Herpetological Conservation and Biology 6(2):297–311.
Submitted: 10 August 2010; Accepted: 6 May 2011.

RAPID HERPETOFAUNAL SURVEYS WITHIN FIVE ISOLATED FORESTS ON SEDIMENTARY ROCK IN WESTERN MADAGASCAR

Hery A. Rakotondravony[1,2,3] and Steven M. Goodman[2,4]

[1]Directorate of Climate Change, Ministry of Environment and Forests, BP 571, Antananarivo 101, Madagascar, email: hery.rado@yahoo.fr
[2]Association Vahatra, BP 3972, Antananarivo 101, Madagascar
[3]Department of Animal Biology, University of Antananarivo, BP 906, Antananarivo 101, Madagascar
[4]Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA

***Abstract.*—Among the most threatened Madagascar ecosystems are the dry deciduous forests situated in the western portion of the island. Associated with varying sedimentary geological substrates, a high degree of microendemism can be found within these habitats. However, they are biologically poorly known and under severe human pressure. We present the first scientific data related to the herpetofaunal communities of five forest relicts resting on sedimentary rock: the Makay sandstone Massif, the Ankara and Kelifely sandstone Tablelands, and the Nosy-Ambositra and Beronto Forests that repose on limestone outcrop. We recorded 70 species (55 reptiles, 15 amphibians) in these habitats. Approximately 97% (n = 68) of these species are endemic to Madagascar and 60% (n = 42) were found exclusively in forest habitats. Sixty-four (91%) of the species are considered endemic to the western dry deciduous forest. A single species was confined to rock outcrops. The field survey data indicate a south-north clinal change in the herpetofauna assemblages occurring at these sites, which is concordant with the north-south biogeographical patterns associated with primates.**

Key Words.— amphibians; biogeography; conservation; endemism; Madagascar; reptiles; sedimentary rock

INTRODUCTION

The high levels of biodiversity and endemism on Madagascar combined with the continuing human pressure on natural habitats render the island one of the most important biotic hot spots in the world (Myers et al. 2000; Groombridge and Jenkins 2002). Further, remarkable levels of microendemism are one of the most striking aspects of the island's terrestrial fauna and flora (e.g. Goodman and Benstead 2005; Wilmé et al. 2006; Ganzhorn et al. 2007; Pearson and Raxworthy 2008). Varying bioclimatic conditions on this 587,000 km² island, together with diversified landscape and complex topography and geology, are some of the key features giving rise to multiple adaptive biotic radiations.

Exposed limestone and sandstone rocks are associated with some landscapes in the western regions of Madagascar. Most of these sedimentary rock outcrops date to the mid-Jurassic (Besairie and Collignon 1972; Battistini 1996; Salomon 1987). Generally, the principal topographic form of these massifs is a series of deep canyons or valleys cutting through the exposed rock. Some of these massifs retain natural vegetation, particularly in valley bottoms. The extent of anthropogenic disturbance of these habitats is closely associated with levels of local human population; areas with low densities are generally reasonably intact, but little in the way of primary forest remains in such zones.

This human pressure and the notable levels of microendemism in western Madagascar call for a documentation of the biological diversity in these threatened habitats before they disappear. Numerous authors have already stressed the importance of such isolated habitats in terms of their conservation value (e.g. Raxworthy and Nussbaum 1994; Mercurio and Andreone 2007; Rakotondravony 2007), and understanding the distributional patterns of such sites is one of the critical tools for the study of the historical biogeography and phylogeography of the exceptionally rich Malagasy fauna.

We present the results of herpetofaunal surveys undertaken at five poorly known sites resting on exposed limestone or sandstone substrates in portions of western Madagascar. Comparative analyses of the herpetological communities at each site are provided here. Considering the fact that amphibian and reptile communities are among the most vulnerable animal groups to habitat destruction and are impacted by other phenomena such as climate change (Glaw and Vences 2008; Raxworthy 2008), we also provide a discussion of the conservation of these natural ecosystems.

MATERIALS AND METHODS

Study sites.*—*The Makay Massif: The Makay Massif is situated in the South-West Region (an administrative

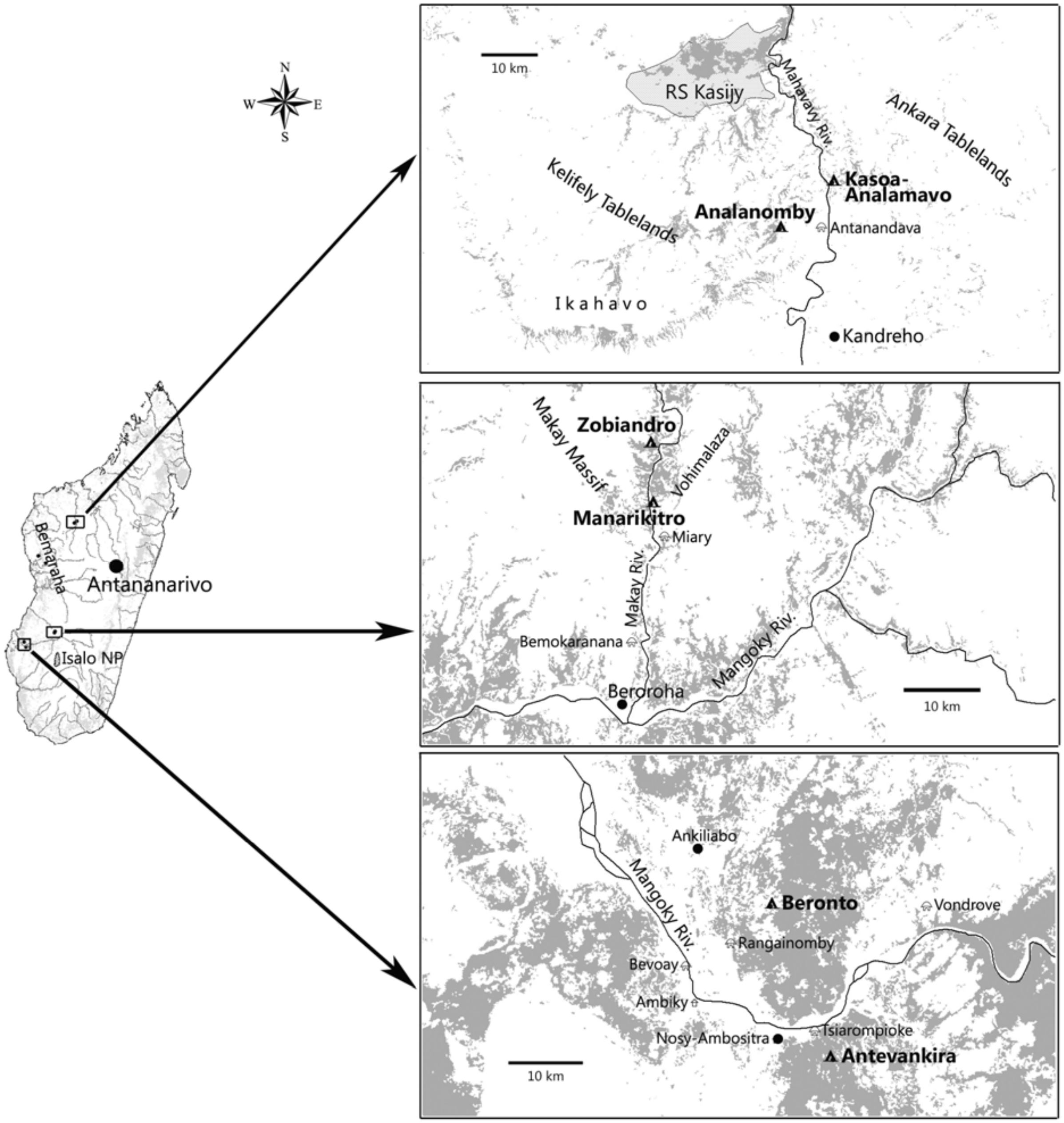


FIGURE 1. Map showing the location of the five study sites (two collecting localities in the Makay Massif – middle panel), all in bold script and indicated with triangular symbols. On the left is a map of Madagascar showing the geographical position of the two protected areas mentioned in the text.

subdivision), 30 km north north-east of Beroroha (21°41.2'S; 045°10.2'E; Fig. 1). The Makay Massif is among the most spectacular natural features of the central southwestern Madagascar. The riparian plain along the Makay River ranges from 250 to 360 m elevation and the associated towering sandstone cliff faces above the river reach 760 m elevation.

No long-term climatic data are available for the region. Based on Chaperon et al. (1993), the mean annual temperature is about 25–26º C and the average annual rainfall is 796 mm at Beroroha. The hottest period is from October to December, and the coolest months are July and August.

The natural forested habitats of the Makay Massif are surrounded by denuded areas and isolated from the nearest natural woodland by at least 50 km. The nearest protected areas are the Isalo National Park, about 100 km to the south, and the Zombitse-Vohibasia National Park, 125 km to the south-west and both on the opposite bank (south) of the Mangoky River. Little primary vegetation remains on the Makay Massif, and much of this is gallery forest in the canyon bottoms. The remaining natural forests are generally degraded and perturbed by human activities (slash-and-burn agriculture, forest fire, cattle grazing), and are now restricted to two areas, Zobiandro Canyon and the Manarikitro riparian forest along the Makay River, facing a hill known as Vohimalaza (Fig. 1). The Zobiandro River, which has its source near the highest peak of the massif, is the only permanent watercourse passing through forested canyons. The vast former marshland ecosystems along the Mangoky River led to widespread reclamation and in the past the region was one of the most important rice producers in Madagascar.

Typical dry forest plants, such as *Commiphora* spp. (Burseraceae) and *Tamarindus indicus* (Fabaceae), compose the principal vegetation of the Manarikitro Forest. There is strong evidence that this latter tree is native to Madagascar (Diallo et al. 2007). In the Zobiandro Canyon, the flora is mixed with a few humid forest elements, including evergreen trees; *Pandanus* sp. (Pandanaceae) is abundant. Rupicolous species, such as *Pachypodium* spp. (Apocynaceae), *Euphorbia* spp. (Euphorbiaceae), and *Aloe* spp. (Liliaceae) are common on exposed rocks.

The Tablelands of Kelifely and Ankara: The sandstone tableland formations (or "*causses*" in French) of Kelifely and Ankara are situated in the central northwestern portion of the island (in the Betsiboka Region) and about 26 km north of Kandreho (17°29.1'S; 046°05.7'E; Fig. 1). The Mahavavy River runs between these two areas. Elevation ranges from about 200 m to 740 m on the highest peak of the Kasoa-Analamavo area. At Kandreho, average annual rainfall is 1591 mm and annual mean temperature of 26º C (Chaperon et al. 1993). The hottest season is from October to December, and the coolest months are July and August.

Bare lands surround these areas, the closest natural woodlands being the Kasijy Special Reserve located 50 km further north (Fig. 1). In the Ankara, forest remnants grow along riparian zones. In Kelikely, some cuestas are still covered by degraded natural forest of a dry deciduous type. More evergreen trees can be found in valley bottoms. Human-caused fires are widespread in the region surrounding these two sites from September to November, causing annual damage to forest remnants. Local people use these forested areas to obtain wood for construction and there is cattle grazing during austral winter.

Nosy-Ambositra and Beronto: Nosy-Ambositra (Fig. 1) is located in the south-west region, about 175 km north of Toliara and 24 km east north-east of Befandriana-Sud (22°06.4'S; 043°53.7'E), on the south bank of the Mangoky River. The local topography is essentially composed of elevated limestone hills with alternating plains and riparian valleys. At Befandriana-Sud, data indicate an annual mean temperature of 25° C, and an average annual rainfall of 778 mm (Chaperon et al. 1993). The hottest season is from October to December and the coolest months are July and August.

Subsistence slash-and-burn agriculture is widespread in the region, mostly confined to rice, corn, and peanuts. Forest relicts are of the dry deciduous type, and at least two species of baobabs (*Adansonia*: Bombacaceae) are present. *Cedrelopsis grevei* (Meliaceae), locally known as *Katrafay*, is one of the most common forest tree species.

In the Nosy-Ambositra region, a north-south aligned limestone outcrop spanning a considerable portion of western Madagascar is severed by the Mangoky River, and recommences on the north bank as the Beronto-Rangainomby hills. Climatic conditions, topography, forest structure, and human pressures are very similar at Beronto as to those observed at Nosy-Ambositra.

Survey periods.—*Makay Massif:* We conducted inventories at two sites; the Zobiandro Valley (21°23.6'S, 45°12.3'E, 360–520 m) 2–10 November 2007, and the Manarikitro Forest (21°27.6'S, 45°12.1'E, 250–350 m) 10–16 November 2007.

Kelifely Tablelands: We inventoried the Analanomby Forest (17°18.9'S, 46°00.2'E, 250–410 m) 25–31 October 2006.

Ankara Tablelands: We inventoried the Kasoa-Analamavo Forest (17°14.6'S, 46°06.1'E, 190–270 m) 18–24 October 2006.

Nosy-Ambositra: We conducted inventories at the Antevankira Forest (21°56.8'S, 44°02.8'E, 100–350 m) 2–9 February 2007.

Beronto-Rangainomby: We inventoried the Beronto Forest (21°46.8'S, 43°58.7'E, 100–130 m) 22–28 January 2007.

Field techniques.—We used three different field techniques: (1) opportunistic diurnal and nocturnal searches along paths in forest and open areas; (2) intensive crevice examination: under rocks, tree-bark, fallen logs, and inside vegetation, especially in the leaf axils of *Pandanus* along the Zobiandro River in the Makay Massif; and (3) 100 m long pitfall lines with 11 15-l buckets with drift fences of 0.5 m tall plastic material. We installed three trap lines at each site, generally in different local microhabitats (to the extent possible).

We euthanized voucher specimens with chlorobutanol solutions and subsequently fixed them in 12% formalin for a minimum of seven days. Specimens were then rinsed in water, transferred to 70% ethanol solution, and deposited in the collection of the Department of Animal Biology at the University of Antananarivo, Madagascar. We recorded the following data for each specimen: date, time, latitude and longitude, altitude, method of capture, microhabitat, and activity. Liver or muscle were removed from all collected specimens prior to fixation and stored in ethylene diamine tetra-acetic acid (EDTA). For amphibians and reptiles, the taxonomy used herein follows Glaw and Vences (2007) as updated by subsequent authors (Raxworthy et al. 2007; Cadle and Ineich 2008; Nagy et al. 2010).

Biogeographical analysis.—We conducted a hierarchical cluster analysis (furthest neighbor [complete linkage], Euclidean distance) to compare the affinities of the herpetofauna assemblages of the five sites. We produced the analysis using SPSS® For Windows® vers. 10.0.1 (SPSS Inc., Chicago, Illinois, USA). We also employed data from the Isalo National Park (Hawkins, F. 1994. Isalo faunal inventory. Final report to the Association Nationale pour la Gestion des Aires Protégées. Landell Mills Limited, City, UK) and from the Bemaraha Plateau (Tsiandro Forest: 18º47.8'S, 44º52.9'E, and Ampasibe Forest: 18º30.9'S, 44º39.6'E; Hery A. Rakotondravony unpubl. data) for this analysis. As these lists were compiled from short term surveys using the same techniques, the associated results are presumed to reflect similarities between the sites species assemblages, particularly dominant species. Excluded from the analysis taxa with uncertain specific attribution (i.e., species name containing "sp.", "cf.", and/or "aff.").

Results

Species diversity.—We documented 70 species of herpetofauna (55 reptiles and 15 amphibians) at the five localities (Table 1). With the exception of the frog *Ptychadena mascareniensis* and the turtle *Pelomedusa subrufa*, all species were endemic to Madagascar. Forty-two species (60%) were found exclusively in forest habitats. Nine reptile species (12.9%) occurred only in open areas; whereas 18 species (25.7%) were collected in both open and forest habitats. A single species, *Oplurus quadrimaculatus*, was confined to rock outcrops. *Pelomedusa subrufa* was recorded at Nosy-Ambositra in a temporary pond close to the forest. The presence of *Erymnochelys madagascariensis* in the Nosy-Ambositra region was confirmed by some carapaces found in the Bevoay village and used as domestic tools. We recorded seven amphibians and 28 reptiles (35 species) in Nosy-Ambositra, Makay Massif; six amphibians and 22 reptiles (28 species) in the Beronto Forest; nine amphibians and 22 reptiles (31 species) in the Ankara Tablelands; and six amphibians and 22 reptiles (28 species) in the Beronto Forest. The lowest herpetofaunal diversity was observed in the Kelifely Tablelands (23 species: five amphibians and 18 reptiles).

The most diverse reptile families were the Colubridae (18 species) and Gekkonidae (14 species; Table 1). Plated-lizards were the least diverse, with only two species (*Zonosaurus laticaudatus* and *Tracheloptychus petersi*). We recorded five reptile species across the five rocky areas (Causses de l'Ankara and Kelifely, Nosy-Ambositra, and Beronto): *Blaesodactylus sakalava*, *Lygodactylus tolampyae*, *Madagascarophis colubrinus*, *Madascincus intermedius*, *Sanzinia madagascariensis volontany*, and *Zonosaurus laticaudatus*. Two species of boid snake (*Acrantophis dumerili* and *Sanzinia madagascariensis volontany*) and two species of iguanid lizard occur sympatrically in the Makay Massif (*Chalarodon madagascariensis* and *Oplurus quadrimaculatus*) and Nosy-Ambositra (*C. madagascariensis* and *O. cyclurus*; Table 1).

The most diverse family of amphibians was Mantellidae (six species). We recorded only three amphibian species across the five rocky areas (*Mantidactylus* sp. aff. *ulcerosus*, *Ptychadena mascareniensis*, and *Scaphiophryne calcarata*). During these surveys, we only observed hyperoliid frogs in Nosy-Ambositra (*Heterixalus* sp.) and the Beronto Forest (*H. luteostriatus*).

Pitfall trap results.—A combined effort of 1221 pitfall-days at the five sites yielded the capture of 375 individuals (288 amphibians and 87 reptiles; 30.7% overall capture rate; Table 2). We obtained twelve reptile species and three amphibians using this trapping technique. One amphibian species (*Scaphiophryne brevis*) and five reptile species (*Amphiglossus reticulatus*, and *Amphiglossus* sp. 2; *Madascincus* cf. *intermedius*; *Liophidium* sp.; and *Typhlops* sp.) were only captured using pitfall traps. The *Amphiglossus* sp. 2 appears to be an undescribed species. The highest capture rate was observed at the Nosy-Ambositra site (51.0%), the lowest being in the Kelifely and Ankara Tablelands (respectively 19.7 and 18.6%). For the Makay and the Beronto regions, the daily pitfall trap rates were 38.9 and 22.7%, respectively. *Scaphiophryne calcarata* was the most captured species (265 individuals), with capture rates for this taxon varying from 8.1 to 34.9% per site (21.8% average capture rate).

Biogeographical affinities.—The cluster analysis (Fig. 2) shows two main biogeographical groups. The first includes sites localized in the south-western part of

TABLE 1. Amphibian and reptile species diversity found within the five areas sampled during this study (*continued on next page*).

	Kelifely	Ankara	Beronto	Nosy-Ambositra	Makay	
Surveyed elevational ranges (m)	190-270	250-410	100-130	100-350	250-520	
Surveyed amplitude altitudinal (m)	80	160	20	250	270	
Species / Date	18-24 Oct. 06	25-31 Oct. 06	22-28 Jan. 07	02-09 Feb. 07	02-16 Nov. 07	Habitat[1]
Amphibia						
Hyperoliidae						
Heterixalus sp.				*		a
Heterixalus luteostriatus			*			a
Mantellidae - Boophinae						
Boophis doulioti	*	*			*	a, b
Mantellidae - Laliostominae						
Aglyptodactylus securifer	*	*			*	a, b
Laliostoma labrosum	*	*	*	*		a, b
Mantellidae - Mantellinae						
Gephyromantis corvus					*	a
Gephyromantis pseudoasper	*	*				a
Guibemantis cf. *flavobrunneus*					*	a
Mantella betsileo		*		*		a, b
Mantidactylus sp.	*					a
Mantidactylus sp. aff. *ulcerosus*[2]		*		*	*	
Microhylidae						
Dyscophys insularis			*			a, b
Scaphiophryne brevis		*	*	*		a
Scaphiophryne calcarata		*	*	*	*	a
Ptychadenidae						
Ptychadena mascareniensis		*	*	*	*	a, b
Reptilia						
Boidae						
Acrantophis dumerili			*	*	*	a, b
Sanzinia madagascariensis volontany	*	*		*	*	a
Chamaeleonidae						
Brookesia brygooi		*			*	a
Furcifer labordi			*	*		a
Furcifer lateralis	*				*	a, b
Furcifer oustaleti	*	*			*	a, b
Furcifer verrucosus			*	*		a, b
Colubridae						
Alluaudina bellyi		*				a
Dromicodryas bernieri			*	*	*	b
Dromicodryas quadrilineatus	*	*				b
Heteroliodon occipitalis		*		*		a, b
Ithycyphus miniatus	*				*	a
Ithycyphus oursi					*	a
Leioheterodon geayi			*			a
Leioheterodon madagascariensis			*		*	a
Leioheterodon modestus			*	*		b
Liophidium sp.			*	*		a
Liophidium torquatum	*				*	a
Lycodryas cf. *gaimardi*		*				a
Madagascarophis colubrinus	*	*			*	a, b
Mimophis mahfalensis	*	*	*	*		b
Phisalixella tulearensis				*		a
Phisalixella variabilis	*					a
Pseudoxyrhopus quinquelineatus		*				a, b
Thamnosophis lateralis					*	a

TABLE 1 (*continued*). Amphibian and reptile species diversity found within the five areas sampled during this study.

Gekkonidae						
Blaesodactylus sakalava		*		*	*	a
Geckolepis maculata	*	*			*	a
Geckolepis typica		*	*	*		a
Hemidactylus frenatus		*				b
Hemidactylus mercatorius			*	*	*	a
Lygodactylus cf. *madagascariensis*			*			a
Lygodactylus tolampyae	*	*	*	*	*	a
Paroedura bastardi					*	a
Paroedura oviceps		*				a
Paroedura picta			*	*	*	a, b
Phelsuma kochi	*	*				a
Phelsuma mutabilis			*	*	*	a, b
Uroplatus guentheri	*					a
Uroplatus henkeli	*	*				a
Gerrhosauridae						
Tracheloptychus petersi			*			b
Zonosaurus laticaudatus	*	*	*	*	*	a, b
Iguanidae						
Chalarodon madagascariensis				*	*	b
Oplurus cuvieri	*	*				a, b
Oplurus cyclurus			*	*		a
Oplurus quadrimaculatus					*	c
Scincidae						
Amphiglossus sp. 2		*				a
Amphiglossus reticulatus	*					a
Madascincus cf. *intermedius*				*	*	a
Madascincus sp. “vitreus”[3]			*	*		a
Trachylepis aureopunctata			*	*	*	a
Trachylepis elegans		*	*	*		a, b
Trachylepis gravenhorstii					*	b
Pelomedusidae						
Erymnochelys madagascariensis				*[4]		
Pelomedusa subrufa				*		b, d
Typhlopidae						
Typhlops decorsei				*		a
Typhlops sp.	*					a
Total	23	31	28	34	33	

[1] Habitats: a = forest, b = open areas, c = rock outcrops, d = temporary pond;
[2] See Glaw and Vences 2007, p. 232;
[3] See Glaw and Vences 2007, p. 332;
[4] Evidence of *Erymnochelys madagascariensis* (Podocnemididae) in the Nosy-Ambositra region is confirmed by turtle shells found in the village of Bevoay along the Mangoky river.

Madagascar (Beronto, Nosy-Ambositra, Makay, and Isalo). The second comprises the Ankara and Kelifely Tablelands, together with the Bemaraha Plateau. On the basis of this field survey data, there is a south-north clinal demarcation in the herpetofauna assemblages occurring at these sites. This partition is not associated with substrate as, for example, limestone occurs in both of the main biogeographical areas.

DISCUSSION

Species richness.—Species richness found within the five regions during these rapid assessment surveys was largely similar; the surveyed elevational ranges of the sites were comparable (approx. 250 m). The seasonal period the inventories were conducted were different (see Materials and Methods). For the Makay Massif and the Kelifely and Ankara Tablelands, surveys were

TABLE 2. Species and the number caught in pitfall traps within the five survey sites (two collecting localities in the Makay Massif) from western Madagascar. Numbers under sites are the pitfall numbers. There were 66 trap days for all sites except Ankara Kasoa, for which there were 77 trap days.

	Makay						Ankara			Kelifely			Nosy-Ambositra			Beronto		
	Zobiandro			Manarikitro			Kasoa			Analanomb			Antevankira			Beronto		
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Dyscophus insularis																1		6
Laliostoma labrosum	1			1									1		3	2		
Scaphiophryne brevis													8	3	4			
Scaphiophryne calcarata	21	15	19	25	26	17	2	11	19	4	12	9	38	19	12	3		13
Amphiglossus sp. 2		1	1				1											
Amphiglossus waterloti											1							
Furcifer oustaleti															1			
Liophidium sp.														1				
Madascincus cf. *intermedius*	2		1		1	3		3	2		3	2	2	1				
Madascincus sp. "vitreus"													1		1			
Pseudoxyrhopus quinquelineatus											1							
Trachylepis auropunctata																1		
Trachylepis elegans	3		2	3	2	1	1	2	1	1	2	1	2		2	10		9
Trachylepis gravenhorstii	1	2		1		2					1							
Typhlops decorsei													1		1			
Typhlops sp.								1										
Zonosaurus laticaudatus	2					1				1	1							
Total	30	18	23	30	29	24	4	17	22	6	21	12	53	24	24	17	0	28
Total capture		71			83			43			39			101			45	
Capture rate per site (%)		35.9			41.9			18.6			19.7			51.0			22.7	

carried at the end of the austral winter/beginning of rainy season when these sites are accessible.

***Taxonomy and local endemism.*—**The species list shown by Table 1 contains mostly taxa with widespread distributions across Western Madagascar (e.g. *Heterixalus luteostriatus*, *Dyscophus insularis*, *Aglyptodactylus securifer*, *Laliostoma labrosum*, *Boophis doulioti*, *Scaphiphryne calcarata*, *Furcifer oustaleti*, *Dromicodryas bernieri*, *D. quadrilineatus*, *Geckolepis maculata*, *Lygodactylus tolampyae*, *Phelsuma kochi*, *Chalarodon madagascariensis*, and *Trachylepis elegans*). However, some of the five surveyed rocky areas sites contain species that may represent local endemic. For example, the hyperoliid frog *Heterixalus* sp. was only recorded in Nosy-Ambositra. Also, a specimen identified as *Guibemantis* sp. *flavobrunneus* was collected from the Makay Massif. This western record of a *Guibemantis* (Amphibia: Mantellidae: Mantellinae) is remarkable, as this genus was previously known only from eastern (more humid) forest belts. Other examples of potential microendemics are *Mantidactylus* sp. and *Typhlops* sp. that were collected from Kelifely Tablelands; and *Stenophis* cf. *gaimardi* from the Ankara Tablelands.

The next taxa, also collected by some authors from certain regions of western Madagascar, are not local endemics, but specific attributions remain unclear: *Mantidactylus* sp. (aff. *ulcerosus*; see Glaw and Vences 2007; Bora et al. 2010), *Amphiglossus* sp. 2 (Christian J. Randrianantoandro, pers. comm.; Toky Randriamoria, comm.. pers.); *Madascincus* cf. *intermedius* (see Bora et al. 2010), and *M.* sp. "vitreus" (see Glaw and Vences 2007). The clarification of taxonomic status of these will contribute to understand the highly diversified biological aspects of Western Madagascar.

***Habitat preferences.*—**The proportion of species recorded only within forest habitats (56.3%) was relatively low, as compared to near 61% for the Montagne des Français (D'Cruze *et al*. 2007), but higher than the 48% Bora et al. (2010) have reported from Bemaraha. Assuming that species recorded in open areas can be considered as generalists, this group constitutes 32.4% of the herpetofaunal communities found at these five areas during our rapid assessments. The ratio of generalists to forest-dwelling species

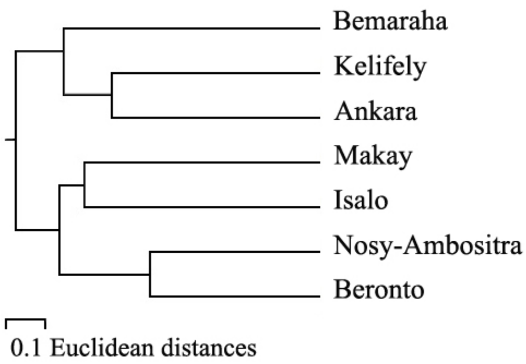


FIGURE 2. Dendrogram resulting from a complete linkage hierarchical cluster analysis using Euclidean distance for seven sites across the western part of Madagascar. A north-south biogeographical cline for vertebrate distribution is corroborated by this study. Data used in this analysis are presented in Appendix 1.

provides evidence that these five forest habitats are in an advanced phase of degradation, with the open canopy favoring heliophilous species.

Cumulative species number.—The daily rate of previously unrecorded species at a given site can be illustrated by species accumulation curves. In all cases, no site shows an asymptote (Fig. 3), which is indicative that with additional survey effort more taxa would have been recorded. This may be associated with the length of each inventory, which was approximately seven days. For the Makay Massif and the Ankara and Kelifely Tablelands, the inventory sessions were situated in the beginning of the hot and rainy season, when the herpetofauna shows maximum of activity. Many reptile and amphibian species are dormant and buried in the ground during the dry (cooler) season, when soil invertebrate activity is low (Huston 1994; Pough et al. 2003). Organizing biological surveys within the Ankara and Kelifely Tablelands during the peak of the rainy season (December to March) is logistically complex associated with inaccessible roads, considerable distances to walk, and the risk of flash flooding.

Certain groups of amphibians and reptiles with discrete or cryptic habits, such as colubrid snakes and skinks, may be more diverse at these sites than current data indicate. Species richness and density of colubrid snakes is presumably correlated with sandy soils, open canopies, presence of microhabitats such as fallen and

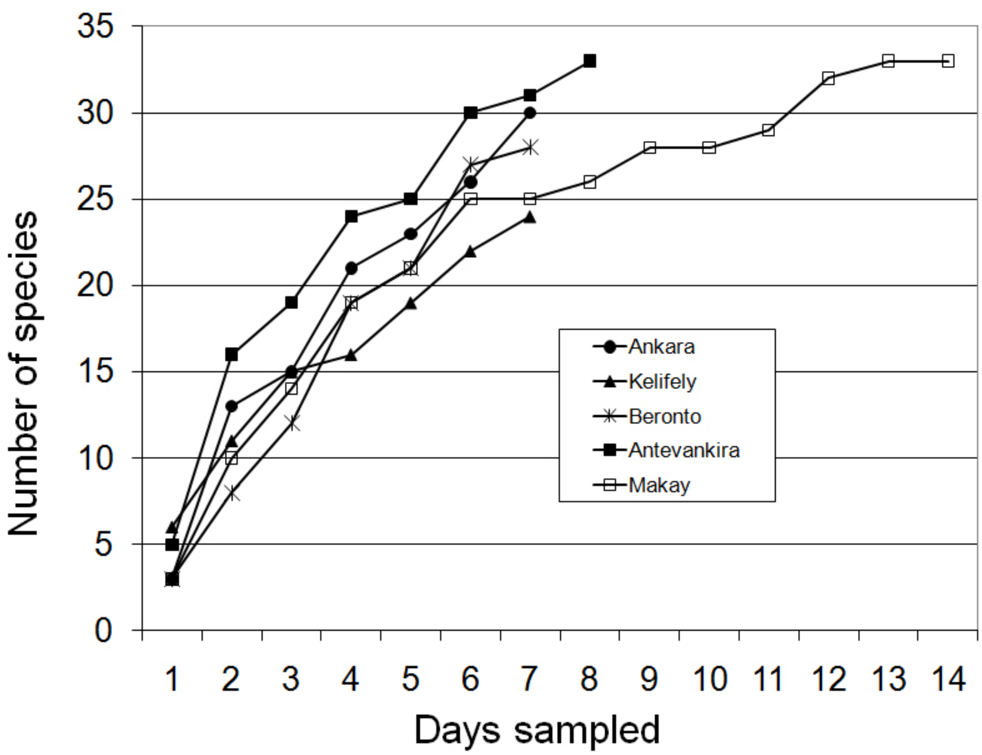


FIGURE 3. Species accumulation curves for the five sites sampled during this study in western Madagascar.

rotten logs, and the abundance of prey (especially frogs) (see Pough et al. 2003). Snakes of the genus *Madagascarophis* were the only nocturnal snakes found during these inventories, but other taxa, for example *Lycodryas* spp. and *Phisalixella* spp., are probably present. The presence of humid microhabitats and leaf litter in riparian valleys is presumably associated with a relatively rich skink community; and the remarkably low species diversity for this group found during this study may partially reflect the relative precocity of the seasonal inventory periods in each site.

Biogeographical analysis.—Numerous species known from the central lowland forests of western Madagascar were not recorded at the five inventoried sites presented herein. Whether this is associated with species that were overlooked or animals that have patchy ranges will require further zoological exploration of these zones. The Bemaraha Plateau has a very complex fauna, with notable levels of beta-diversity turnover (Bora et al. 2010; Parfait Bora, Miguel Vences and Frank Glaw pers. comm; Achille P. Raselimanana, pers. comm.) and the inclusion of other sites from this massif will certainly change the biogeographical relationships presented herein. However, assuming that the species inventoried during our surveys represent the dominant members of the herpetofaunal communities of each site, our results are probably indicative of certain biogeographical patterns of this portion of the island. The biogeographical affinities of the amphibian and reptile communities shown by this study are concordant with the north-south biogeographical clinal patterns associated of primates (e.g., Yoder et al. 2000; Pastorini et al. 2001a, b, 2003), as well as the herpetofauna (e.g., Townsend and Larson 2002; Boumans et al. 2007; Glaw et al. 2009).

Considering that four of the seven sites included within the biogeographical analysis are situated on opposite banks of the Mangoky River (north bank: Makay Massif and Beronto; south bank: Nosy-Ambositra and Isalo), provides an interesting test if this river acts as a dispersal corridor or barrier. Given that the Makay Massif groups with Isalo and Nosy-Ambositra with Beronto, implies the river along the lower portion of its trajectory acts as a dispersal corridor. In the same fashion, given that the Mahavavy River runs through the Ankara and Kelifely Tablelands, the biogeographical analysis conducted here shows that the herpetofaunal communities of these two sites are similar. During periods of climatic shifts during the Pleistocene, these different sites may have experienced certain parallels in the colonization patterns of some members of the herpetofauna community.

Multiple processes are considered giving rise to the extensive adaptive radiation of Malagasy biota. They include isolation by dispersal barriers (e.g. Pastorini et al. 2003), climatic gradient due to an extensively diverse bioclimatic formations (e.g. Goodman & Benstead 2005; Goodman 2008; Pearson and Raxworthy 2008), and the recently developed retreat-dispersion watershed pattern (Wilmé et al. 2006). Pearson and Raxworthy's (2008) climatic gradient model presents 14 clusters having similar climatic conditions, based on four principal components of 19 bioclimatic variables. These authors consider the 14 clusters as potential areas of endemism. On this model, northern and eastern Madagascar areas of endemism are closely linked with elevation, but western and southern areas of endemism are likely affected by latitudinal gradients. This model presents some discrepancies with the Wilmé et al. (2006) retreat-dispersion hypothesis that identifies 14 areas of endemism that are chiefly delimitated by important rivers that have their sources at higher elevation on Central Highlands' higher elevation. The retreat-dispersion watersheds model predicts that river catchments with sources at higher elevation act as zones of retreat during glacial periods and as zones of subsequent dispersal during inter-glacial periods (Wilmé et al. 2006). The partial biogeographical analysis presented here (Fig. 2) reveals a latitudinal clustering of species assemblages that seems to corroborate Pearson and Raxworthy's (2008) climatic gradient endemism model. However, the analysis also seems to be in accordance with aspects of the Wilmé et al. (2006) model. Pearson and Raxworthy (2008) stressed that endemism pattern in Madagascar is the result of multiple processes, and further investigations are needed to understand this aspect of the island's terrestrial biota.

Conservation.—The five sites surveyed during this study are the habitat for at least 15 amphibian species and 55 reptiles. These relatively diverse, but isolated, communities are important for conserving genetic pools. Allopatric speciation or population differentiation in such isolated habitats has already been reported or suggested for a variety of organisms (e.g., Paulian and Viette 2003; Sparks and Stiassny 2003; Imron et al. 2007). Natural isolation, exacerbated by habitat fragmentation caused by environmental changes, play a central role on the extensive adaptive radiation exhibited by Malagasy herpetofauna (Raxworthy and Nussbaum 1995; Glaw et al. 1999; Raxworthy 2008). Such a scenario is certainly plausible for the herpetological communities of these isolated sedimentary rock areas, as in all cases, the remaining natural habitats are actually surrounded by bare anthropogenic landscapes, and any gene flow between isolated sites is not expected for the forest-dwelling species. In the same manner, local extirpation on the medium-term would be expected, especially for forest-dwelling species. Further or continued isolation is anticipated as human pressure on natural habitats remains high, as it is in the remaining forested areas of western Madagascar (Smith 1997; Raselimanana 2008).

There are differences in the degree of anthropogenic pressure on these five areas. For instance, the Makay Massif, the Manarikitro Forest, and the forested riverine zone in the Zobiandro Canyon are exploited by local people for construction and fire wood. Further, cattle grazing in forested habitats may result in notable changes to ground cover and leaf litter dwelling species. This is especially the case during the austral winter when forest-dwelling reptiles and amphibians are subject to considerable mortality (e.g. Rabearivony 1999) and cattle are obliged to find grazing in forest.

The list of amphibians and reptiles reported herin include two species listed on Appendix I of CITES (*Acrantophis dumerilii* and *Sanzinia madagascariensis*), and seven in Appendix II (*Phelsuma kochi*, *P. mutabilis*, *Brookesia brygooi*, *Furcifer labordi*, *F. lateralis*, *F. oustaleti*, and *F. verrucosus*). Based on interviews with local people, commercial collectors for the pet and zoo trade do not visit the five surveyed zones. At all of these sites, there is a representative of the Direction des Eaux et Forêts in the closest larger village or town, but given the physical distance between these urban centers and the forest, effective control of illicit activities is rather difficult. Further, given the rudimentary primary school system, subsistent way of life for many people, and few means for the diffusion of information, local considerations of biodiversity or the importance of ecosystem functioning is poorly understood. These aspects, combined with the human pressures, push these vestigial forested biological communities towards greater levels of fragmentation and isolation.

Acknowledgments.—Fieldwork associated with this paper was conducted with the gracious hospitality of local communities and funding by a National Science Foundation grant to Steven M. Goodman (DEB-0516313). Special thanks to Frank Glaw for valuable comments on the manuscript. We thank the Direction des Eaux et Forêts (Antananarivo, Madagascar) for issuing permits to conduct faunal surveys. Achille P. Raselimanana, Parfait Bora, Miguel Vences, and Frank Glaw provided lists of the Bemaraha herpetofauna.

Literature Cited

Battistini, R. 1996. Paléogéographie et variété des milieux naturels à Madagascar et dans les îles voisines: quelques données de base pour l'étude biogéographique de la "région Malgache." Pp. 1–17 *In* Biogéographie de Madagascar. Lourenço, W.R. (Ed.). ORSTOM, Paris, France.

Besairie, H., and M. Collignon. 1972. Géologie de Madagascar. I. Les terrains sédimentaires. *Annales géologiques de Madagascar*. Imprimerie Nationale, Tananarive, Madagascar.

Bora, P., J.C. Randrianatoandro, R. Randrianavelona, E.F. Hantalalaina, R.R. Andriatsimanarilafy, D. Rakotondravony, O.R. Ramilijaona, M. Vences, R.K.B. Jenkins, F. Glaw, and J. Köhler. 2010. Amphibians and reptiles of the Tsingy de Bemaraha plateau, western Madagascar: checklist, biogeography and conservation. Herpetological Conservation and Biology 5:111–125.

Boumans, L., D.R. Vieites, F. Glaw, and M. Vences. 2007. Geographical patterns of deep mitochondrial differentiation in widespread Malagasy reptiles. Molecular Phylogenetics and Evolution 45:822–839.

Cadle, J.E., and I. Ineich. 2008. Nomenclatural status of the Malagasy snake genus *Bibilava* Glaw, Nagy, Franzen, and Vences, 2007: Resurrection of *Thamnosophis* Jan and designation of a lectotype for *Leptophis lateralis* Duméril, Bibron, and Duméril (Sepentes: Colubridae). Herpetological Review 39:285–288.

Chaperon, P., J. Danloux, and L. Ferry. 1993. Fleuves et Rivières de Madagascar. ORSTOM, Paris, France.

D'Cruze, N., J. Sabel, K. Green, J. Dawson, C. Gardner, J. Robinson, G. Starkie, M. Vences, and F. Glaw. 2007. The first comprehensive survey of amphibians and reptiles at Montagne des Français, Madagascar. Herpetological Conservation and Biology 2:87–99.

Diallo, B.O., H.I. Joly, D. McKey, M. Hossaert-McKey, and M.H. Chevallier. 2007. Genetic diversity of *Tamarindus indica* populations: Any clues on the origin from its current distribution? African Journal of Biotechnology 6:853–860.

Ganzhorn, J.U., S.M. Goodman, and M. Vincelette (Eds.). 2007. Biodiversity, ecology and conservation of littoral ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin). SI/MAB series #11. Smithsonian Institution, Washington, D.C, USA.

Glaw, F., Z.T. Nagy, J. Köhler, M. Franzen, and M. Vences. 2009. Phylogenetic relationships of a new species of pseudoxyrhophiine snake (Reptilia: Lamprophiidae: *Thamnosophis*) suggest a biogeographical link between western and northern Madagascar. Organisms Diversity and Evolution 9: 13–22.

Glaw, F. and M. Vences. 2007. A Fieldguide to the Amphibians and Reptiles of Madagascar. 3rd Edition. Vences und Glaw Verlag, Cologne, Germany.

Glaw, F., and M. Vences. 2008. Les amphibiens. Pp. 311–340 *In* Paysages Naturels et Biodiversité de Madagascar. Goodman, S.M. (Ed.). Muséum National d'Histoire Naturelle, Paris, France.

Glaw, F., M. Vences, T. Ziegler, W. Böhme, and J. Köhler. 1999. Specific distinctness and biogeography of the dwarf chameleons *Brookesia minima*, *B. peyrierasi* and *B. tuberculata* (Reptilia:

Chamaeleonidae): evidence from hemipenial and external morphology. Journal of Zoology 427:225–238.

Goodman, S.M. (ed). 2008. Paysages Naturels et Biodiversité de Madagascar. Muséum National d'Histoire Naturelle, Paris, France.

Goodman, S.M., and J.P. Benstead. 2005. Updated estimates of biotic diversity and endemism for Madagascar. Oryx 39:1–5.

Groombridge, B., and M.D. Jenkins. 2002. World Atlas of Biodiversity. The University of California Press, Berkeley, California, USA.

Huston, M. 1994. Biological Diversity. The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.

Imron, J.B., P. Hale, B.M. Degnan, and S.M.Degnan. 2007. Pleistocene isolation and recent gene flow in *Haliotis asinina*, an Indo-Pacific vetigastropod with limited dispersal capacity. Molecular Ecology 16:289–304.

Mercurio, V., and F. Andreone. 2007. Two new canyon-dwelling frogs from the arid sandstone Isalo Massif, central-southern Madagascar (Mantellidae, Mantellinae). Zootaxa 1574:31–47.

Myers, N., C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nagy, Z.T., F. Glaw, and M. Vences. 2010. Systematics of the snake of genera *Stenophis* and *Lycodryas* (Squamata, Serpentes, Pseudoxyrophiinae) from Madagascar and the Comoros. Zoologica Scripta 39:426–435.

Pastorini, J., M.R.J. Forstner, and R.D. Martin. 2001a. Phylogenetic history of sifakas (*Propithecus*: Lemuriformes) derived from mtDNA sequences. American Journal of Primatology 53:1–17.

Pastorini, J., R.D. Martin, P. Ehresmann, E. Zimmermann, and M.R.J. Forstner. 2001b. Molecular phylogeny of the lemur family Cheirogaleidae (Primates) based on mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 19:45–56.

Pastorini, J., U. Thalmann, and R.D. Martin. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. Proceedings of the National Academy of Sciences of the United States of America 100:5879–5884.

Paulian, R., and P. Viette. 2003. An introduction to terrestrial and freshwater vertebrates. Pp. 503–511 *In* The Natural History of Madagascar. Goodman, S.M., and J.P. Benstead (Eds.). The University of Chicago Press, Chicago, Illinois, USA.

Pearson, R.G., and C.J. Raxworthy. 2008. The evolution of local endemism in Madagascar: watershed versus climatic gradient hypotheses evaluated by null biogeographic models. Evolution 63:959–967.

Pough, H.F., R.M. Andrews, J.E. Cadle, M.L. Crumps, A.H. Savitzky, and K.D. Wells. 2003. Herpetology. 3rd Edition. Prentice Hall, City, New Jersey, USA.

Rabearivony, J. 1999. Conservation and status assessment of *Brookesia*, the dwarf chameleons of Madagascar. M.Sc. thesis, Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK.

Rakotondravony, H.A. 2007. Conséquences de la variation des superficies forestières sur les communautés de reptiles et d'amphibiens dans la région Loky-Manambato, extrême Nord-est de Madagascar. Revue d'Écologie (Terre Vie) 62:209–227.

Raselimanana, A.P. 2008. Aspect de la conservation des forêts sèches malgaches. Malagasy Nature 1:162–167.

Raxworthy, C.J. 2008. Introduction aux reptiles. Pp. 341–366 *In* Paysages Naturels et Diversité de Madagascar. Goodman, S.M. (Ed.) Muséum National d'Histoire Naturelle, Paris, France.

Raxworthy, C.J., and R.A. Nussbaum. 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. Biological Conservation 69:65–73.

Raxworthy, C.J., and R.A. Nussbaum. 1995. Systematic, speciation and biogeography of the dwarf chameleons (Brookesia: Reptilia, Squamata, Chamaeleontidae) of Northern Madagascar. Journal of Zoology, London 235:525–558.

Raxworthy, C.J., C.M. Ingram, N. Rabibisoa, and R.G. Pearson. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. Systematic Biology 56:907–923.

Salomon, J.-N. 1987. Le Sud-ouest de Madagascar. Tome I. Université d'Aix-Marseille, Marseille, France.

Smith, A.P. 1997. Deforestation, fragmentation, and reserve design in western Madagascar. Pp. 415–441 *In* Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Laurance, W.F., and R.O. Bierregaard. (Eds). The University of Chicago Press, Chicago, Illinois, USA.

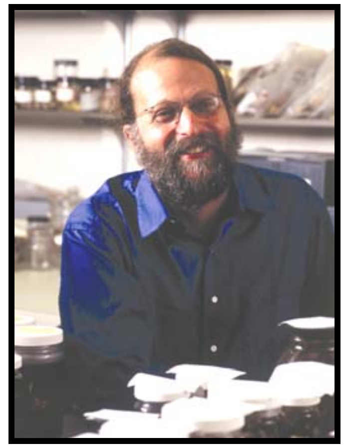
Sparks, J.S., and M.L.J. Stiassny. 2003. Introduction to freshwater fishes. Pp. 849–863 *In* The Natural History of Madagascar. Goodman, S.M., and J.P. Benstead. (Eds). The University of Chicago Press, Chicago, Illinois, USA.

Townsend, T., and A. Larson. 2002. Molecular phylogenetics and mitochondrial genomic evolution in the Chamaeleonidae (Reptilia, Squamata). Molecular Phylogenetics and Evolution 23:22–36.

Wilmé, L., S.M. Goodman, and J.U. Ganzhorn. 2006. Biogeographic evolution of Madagascar's microendemic biota. Science 312:1063–1065.

Yoder, A.D., R.M. Rasoloarison, S.M. Goodman, J.A. Irwin, S. Atsalis, S. Ravosa, and J.U. Ganzhorn. 2000. Remarkable species diversity in Malagasy mouse lemurs (Primates, *Microcebus*). Proceedings of the National Academy of Sciences of the United States of America 97:11325–11330.

HERY A. RAKOTONDRAVONY is a researcher and herpetologist with a Ph.D. from the University of Antananarivo. He is interested in ecology, biogeography, biology, ecotourism management, and climate sciences. Hery is a lecturer at various universities in Madagascar. (Photographed by Devi M. Stuart-Fox).



STEVEN M. GOODMAN holds the post of MacArthur Field Biologist, Field Museum of Natural History, Chicago, and Scientific Advisor, Association Vahatra, Antananarivo, Madagascar. He has a Ph.D. from Hamburg University, Germany, and an H.D.R. from the University of Paris, France. He has been working on different aspects of the vertebrate fauna of Madagascar for over two decades, in close association with Malagasy graduate students. (Photographed courtesy of the Field Museum).

APPENDIX I.

Voucher specimens

AMPHIBIANS: ***Aglyptodactylus securifer***: Ankara Tablelands: UADBA 43104, 43105, 43106, 43107, 43108, 43109, 43110; Kelifely Tablelands: UADBA 43111, 43112; ***Boophis doulioti***: Ankara Tablelands: UADBA 43287; Kelifely Tablelands: UADBA 43288, 43289, 43290, 43291, 43292, 43293; Makay: 43295, 43296, 44327, 44328, 44329, 44330, 44331, 44332, 44333, 44334; ***Dyscophus insularis***: UADBA 43427, 43428, 43429; Beronto: UADBA 43463, 43464; ***Gephyromantis corvus***: Makay: UADBA 44069; ***Guibemantis* cf. *flavobrunneus***: Makay: UADBA 43639; ***Heterixalus luteostriatus***: Beronto: UADBA 43692, 43693, 43694; ***Heterixalus* sp.**: Nosy-Ambositra: UADBA 43696, 43697, 43698, 43699; ***Laliostoma labrosum***: Ankara Tablelands: UADBA 43722; Kelifely Tablelands: UADBA 43723; Beronto: UADBA 43726, 43727; Nosy-Ambositra: UADBA 43728, 43729, 43730; ***Mantella betsileo**:* UADBA 43948, 43949; Ankara Tablelands: UADBA 43957, 43958; Nosy-Ambositra: UADBA 43959, 43960, 43961; ***Mantidactylus* sp. aff. *ulcerosus**:* Ankara Tablelands: UADBA 43968, 43969, 43970, 43971, 43972, 43973, 43974, 43975, 43976, 43977, 43978, 43979, 43980; Nosy-Ambositra: UADBA 43992, 43993, 43994, 43995, 43996, 43997, 43998, 43999; ***Mantidactylus* sp.**: Kelifely Tablelands: UADBA 44023, 44024, 44025, 44026, 44027, 44028, 44029; ***Mantidactylus pseudoasper**:* Ankara Tablelands: UADBA 44060, 44061; Kelifely Tablelands: UADBA 44062, 44063, 44064, 44065; ***Ptychadena mascareniensis**:* Ankara Tablelands: UADBA 44302; Beronto: UADBA 44304, 44305, 44306; Nosy-Ambositra: UADBA 44307, 44308, 44309, 44310, 44311; Makay: UADBA 44317, 44318, 44319, 44320; ***Scaphiophryne brevis***: Beronto: UADBA 44344, 44041, 44042; Nosy-Ambositra: UADBA 44345, 44346, 44347; ***Scaphiophryne calcarata***: Ankara Tablelands: UADBA 44386, 44387, 44388, 44389, 44390, 44391, 44392, 44393, 44394, 44395, 44396, 44397; Beronto: UADBA 44398, 44399, 44000, UADBA 44001; Nosy-Ambositra: UADBA 44002, 44003; Makay: UADBA 44009, 44010, 44011, 44012, 44013, 44014, 44015, 44016, 44017, 44018, 44019, 44020, 44021, 44022, 44023, 44024, 44025, 44026, 44027, 44028, 44029, 44030, 44031, 44032, 44033, 44034, 44035, 44036, 44037, 44038, 44039.

REPTILES: ***Acrantophis dumerili***: Beronto: UADBA 43078; Nosy-Ambositra: UADBA 43079, 43080; Makay: UADBA 43081; ***Alluaudina bellyi***: Ankara Tablelands: UADBA 43125; ***Amphiglossus* cf. *intermedius***: Kelifely Tablelands: UADBA 43139; Nosy-Ambositra: UADBA 43140; Makay: UADBA 43145, 43146, 43147, 43148, 43149, 43150, 43151, 43152, 43153, 43154; ***Amphiglossus* sp. 2**: Ankara Tablelands: UADBA 43171; ***Amphiglossus reticulatus***: Ankara Tablelands: UADBA 43192; ***Thamnosophis lateralis***: Makay: UADBA 43193, 43194; ***Blaesodactylus sakalava***: Ankara Tablelands: UADBA 43206; Nosy-Ambositra: UADBA 43210, 43211; Makay: UADBA 43215, 43216, 43217, 43218, 43219; ***Brookesia brygooi***: Ankara Tablelands: UADBA 43307; Makay: UADBA 43312, 43313, 43314; ***Chalarodon madagascariensis***: Nosy-Ambositra: UADBA 43391, 43392, 43393, 43394, 43395, 43396; Makay: UADBA 43402, 43403, 43404; ***Dromicodryas bernieri***: Beronto: UADBA 43412; Nosy-Ambositra: UADBA 43413; Makay: UADBA 43416; ***Dromicodryas quadrilineatus***: Ankara Tablelands: UADBA 43422, 43423; Kelifely Tablelands: UADBA 43424; ***Furcifer labordi***: UADBA 43483, 43484, 43485, 43486; Nosy-Ambositra: UADBA 43487, 43488, 43489, 43490, 43491; ***Furcifer lateralis***: Kelifely Tablelands: UADBA 43498; Makay: UADBA 43502, 43503; ***Furcifer oustaleti***: Ankara Tablelands: UADBA 43541, 43542, 43543, 43544; Kelifely Tablelands: UADBA 43545, 43546, 43547; Makay: UADBA 43573, 43574, 43575; ***Furcifer verrucosus***: UADBA 43589, 43590, 43591, 43592; UADBA 43593, 43594, 43595, 43596, 43597, 43598, 43599, 43600, 43601; ***Geckolepis maculata***: Ankara Tablelands: UADBA 43610, 43611; Kelifely Tablelands: UADBA 43613, 43614, 43615; Makay: UADBA 43608, 43609; ***Geckolepis typica***: Ankara

Tablelands: UADBA 43612; Beronto: UADBA 43620, 43621; Nosy-Ambositra: UADBA 43622, 43623; ***Hemidactylus frenatus***: Ankara Tablelands: UADBA 43657, 43658, 43659, 43660; ***Hemidactylus mercatorius***: Beronto: UADBA 43666; Nosy-Ambositra: UADBA 43667, 43668; Makay: UADBA 43669; ***Itycyphus miniatus***: Kelifely Tablelands: UADBA 43702; Makay: UADBA 43705; ***Itycyphus oursi***: Makay: UADBA 43706, 43707; ***Leioheterodon geayi***: UADBA 43750; ***Leioheterodon madagascariensis***: Beronto: UADBA 43754; Makay: UADBA 43757, 43758, 43759; ***Leioheterodon modestus***: Beronto: UADBA 43766, 43767; Nosy-Ambositra: UADBA 43768; ***Liophidium* sp.**: Beronto: UADBA 43775; Nosy-Ambositra: UADBA 43776; ***Liophidium torquatum***: Kelifely Tablelands: UADBA 43779; Makay: UADBA 43783; ***Lycodryas* cf. *gaimardi***: Ankara Tablelands: UADBA 43798; ***Madascincus* sp. "vitreus"**: Beronto: UADBA 43164, 43165, 43166; Nosy-Ambositra: UADBA 43167; ***Lygodactylus* cf. *madagascariensis***: Beronto: UADBA 43814, 43815, 43816, 43817; ***Lygodactylus tolampyae***: Ankara Tablelands: UADBA 43830, 43831, 43832, 43833, 43834, 43835, 43836; Kelifely Tablelands: UADBA 43837, 43838; Beronto: UADBA 43870, 43871; Nosy-Ambositra: UADBA 43843, 43844, 43845, 43846, 43847, 43848; ***Madagascarophis colubrinus***: Ankara Tablelands: UADBA 43890, 43891, 43892, 43893, 43984, 43895, 43896; Kelifely Tablelands: UADBA 43897, 43898, 43899, 43900, 43901, 43902, 43903, Beronto: UADBA 43906; Nosy-Ambositra: UADBA 43907, 43908, 43909, 43910, 43911; Makay: UADBA 43907, 43908, 43909, 43910, 43911; ***Mimophis mahfalensis***: Ankara Tablelands: UADBA 44096; Kelifely Tablelands: UADBA 44097, 44098; Beronto: UADBA 44014, 44105, 44106, 44107; Nosy-Ambositra: UADBA 44108, 44109, 44110; ***Oplurus cuvieri***: Ankara Tablelands: UADBA 44133, 44134, 44135; Kelifely Tablelands: UADBA 44136, 44137, 44138; ***Oplurus cyclurus***: Beronto: UADBA 44153, 44154, 44155, 44156, 44157, 44158; Nosy-Ambositra: UADBA 44159, 44160, 44161, 44162, 44163, 44164; ***Oplurus quadrimaculatus***: Makay: UADBA 44172, 44173, 44174, 44175, 44176; ***Paroedura bastardi***: Makay: UADBA 44189, 44190, 44191, 44192, 44193; ***Paroedura oviceps***: Ankara Tablelands: UADBA 44194, 44195, 44196, 44197, 44198, 44199; ***Paroedura picta***: Beronto: UADBA 44203, 44204, 44205, 44206, 44207, 44208, 44209; Nosy-Ambositra: UADBA 44210, 44211, 44212, 44213, 44214, 44215; Makay: UADBA 44224; ***Paroedura vahiny***: Beronto: UADBA 44241; ***Phelsuma kochi***: Ankara Tablelands: UADBA 44260, 44261, 44262, 44263; Kelifely Tablelands: UADBA 44264, 44265, 44266, 44267, 44268; ***Phelsuma mutabilis***: Beronto: UADBA 44279, 44280; Nosy-Ambositra: UADBA 44281, 44282; Makay: UADBA 44285, 44286; ***Phisalixella tulearensis***: Nosy-Ambositra: UADBA 43809; ***Phisalixella variabilis***: Ankara Tablelands: UADBA 43808; ***Pseudoxyrhopus quinquelineatus***: Ankara Tablelands: UADBA 44299; ***Sanzinia madagascariensis volontany***: Ankara Tablelands: UADBA 44340; Kelifely Tablelands: UADBA 44341; Nosy-Ambositra: UADBA 44342; Makay: UADBA 44343; ***Tracheloptychus petersi***: Beronto: UADBA 44064, 44065; ***Trachylepis aureopunctata***: Beronto: UADBA 44068, 44069; Nosy-Ambositra: UADBA 44070, 44071, 44072, 44073; Makay: UADBA 44076; ***Trachylepis elegans***: Ankara Tablelands: UADBA 44085, 44086, 44087, 44088, 44089; Beronto: UADBA 44106, 44107, 44108, 44109, 44110; Nosy-Ambositra: UADBA 44111, 44112, 44113, 44114, 44115, 44116; ***Trachylepis gravenhorstii***: Makay: UADBA 44131, 44132, 44133, 44134, 44135, 44136, 44137, 44138, 44139; ***Pelomedusa subrufa***: Nosy-Ambositra: UADBA 44165, 44166; ***Typhlops decorsei***: Nosy-Ambositra: UADBA 44168; ***Typhlops* sp.**: Ankara Tablelands: UADBA 44167; ***Uroplatus guentheri***: Kelifely Tablelands: UADBA 44178, 44179; ***Uroplatus henkeli***: Ankara Tablelands: UADBA 44182; Kelifely Tablelands: UADBA 44183, 44184, 44185, 44186, 44187, 44188; ***Zonosaurus laticaudatus***: Ankara Tablelands: UADBA 44220, 44221, 44222; Kelifely Tablelands: UADBA 44223, 44224, 44225, 44226; Beronto: UADBA 44230; Nosy-Ambositra: UADBA 44231, 44232, 44233, 44234, 44235, 44236; Makay: UADBA 44211, 44243, 44244, 44245, 44246, 44247, 44248, 44249, 44250, 44251, 44252.

APPENDIX II. Binary matrix table used for hierarchical cluster analysis for the biogeographical analysis. Species with uncertain taxonomic attribution are omitted from the table (see **MATERIALS AND METHODS**: ***Biogeographical analysis***).

Species	Ankara[1]	Kelifely[1]	Bemaraha[2]	Nosy-Ambositra[1]	Beronto[1]	Makay[1]	Isalo[3]
Acrantophis dumerili	0	0	0	1	1	1	1
Aglyptodactylus securifer	1	1	1	0	0	1	0
Alluaudina bellyi	1	0	0	0	0	0	0
Amphiglossus reticulatus	0	1	1	0	0	0	0
Blaesodactylus sakalava	1	0	1	1	0	1	1
Boophis doulioti	1	1	1	0	0	1	0
Brookesia brygooi	1	0	1	0	0	1	1
Chalarodon madagascariensis	0	0	1	1	0	1	1
Dromicodryas bernieri	0	0	0	1	1	1	1
Dromicodryas quadrilineatus	1	1	1	0	0	0	0
Dyscophys insularis	0	0	1	0	1	0	0
Furcifer labordi	0	0	0	1	1	0	0
Furcifer lateralis	0	1	1	0	0	1	1
Furcifer nicosiai	0	0	1	0	0	0	0
Furcifer oustaleti	1	1	0	0	0	1	1
Furcifer verrucosus	0	0	0	1	1	0	0
Geckolepis maculata	1	1	1	0	0	1	0
Geckolepis typica	1	0	1	1	1	0	1
Gephyromantis corvus	0	0	0	0	0	1	1
Gephyromantis pseudoasper	1	1	0	0	0	0	0
Hemidactylus frenatus	1	0	0	0	0	0	0
Hemidactylus mercatorius	0	0	0	1	1	1	1
Heterixalus luteostriatus	0	0	1	0	1	0	0
Heteroliodon occipitalis	1	0	0	1	0	0	0
Ithycyphus miniatus	0	1	1	0	0	1	0
Ithycyphus oursi	0	0	0	0	0	1	0
Laliostoma labrosum	1	1	1	1	1	0	1
Leioheterodon geayi	0	0	0	0	1	0	0
Leioheterodon madagascariensis	0	0	1	0	1	1	1
Leioheterodon modestus	0	0	1	1	1	0	1
Liophidium torquatum	0	1	1	0	0	1	0
Lycodryas granuliceps	0	0	1	0	0	0	0
Lygodactylus madagascariensis	0	0	0	0	1	0	0
Lygodactylus tolampyae	0	1	1	1	1	1	1
Madagascarophis colubrinus	1	1	1	0	0	1	1
Madagascarophis meridionalis	0	0	1	1	1	1	0
Madascincus intermedius	0	0	1	1	0	1	0
Mantella betsileo	1	0	1	1	0	0	0
Mimophis mahfalensis	1	1	1	1	1	0	1
Oplurus cuvieri	1	1	1	0	0	0	0
Oplurus cyclurus	0	0	0	1	1	0	1
Oplurus quadrimaculatus	0	0	0	0	0	1	1
Paroedura androyensis	0	0	0	0	0	0	1
Paroedura bastardi	0	0	0	0	0	1	1
Paroedura oviceps	1	0	0	0	0	0	0
Paroedura picta	0	0	0	1	1	1	1

Paroedura tanjaka	0	0	1	0	0	0	0
Pelomedusa subrufa	0	0	0	1	0	0	1
Phelsuma hielscheri	0	0	0	0	0	0	1
Phelsuma kochi	1	1	1	0	0	0	0
Phelsuma lineata	0	0	1	0	0	0	0
Phelsuma mutabilis	0	0	1	1	1	1	1
Phisalixella tulearensis				1			
Phisalixella variabilis	0	1	1	0	0	0	0
Pseudoxyrhopus quinquelineatus	1	0	1	0	0	0	1
Ptychadena mascareniensis	1	0	0	1	1	1	1
Sanzinia m. volontany	1	1	1	1	0	1	0
Scaphiophryne brevis	1	0	0	1	1	0	1
Scaphiophryne calcarata	1	0	1	1	1	1	0
Scaphiophryne gottlebei	0	0	0	0	0	0	1
Stenophis gaimardi	0	0	0	0	0	0	1
Stenophis granuliceps	0	0	1	0	0	0	0
Thamnosophis lateralis	0	0	1	0	0	1	1
Trachylepis aureopunctata	0	0	0	1	1	1	0
Trachylepis elegans	1	0	1	1	1	0	0
Trachylepis gravenhorstii	0	0	0	0	0	1	0
Trachylepis vato	0	0	0	0	0	0	1
Tracheloptychus petersi	0	0	0	0	1	0	0
Typhlops decorsei	0	1	0	1	0	0	0
Uroplatus ebenaui	0	0	1	0	0	0	0
Uroplatus guentheri	0	1	1	0	0	0	0
Uroplatus henkeli	1	1	1	0	0	0	0
Zonosaurus bemaraha	0	0	1	0	0	0	0
Zonosaurus karsteni	0	0	1	0	0	0	1
Zonosaurus laticaudatus	1	1	1	1	1	1	1
Zonosaurus madagascariensis	0	0	0	0	0	0	1

Sources: [1] This study; [2] H.A. Rakotondravony (unpublished data); [3] Hawkins (1994).