Belg. J. Zool., 135 (supplement) : 21-29 December 2005

Investigating the role of natural gallery forests outside the Congolese rainforest as a refuge for African forest shrews

Patrick Barrière[1,2], Rainer Hutterer[3], Violaine Nicolas[4,2], Sophie Quérouil[5,2] and Marc Colyn[1,2]

[1] **Laboratoire Ecobio : Ecosystèmes, Biodiversité et Evolution, UMR 6553 - CNRS, Université de Rennes 1, Station Biologique, F-35380 Paimpont, France.**
[2] **Laboratoire EVE : Ethologie, Evolution et Ecologie, UMR 6552 - CNRS, Université de Rennes 1, Station Biologique, F-35380 Paimpont, France.**
[3] **Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany.**
[4] **Museum National d'Histoire Naturelle, Département de Systématique et Evolution, UMR 5202 - CNRS, USM 601, Laboratoire Mammifères et Oiseaux, 55 rue Buffon, F-75005 Paris, France.**
[5] **Instituto do Mar (IMAR), Departamento de Oceanografia e Pescas, cais Santa Cruz, 9901-862 Horta, Portugal.**
Corresponding author : P. Barrière, e-mail : Patrick.Barriere@laposte.net

---

ABSTRACT. Conditions that prevailed in rainforest faunal refuges during glacial periods of the Pleistocene, particularly their size, position and habitat characteristics, remain little investigated. After the peak of the last interglacial period of the Holocene (7000 years B.P.), the Guineo-Congolese rainforest has been reduced in size and isolated gallery forests emerged in the peripheral Northern Congo forest-savanna mosaic, mainly because of the reduction in rainfall. In the north of the Central African Republic, 400 km north of the present rainforest zone, up to the Sudano-Sahelian savannas, such gallery forests harbour several forest species of plants, birds and mammals related to West and/or East Congo faunal regions. This suggests that since the catastrophic destruction of central African rainforests, that culminated about 2500 years ago, these galleries could have mimicked the conditions that occurred in the Pleistocene refuges. We tested whether these natural gallery forests, outside the Congolese rainforest, could act as refuges for small forest mammals such as shrews. Composition and structure of shrew communities were studied in three main regions belonging to three river basins and two distinct phytoregions. They were compared to two other shrew communities located within the main Congolese rainforest, also in C.A.R.. None of the typical rainforest shrew species was collected within the studied isolated gallery forests. Thus, climatic and habitat characteristics within these gallery forests were presumably not suitable for these forest patches to act as climatic refuges for the forest shrew fauna.

KEY WORDS : Soricidae, *Crocidura*, *Suncus*, Central African Republic, Community structure, Biogeography, Refuge theory.

INTRODUCTION

In the Quaternary period (from 1.8 My B.P. to present), Africa underwent climatic oscillations resulting in several phases of forest fragmentation and extension. During the last glacial maximum of the Pleistocene (between about 20000 and 15000 years B.P.), as a result of the very cold and dry climate, tropical rainforest decreased in size and became fragmented. Paleontological and biogeographic data suggest that it was limited to lowland forest patches in the downstream zone of the large rivers and on lower slopes of mountains (HUTTERER et al., 1987; MALEY, 1987; COLYN, 1991; COLYN et al., 1991; MALEY, 1996; MALEY & BRENAC, 1998). According to HAFFER (1969), these forest patches may have acted as refuges for the forest flora and fauna. In contrast, during the inter-glacial periods, the warmer and wetter climate favoured an extension of the rainforest. The last inter-glacial period culminated at 7000-8000 years B.P., during the Holocene (MALEY, 2001). The central African rainforest extended to the north, up to the present Sudano-Sahelian savanna zone. Since 5000 years B.P., the reduction in rainfall (BERTAUX et al., 2000), associated with climatic disturbance, resulted in contraction of the central African rainforests that culminated about 2500 years ago (MALEY, 2001). In the north of the Central African Republic (C.A.R.), since 7000 years B.P., the extension of the savannas (MALEY & BRENAC, 1998) resulted in the isolation of gallery forests outside the Congolese rainforest. Despite a new phase of forest extension that began 2000 years ago (MALEY, 2001), it is probable that these Holocene gallery forests remained isolated from the Congolese rainforest and could have acted as forest refuges. It is hypothesised that Pleistocene and Holocene refuges probably formed a network of forest isolates within a forest-savanna mosaic zone rather than small homogenous forest isolates (LEAL, 2000; MALEY, 2001). The principal refuges of the Pleistocene were probably located in the downstream zone of the large rivers, within the present rainforest zone. However, the conditions that prevailed in these forest refuges, particularly their size and habitat characteristics remain poorly investigated.

In the North of the C.A.R., more than 400 km north of the present northern boundary of the rainforest, Holocene gallery forests are known to harbour typical Congolese forest plants, birds and mammals (Fay, 1988; Christy, 1999; ECOFAC, 2001). These taxa also occur in the West Central or East Central regions (*sensu* Colyn, 1999; Colyn & Deleporte, 2002b) and these galleries represent their northernmost range limit. In particular, Fay (1988) showed that three strictly arboreal species of forest primates (*Cercopithecus pogonias*, *C. nictitans* and *C. ascanius*), known to be widely distributed in the Congolese rainforest, can be found in the northern C.A.R. gallery forests, in the south-western sector of Manovo-Gounda-St. Floris National Park. The aim of this study is to test whether these natural gallery forests, located outside the Congolese rainforest, may act as refuge for terrestrial small forest mammals such as shrews. This may help to understand the conditions that could have prevailed in the Pleistocene refuges.

MATERIAL AND METHODS

Study area

The study area (80000 km^2) is located in the north of C.A.R., more than 400 km north of the present northern boundary of the Congolese rainforest (Fig. 1). It has been managed until the end of the year 2000 by the "Programme de Développement de la Région Nord" (P.D.R.N.). Since then, it has been associated with the ECOFAC project under the name "Zones Cynégétiques Villageoises" (Z.C.V.). Shrews were collected at eleven sites (Fig. 1) located within National Parks (Bamingui-Bangoran N.P., sites 5-7; Manovo-Gounda-St Floris N.P., 8-9 and its periphery, 10), within a hunting zone (Sangba, sites 3 and 4) or in neighbouring zones (sites 1, 2 and 11) within the project's action area (Téllo, 2000; ECOFAC online). All these sites, which are located in the upstream zone of several rivers, were pooled in three main regions : Bohou (sites 1 and 2), Bamingui-Bangoran (sites 3-7) and Manovo-Mara (sites 8-11) They belong to three river basins (Bahr Aouk, Bamingui and Kotto) and two distinct phytoregions (medio-Sudanian savanna and Sudano-Sahelian savanna; (Table 1; Fig. 1).

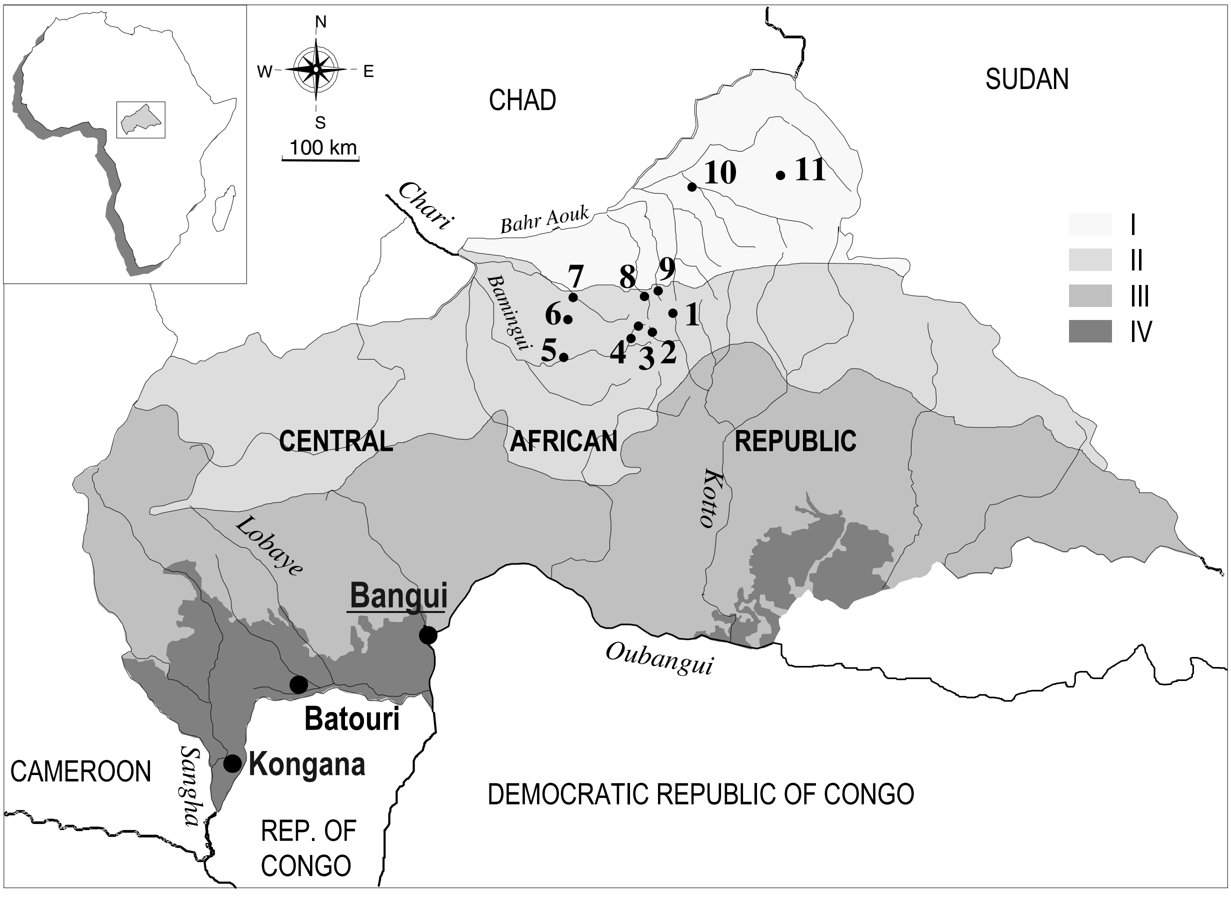

Fig. 1. – Study sites in the north of the Central African Republic : 1, Kpata; 2, Bohou; 3, Bamingui-Brendja; 4, Sangba; 5, Kaha pond, near Bamingui; 6, Kivou pond; 7, Bangoran; 8, Manovo; 9, Koumbala; 10, Gordil; 11, Délembé. Phytoregions *sensu* Boulvert (1986) : I, Sudano-Sahelian savanna; II, medio-Sudanian savanna; III, Sudano-Guinean savanna and peri-forest sector of the Guineo-Congolian rainforest and savanna domain; IV, rainforest sector of the Guineo-Congolian domain. The two sites located within the Congolese rainforest and selected for comparison (Batouri and Kongana) are also plotted.

The Bohou region is located in the upstream zone of the Kotto River within the Congo River basin, while the two other regions are located in the upstream zone of the Chari River, within the Chad River basin. A savanna zone of ca. 5 km has been separating the two river basins for the past few hundred years (Fay, 1988). The southernmost sites (1-9) belong to the medio-Sudanian savanna domain *sensu* Boulvert (1986), while the other two (10 and 11) belong to the Sudano-Sahelian savanna. The typical medio-Sudanian sector is of *Encephalartos septentrionalis* type at the sites 1-4 and 8-9, with included bamboo savannas of *Oxytenanthera abyssinica* type (e.g. site 3), and of *Butyrospermum paradoxum parkii* type at sites 5-7 (Boulvert, 1986). It harbours gallery forests of *Anogeissus leiocarpus* type at all sites (1-9). The northernmost sites (10, 11) belong to the Sudano-Sahelian domain and are of *Terminalia lexiflora* type.

TABLE 1

Characteristics of each study site. Site numbers refer to Figure 1. Main habitat types : BS, bamboosian savanna; GF, gallery forest; RS, riparian savanna; S, undifferentiated savanna.

Site No	**Study Site**	**Coordinates**	**Main Region**	**Main habitat**		**Sub-climate**	**Annual Rainfal (mm)**
				GF	**S**		
1	Kpata	08°03'N; 21°24'E	Bohou	GF		sub-Sudanian	1200-1400
2	Bohou	07°43'N; 21°20'E	Bohou	GF		sub-Sudanian	1200-1400
3	Bamingui-Brendja	07°47'N; 20°57'E	Bamingui-Bangoran	GF	BS	sub-Sudanian	1200-1400
4	Sangba	07°45'N; 20°43'E	Bamingui-Bangoran		RS	sub-Sudanian	1200-1400
5	Kaha pond near Bamingui	07°26'N; 20°08'E	Bamingui-Bangoran	GF	S	sub-Sudanian	1000-1200
6	Kivou pond (= Kaga Yara)	07°51'N; 20°11'E	Bamingui-Bangoran		RS	sub-Sudanian	1000-1200
7	Bangoran	08°05'N; 20°21'E	Bamingui-Bangoran		S	sub-Sudanian	1000-1200
8	Manovo	08°22'N; 20°57'E	Manovo-Mara		RS	sub-Sudanian	1200-1400
9	Koumbala	08°19'N; 21°17'E	Manovo-Mara	GF		sub-Sudanian	1200-1400
10	Gordil	09°36'N; 21°41'E	Manovo-Mara		RS	Sudano-Sahelian	1200-1400
11	Délembé	09°44'N; 22°39'E	Manovo-Mara		RS	Sudano-Sahelian	1000

All the sites have a Sudano-Guinean climate, with sub-Sudanian or Sudano-Sahelian sub-climates (Table 1). Gallery forests were surveyed in each of the three regions, and the surrounding savanna was also surveyed within the Chad River basin (Table 1). Sampling in different river basins and phytoregions, rather than focusing on sampling within a single gallery forest, was considered the best way to have a good representation of the shrew community in the study area. Human populations in the area have a density lower than 0.5 persons/km^2 and have a low disturbance effect on the small mammal fauna, especially on shrews that are never hunted nor eaten.

Two sites located within the Congolese rainforest were selected for comparison (Fig. 1). The Batouri River site, in the Ngotto forest, consists of a mixed-species semi-deciduous rainforest at the northern limit of the Guineo-Congolese rainforest (more details in Boulvert, 1986). This primary rainforest is often affected by storms and numerous tree falls have created openings in the canopy (Barrière et al., 2000). With a typical forest Guinean climate, the rainfall, occurring mainly from May to October, averages 1600 mm per year. The Kongana study area consists mainly of a mixed-species semi-deciduous rainforest and a mono-dominant *Gilbertiodendron dewevrei* forest, and has a climate similar to that of Ngotto (Ray & Hutterer, 1996).

Sampling

Trapping was mainly performed from May to August 1998 and from June to August 1999 (Table 2), i.e. during the early wet season, by J.L. Téllo and/or a member of the University of Rennes 1. Our major method of collecting shrews was by dry, not-baited pitfall traps, with 10-litre buckets positioned at 5 m intervals along a linear plastic drift fence. All the lines were constructed as described in Nicolas et al. (2003). Trapping period, number of pitfall lines and cumulated trapping effort varied between sites (Table 2). The thirty-five pitfall lines totalled a pitfall trapping effort of 8581 bucket-nights.

Mixed Sherman traps and metal snap-traps were also used in transects, mainly to capture rodents, and totalled 32844 trap-nights. In addition, a few specimens were incidentally collected by J.L. Téllo since June 1997. Most of the small mammals captured were weighed, measured, autopsied and preserved in 10% formalin. Species identification was performed by two of the authors (R.H. and P.B.) on the basis of morpho-anatomical analyses, and in some instances supported by molecular analyses (Quérouil et al., 2001; in press). The taxonomic nomenclature follows Hutterer (1993), except for *Suncus megalura*, previously considered as a *Sylvisorex* species, but now considered as a *Suncus* species according to Quérouil et al. (2001). Three problematic *Crocidura* taxa, belonging to species complexes still in need of revision, were named *Crocidura* cf. *denti*, *C.* cf. *hildegardeae* and *C.* cf. *poensis* as they could not be definitively identified. The material was deposited at the Station Biologique de Paimpont, University of Rennes 1, France and the Museum Alexander Koenig, Bonn, Germany.

Data analysis

The trapping effort (TE, in trap-nights) was defined as the number of traps (or buckets) set for a 24-hour period, and the trap success (TS) as the number of individuals captured per 100 trap-nights; i.e. TS = (N/TE)*100, where N is the number of shrews captured. Genus and species richness (G and S) were defined as the number of distinct genera and species identified, respectively. Species relative abundance (pi, %) was defined as the number of individuals (ni) of species i captured per 100 individuals of all species, i.e. pi = (ni/N)*100. For the estimation of species richness, all shrew captures were considered, but for the estimation of trap success and species relative abundance, only the individuals captured by pitfall traps were selected.

TABLE 2

Trapping characteristics (trapping period, number of lines and trapping effort, mainly in pitfall (P)), shrew trap success, identity and number of shrews captured. Site numbers refer to Table 1 and Figure 1. Number of shrews collected in mixed Sherman and metal snap-traps line (L) are in brackets and those collected by hand (H) in square-brackets. Main habitat type codes refer to Table 1. A species code (A-N) was attributed to each shrew taxon.

Main region	**Bohou**		**Bamingui-Bangoran**							**Manovo-Mara**				**Total**			
Site number	**1**	**2**	**3**		**4**	**5**		**6**	**7**	**8**	**9**	**10**	**11**				
Mean of collect	**P**	**L**	**P**	**P**	**P**	**P**	**H**	**P**	**L**	**L**	**P**	**P**	**P**	**P**	**L**	**H**	**Total**
Main Habitat type	**GF**	**GF**	**GF**	**BS**	**RS**	**GF**	**S**	**RS**	**S**	**RS**	**GF**	**RS**	**RS**				
Trapping period	Jun-98		May-98	Aug-98	Aug-99	Jul-99		Jul-99			Jul-98	Jun-99	Jun-99				
No of pitfall lines	4		5	3	4	4		4			6	3	2	35			
Trapping effort (TE)	1,584		1,500	648	700	900		700			1,584	600	365	8,581	32,844		
No of shrews captured (N)	58	(1)	41 (1)	26	29 [4]	23	[1]	16	(4)	(4)	47 (2)	23 [4]	7 (1)	270	(13)	[9]	292
Trap success (TS)	3.66		2.73	4.01	4.14	2.56		2.29			2.97	3.83	1.92	3.15	0.04		
A *Crocidura* cf. *denti* Dollman, 1915	4	(1)	15	4	4 [1]	5		2			18 (1)	1 [1]		53	(2)	[2]	57
B *Crocidura* cf. *hildegardeae* Thomas, 1904			23 (1)	4	16	1	[1]	6			2	1	1	54	(1)	[1]	56
C *Crocidura* cf. *poensis* (Fraser, 1843)					2					(1)		12 [1]	3 (1)	17	(2)	[1]	20
D *Crocidura fuscomurina* (Heuglin, 1865)					1									1			1
E *Crocidura lamottei* Heim de Balsac, 1968	1								(2)					1	(2)		3
F *Crocidura littoralis* Heller, 1910	4					9					5			18			18
G *Crocidura ludia* Hollister, 1916	41													41			41
H *Crocidura nanilla* Thomas, 1909								1					1	2			2
I *Crocidura olivieri* (Lesson, 1827)	5		1	4	2 [3]	1		7	(2)	(3)	3 (1)	1	1	25	(6)	[3]	34
J *Crocidura roosevelti* (Heller, 1910)	1			2							1			4			4
K *Crocidura turba* Dollman, 1910												[2]				[2]	2
L *Crocidura yankariensis* Hutterer & Jenkins, 1980												7		7			7
M *Suncus infinitesimus* (Heller, 1912)	2		2	7	2	6					18	1	1	39			39
N *Suncus megalura* (Jentink, 1888)					2									2			2
Specimens not seen				5		1								6			6
Genus richness (G)	2	1	2	2	2	2	1	1	1	1	2	2	2	2	1	1	2
Species richness (S)	7	1	4	5	7	5	1	4	2	2	6	7	5	13	5	5	14

RESULTS

Overall community composition

A total of 292 shrews representing two genera and fourteen species were collected. One genus (*Suncus*) was only represented by two species and the other one (*Crocidura*) by 12 species (Table 2). More than ninety-two percent of shrews were collected in pitfall traps (N=270; TS=3.15) while only 13 individuals were captured in Sherman traps (TS=0.04), nine were collected by hand and none in metal snap-traps. While only five species were trapped in Sherman traps, thirteen species were captured in pitfalls. *Crocidura turba* was only collected by hand. Two species were numerous (*C.* cf. *hildegardeae* and *C.* cf. *denti*, each comprising about 20% of all shrews), five were common (*C. ludia*, *S. infinitesimus*, *C. olivieri*, *C.* cf. *poensis* and *C. littoralis*) and the other seven were captured infrequently. The three specimens of the savanna species *C. lamottei*, described from Lamto (Ivory Coast) and since then widely recorded within Sudanian and Guinean savannas from Senegal to western Cameroon, constitute the first known record of the species in C.A.R. and the easternmost limit of its distribution range. The seven specimens of the uncommon savanna shrew *C. yankariensis* also constitute the first known record of the species in C.A.R.

Community structure within the gallery forests

In the gallery forests, with a pitfall trapping effort of 5568 bucket-nights, 169 shrews (TS=3.04) representing two genera and eight species were recorded (Fig. 2a). The two genera (*Crocidura* and *Suncus*) were captured in each of the three main regions. The number of species varied from five to seven according to the region. It is noteworthy that the shrew community had a higher species richness and trap success at Bohou (S=7 and TS=3.66, respectively), within the Congo River basin. All the species recorded are either savanna species or species occurring within the rainforest and at its margin (see Table 3) but preferentially in open habitat. *Crocidura ludia*, the most forest-dependent species amongst the recorded species, was highly dominant at Bohou, while it was absent from all pitfall traps in the Chad River basin. Within the latter, the structure of the community differed between the two studied regions : the medium-sized *C.* cf. *hildegardae* was more abundant at Bamingui-Bangoran (pi=37.5%) while the medium-sized *C.* cf. *denti* and the tiny *S. infinitesimus* co-dominated in the Manovo-Mara region (pi=38.3%).

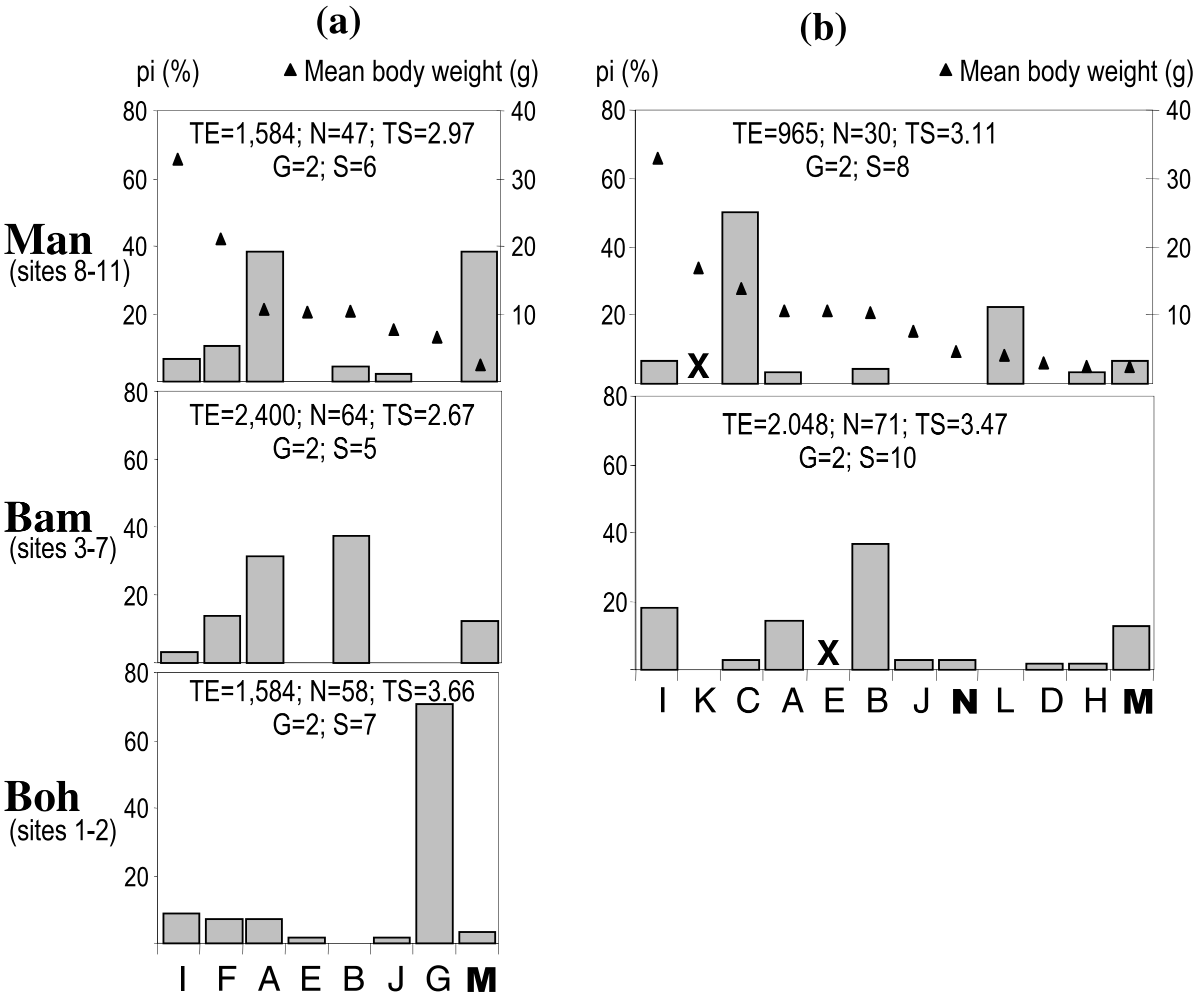

Fig. 2. – Pitfall trapping effort (TE); number of individuals (N), of genera (G) and of species (S) pitfall-trapped; trap success (TS) and distribution of relative abundance (pi) of the shrew species within (a) the gallery forests and (b) the surrounding savanna of the three main regions studied : Boh (Bohou), Bam (Bamingui-Bangoran) and Man (Manovo-Mara). Species codes (A-N) are defined in Table 2 and codes of the two *Suncus* species (M and N) are in bold. Species are ordered by decreasing mean body weight (as indicated by the triangles). Crosses indicate records by another mean than pitfall.

Community structure within the savanna

In the savanna zone of the two regions belonging to the Chad River basin, with a pitfall trapping effort of 3013 bucket-nights, 101 shrews (TS=3.35) representing two genera and ten species were recorded (Fig. 2b). Two additional species were collected by other means than pitfall trapping. The two genera (*Crocidura* and *Suncus*) were captured in each of the two regions. The number of species and the trap success were higher at Bamingui-Bangoran (S=10 and TS=3.47, respectively) than at Manovo-Mara (S=8 and TS=3.11). While the medium-sized *Crocidura* cf. *hildegardae* was dominant at Bamingui-Bangoran (pi=36.6%), the shrew community of Manovo-Mara was dominated by *C.* cf. *poensis* (pi=50%) of higher size.

Differences in the community structure between gallery forest and savanna

Species richness and trap success were higher in the two savanna habitats (S=12 and TS=3.35, respectively) than in the gallery forests (S=8 and T=3.04), despite a lower pitfall trapping effort (TE=3013). The difference in term of trap-success was mainly due to the capture of one additional species (*C.* cf. *poensis*), absent from the gallery forests and dominant at Manovo-Mara. *Suncus megalura* was captured only in the riparian savanna of the Bamingui-Bangoran region and the other species that were not captured in gallery forest are four savanna species (*C. fuscomurina, C. nanilla, C. turba* and *C. yankariensis*) and the problematic *C.* cf. *poensis*. The latter is taxonomically closely related to the savanna species *C. turba* and both belong to the poensis species complex, still in need of revision (Quérouil et al., in press). It could refer to a species different from the true

C. poensis, which could mainly occur in rainforest. For a given region, the shrew community structure varied between gallery forest and savanna, especially at Manovo-Mara where *C.* cf. *denti* and *S. infinitesimus* co-dominated in gallery forest (pi=38.3% each), while *C.* cf. *poensis* and *C. yankariensis* were the most abundant species in savanna (pi=50% and 23.3%, respectively). Whatever the habitat type the shrew community structure and the identity of the dominant species varied also between regions.

DISCUSSION

In order to test whether the natural gallery forests outside the Congolese rainforest could act as refuge for rainforest shrews, comparison of the shrew community within these galleries were made with two other communities in the northernmost part of the Congolese rainforest (Ray & Hutterer, 1996; Barrière et al., 2000; see Fig. 1 and Table 3), also situated in C.A.R. and within the West Central faunal region. In the Ngotto forest (Batouri River site), shrews were mainly pitfall-trapped (Barrière et al., 2000) while in Kongana, shrew remains were collected in carnivore scats (Ray & Hutterer, 1996). For the two communities combined, five genera and 20 species were collected (Table 3). In each of these two localities, rainforest species were the most numerous and represented altogether more than 88% of the whole collection.

TABLE 3

Comparison between the structure of shrew communities (pi, relative abundance) within gallery forests outside the Congolese rainforest and within the rainforest zone at two sites. "Forest I" means primary forest and "II" means secondary. When absent in the gallery forests, the presence of the species in the adjacent savanna is indicated by an "X" for each of the three regions. Region abbreviations : Boh (Bohou); Bam (Bamingui-Bangoran); Man (Manovo-Mara). Species in bold are known to occur within the rainforest zone. Habitat preferences (HP) : F, predominantly dense forest species; FS, species mainly occurring in transition zones such as secondary forest or forest-savanna mosaic; S, predominantly savanna species. Mean body weight (MBW) is given in grams.

				Within the Congolese rainforest		**Outside the rainforest**			
	Study location			**Batouri**	**Kongana**	**Boh**	**Bam**	**Man**	Total
	Main habitat type			Forest I	Forest I & II	Gallery forests			
	Period			Oct98 – Nov99	May92 – May94	May98 – Jul99			
	Mean of sampling			Pitfall	carnivore scats	Pitfall			
	Pitfall trapping effort (bucket-nights)			43,240	–	1,584	2,400	1,584	5,568
	Genus richness (G)			5	4	2	2	2	2
	Species richness (S)			18	16	7	5	6	8
	No of captures (N)			1,339	311	58	64	47	169
	Trap success (TS)			3.1		3.66	2.67	2.97	3.05
		HP	**MBW**						
	Sylvisorex johnstoni	F	2,9	**25.0**	**36.7**				
	Sylvisorex ollula	F	16,1	9.3	3.5				
	Crocidura nigrofusca	F	11,2	0.1	13.5				
	Sylvisorex konganensis	F	4,9	0.8	1.3				
	Paracrocidura schoutedeni	F	7,4	**17.6**	**24.1**				
	Congosorex verheyeni	F	7,1	1.8					
	Crocidura crenata	F	7,6	8.1					
	Crocidura dolichura	F	6,1	8.4	3.9				
	Suncus remyi	F	1,9	3.6	2.3				
	Crocidura batesi	F	16,0	11.1	3.2				
	Crocidura goliath	F	70,0	0.1	0.3				
	Sylvisorex pluvialis	F	5,0		1.0				
	Crocidura grassei	F	11,0	0.5					
	Crocidura poensis	F	14,0	2.1					
	Crocidura cf. _mutesae_	FS	16,1	0.3	2.3				
G	***Crocidura ludia***	FS	6,5	0.6	1.3	**70.7**			24.3
F	***Crocidura littoralis***	FS	21,0		2.3	6.9	14.1	10.6	10.7
B	**_Crocidura_ cf. _hildegardeae_**	FS	10,3	0.1	1.3		**37.5**	4.3	15.4
A	**_Crocidura_ cf. _denti_**	FS	10,5	0.9	2.9	6.9	**31.3**	**38.3**	24.9
I	***Crocidura olivieri***	FS	32,8	9.4	0.3	8.6	3.1	6.4	5.9
N	***Suncus megalura***	FS	4,5				x		x
M	*Suncus infinitesimus*	FS	2,5			3.5	12.5	**38.3**	16.6
J	*Crocidura roosevelti*	FS	7,6			1.7	x	2.1	1.2
E	*Crocidura lamottei*	S	10,5			1.7	x		0.6
D	*Crocidura fuscomurina*	S	3,0				x		x
H	*Crocidura nanila*	S	2,5				x	x	x
K	*Crocidura turba*	S	17,0					x	x
L	*Crocidura yankariensis*	S	4,4					x	x
C	*Crocidura* cf. *poensis*	S	14,0				x	x	x

In comparison, among the five genera occurring within the West Central region, only two (*Crocidura* and *Suncus*) were recorded in the gallery forests. A lower number of species was also recorded in the gallery forests (S=8). However, it is important to note that, at Batouri, when the cumulated pitfall trapping effort reached the value obtained at the northern galleries (5568 bucket-nights), four species had not been collected yet. None of the typical forest species of the genera *Sylvisorex, Paracrocidura, Suncus* and *Congosorex* was recorded in the gallery forests. *Suncus* was represented by *S. infinitesimus*, previously recorded from forest patches in forest-savanna mosaic, in eastern Congo and by *S. megalura*, which was only recorded within the savanna zone and is actually not a typical rainforest dweller but a widely distributed species (HUTTERER et al., 1987). Among the five *Crocidura* species recorded in both Congolese rainforest and gallery forest, all have ecological preferences directed towards open rainforest or forest patches within forest-savanna mosaic, and are medium or large sized. Three species, absent from the rainforest, were recorded within the gallery forests : *C. roosevelti* occurs at the margin of the rainforest in forest-savanna mosaic, and *C. lamottei* and *S. infinitesimus* occur only in savannas or in savanna-forest mosaic. Despite the absence of the typical forest shrew fauna within the gallery forests, it is noteworthy that *C. ludia*, which is listed as vulnerable (B1+2c) by the IUCN (HILTON-TAYLOR, 2000), was common at Bohou.

In Afro-tropical primary lowland rainforest, shrew communities, when surveyed by an adequate trapping protocol (i.e. pitfall traps with drift fence, NICOLAS et al., 2003) appear to be dominated by one of the smallest species, such as *Sylvisorex johnstoni* in West Central Africa (e.g. in Gabon : BARRIÈRE, 1997; GOODMAN et al., 2001; NICOLAS et al., 2004; in C.A.R. : BARRIÈRE et al., 2000; in Republic of Congo : BARRIÈRE, 1997; in Equatorial Guinea : LASSO et al., 1996; and in Cameroon : HUTTERER & SCHLITTER, 1996); or by *Crocidura obscurior* (3.6 g of mean body weight) in West Africa (Ivory Coast : BARRIÈRE et al., 1999; CHURCHFIELD et al., 2004). By contrast, in secondary forest or open habitats within the Congo River basin, the dominant shrews are usually larger, such as *C.* cf. *hildegardeae* (more than 10 g) in included savanna at Odzala National Park, Republic of Congo (Marc Colyn & Patrick Barrière, unpublished data) and at Ngotto forest, C.A.R. (BARRIÈRE et al., 2000), or such as *C. buettikoferi* (11 g) in cacao-coffee plantations included in the Taï National Park, Ivory Coast (BARRIÈRE et al., 1999). In the gallery forests of the Z.C.V., the tiny *S. infinitesimus* co-dominated (with *C.* cf. *denti*) the shrew community of Manovo-Mara and the small *C. ludia* highly dominated the community of Bohou. Nevertheless, it is noteworthy that the medium-sized *C.* cf. *hildegardeae* and *C.* cf. *denti* were co-dominant in Bamingui-Bangoran and that *C.* cf. denti was co-dominant (which *S. infinitesimus*) in Manova-Mara.

Among the 169 shrews, representing eight species, collected in gallery forests within three main regions, none of the typical rainforest shrews occurring within the Congo River basin was recorded. Similarly, no typical rainforest muroid rodent species was identified among a collection of 449 individuals, at the present state of analysis (Marc Colyn & Violaine Nicolas, unpublished data). The gallery forests harbour several plant, bird, primate and other larger mammal species, typical of the Congolese rainforest, suggesting that these galleries may presently act as refuge for these forest taxa. However, it is not the case for terrestrial small mammals. At first sight, these contrasting results are surprising. The observed differences may be attributed to distinct climatic and habitat characteristics as food resources, between the gallery forests and the Congolese rainforest. Being amongst the smallest mammals, shrews have high metabolic rates resulting in high energy requirements and water loss (CHURCHFIELD, 1990), especially the smallest species (VOGEL et al., 1981). These characteristics may be constraining life histories to a greater extent than occurs in larger mammals (SYMONDS, 1999) and could explain the differences observed between small mammals and larger ones. It is then possible that the typical rainforest shrews would not have survived in the gallery forests because the conditions would have been too dry and too hot in comparison to the more clement conditions of the Congo River basin.

Differences in food resources could also have an influence. Afro-tropical shrews, closely dependent on the understorey leaf litter, feed mainly on small arthropods. These shrews have a high level of food niche overlap and very small prey is of greatest importance to the smaller species (CHURCHFIELD et al., 2004; DUDU et al., in press). Therefore, shrews would be more dependent on the climatic conditions and food availability than larger mammals, and they could not have been able to survive in the warm and dry gallery forests in comparison to the Congolese rainforest. As previously suggested, central African endemic shrews are highly dependent on primary forest environments (HUTTERER et al., 1987). The unsuitability of these galleries to act as refuge for terrestrial small forest mammals could also be attributed to the small size of the patches, their peripheral location outside the present Congolese rainforest, more than 400 km from its margin, and the time elapsed since their isolation from the Congolese rainforest. This is in agreement with hypotheses which suggest that refuges could have been much larger, close to one another, on the margins of the rainforest zone and in the downstream zone of large rivers (HUTTERER et al., 1987; MALEY, 1996; DELEPORTE & COLYN, 1999).

CONCLUSION

Altogether, these findings support the hypotheses that Pleistocene refuges would have been composed of a network of forest patches within a forest-savanna mosaic rather than of small homogenous forest isolates and localised in the downstream zone of large rivers. The knowledge of the location and size of refuges is essential for the understanding of evolutionary scenarios. The refuges could probably not maintain the whole mammalian fauna, but rather a limited number of taxonomic units with suitable anatomy, physiology and ecological preferences. The knowledge of the history of tropical African floras and faunas will progress thanks to the multiplication of comparative phylogeographic studies (QUÉROUIL, 2001; QUÉROUIL et al., 2002; 2003) using relevant biological markers (COLYN & DELEPORTE, 2002a).

ACKNOWLEDGEMENTS

Field studies were supported by EU-DGVIII-PDRN, "Programme de Développement de la Région Nord" (NORCADEV); EU-DGVIII-Ecofac program, "Conservation et Utilisation Rationnelle des Ecosystèmes Forestiers en Afrique centrale", http.www.ecofac.org, (managed by AGRECO, GEIE, BDPA, SCETAGRI, SECA, CIRADFORET) and EU-DGVIII-

Biofac program, "Origine et maintien de la biodiversité en Afrique centrale" (University of Rennes 1-CNRS, UMR 6552). P. Barrière and V. Nicolas received a fellowship from the Ministère de l'Education Nationale de l'Enseignement Supérieur et de la Recherche (France). We thank J. Lobão Téllo (PDRN) and A. Pénelon (ECOFAC) for their logistic support in the field, Olivier Perpète and the local teams of Sangba and Ngotto. We are also grateful to E. Verheyen and M. Dillen for their contribution to molecular analyses.

REFERENCES

Barrière, P. (1997). Ecologie des Peuplements de Soricidae Forestiers d'Afrique Centrale : considérations nouvelles sur base de la méthode de piégeage Pitfall. *Report to the University of Rennes 1*, Rennes : 26 pp.

Barrière, P., P. Formenty, R. Hutterer, O. Perpète & M. Colyn (1999). Shrew community from Taï forest (Côte d'Ivoire); ecological vigil searching the Ebola virus reservoir. *Abstracts of the 8th International African Small Mammal Symposium*, MNHN, Paris : 57.

Barrière, P., V. Nicolas, R.K. Maro, G. Yangoundjara & M. Colyn (2000). Ecologie et structuration des peuplements de micromammiferes musaraignes et rongeurs. *ECOFAC-CEE report*, Libreville : 55 pp.

Bertaux, J., D. Schwartz, A. Vicens, A. Siffedine, H. Elenga, M. Mansour, A. Mariotti, M. Fournier, L. Martin, D. Wirrmann & M. Servant (2000). Enregistrement de la phase sèche d'Afrique centrale vers 3000 ans B.P. par la spectrométrie IR dans les lacs Sinnda et Kitina (sud-Congo). In : Servant & Servant-Vildary (eds), *Dynamique à long terme des écosystèmes forestiers intertropicaux*, Mémoires UNESCO, Paris : 43-49.

Boulvert, Y., (1986). *République centrafricaine, carte phytogéographique*. Editions de l'ORSTOM, Paris : 131 pp.

Churchfield, S. (1990). *The natural history of shrews*. Christopher Helm (ed), London : 175 pp.

Churchfield, S., P. Barrière, R. Hutterer & M. Colyn (2004). First results on the feeding ecology of sympatric shrews (Insectivora : Soricidae) in the Tai National Park, Ivory Coast. *Acta Theriologica,* 49(1) : 1-15.

Christy, P. (1999). La République Centrafricaine, carrefour biogéographique. *Canopée, Bulletin sur l'Environnement en Afrique Centrale,* 14 : 6.

Colyn, M. (1991). L'importance zoogéographique du bassin du fleuve Zaïre pour la spéciation : le cas des primates simiens. *Ann. Mus. R. Afr. Centr.*, Tervuren, Belgique : 264.

Colyn, M. (1999). Un nouveau statut biogéographique pour l'Afrique centrale. *Canopée, Bulletin sur l'Environnement en Afrique Centrale,* 14 : 3-5.

Colyn, M., & P. Deleporte (2002a). Marqueurs biologiques en biogéographie historique : problèmes de taxonomie, de distribution et de filtre écologique. *Biosystema,* 20 : 41-48.

Colyn, M., & P. Deleporte (2002b). Biogeographic analysis of central African forest Guenons. In : Glenn & Cords (eds), *The Guenons : Diversity and Adaptation in African Monkeys.*, Kluwer Academic/Plenum Publishers, New-York : 61-78.

Colyn, M., A. Gauthier-Hion & W. Verheyen (1991). A reappraisal of the paleoenvironment history in Central Africa : evidence for a major fluvial refuge in the Zaire basin. *J. Biogeogr.,* 18 : 403-407.

Deleporte, P., & M. Colyn (1999). Biogéographie et dynamique de la biodiversité : application de la PAE aux forêts planitiaires d'Afrique centrale. *Biosystema,* 17 : 37-43.

Dudu, A., S. Churchfield & R. Hutterer (in press). Community structure and food niche relationships of coexisting rainforest shrews in the Masako Forest, north-eastern Congo. In : Merritt, Churchfield, Hutterer & Sheftel (eds), *The Biology of the Soricidae II*, Carnegie Museum of Natural History Special Publication.

ECOFAC online : (http ://www.ecofac.org).

ECOFAC (2001). Composante RCA, Projet de développement des zones cynégétiques villageoises. Rapport d'activités juillet-décembre 2001 (http ://www.ecofac.org/Composantes/ZonesCynegetiquesVillageoises.htm). *ECOFAC-CEE report*, Libreville : 116-137.

Fay, M. (1988). Faunal monkey populations in the Central African Republic : the northern limits. A census in Manovo-Gounda-St. Floris National Park. *Mammalia,* 52 : 57-74.

Goodman, S.M., R. Hutterer & P.R. Ngnegueu (2001). A report on the community of shrews (Mammalia : Soricidae) occurring in the Minkebe Forest, northeastern Gabon. *Mammal. Biol.,* 66 : 22-34.

Haffer, J. (1969). Speciation in neotropical birds. *Science,* 165 : 131-137.

Hilton-Taylor, C. (2000). 2000 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland and Cambridge, UK : xviii + 61 pp.

Hutterer, R., E. Van der Straeten & W.N. Verheyen (1987). A checklist of the shrews of Rwanda and biogeographical considerations of African Soricidae. *Bonn. Zool. Beiträge,* 38 : 155-172.

Hutterer, R. (1993). Order Insectivora. In : Wilson & Reeder (eds), *Mammal species of the world, a taxonomic and geographic reference*, second edition, Washington, D.C. : 69-130.

Hutterer, R., & D.A. Schlitter (1996). Shrews of the Korup National Park, Cameroon, with the description of a new *Sylvisorex* (Mammalia : Soricidae). *Spec. Publ. Mus. Texas Tach. Univ.,* : 57-66.

Lasso, C., R. Hutterer & A. Rial (1996). Records of shrews (Soricidae) from Equatorial Guinea, especially from Monte Alen National Park. *Mammalia,* 60 : 69-76.

Leal M. (2000). Microrefugia, small scale ice age forest remnants. In : Robbrecht & Degreef (eds), *Abstracts XVIth AETFAT Congress. Scripta Bot. Belg.* : 3.

Maley J. (1987). Fragmentation de la Forêt Dense Humide Africaine et extension des biotopes montagnards au Quaternaire récent : nouvelles données polliniques et chronologiques. Implications paléoclimatiques et biogéographiques. *Palaeoecology of Africa* 18 : 307-334.

Maley, J. (1996). The African rain forest - main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proc. R. Soc. Edinburgh* 104B : 31-73.

Maley, J. (2001). La destruction catastrophique des forêts d'Afrique centrale survenue il y a environ 2500 ans exerce encore une influence majeure sur la répartition actuelle des formations végétales. *Syst. Geogr. Pl.*, 71 : 777-796.

Maley, J., & P. Brenac (1998). Vegetation dynamics, palaeoenvironments and climatic changes in the forests of west Cameroon during the last 28,000 years. *Rev. Palaeobot. Palyno.*, 99 : 157-188.

Nicolas, V., P. Barrière & M. Colyn (2003). Impact of removal pitfall trapping on the community of shrews (Mammalia : Soricidae) in two African tropical forest sites. *Mammalia,* 67 : 133-138.

Nicolas, V., P. Barrière, S. Guimondou & M. Colyn (2004). Variabilité structurale des peuplements forestiers de rongeurs (Muridae) et musaraignes (Soricidae) dans les Monts Doudou, Gabon. In : Fischer (ed), *A floral and faunal inventory of Monts Doudou : Gabon with reference to elevation variation*, Proceedings of the California Academy of Sciences, Memoir 28, San Francisco : 107-127.

Quérouil, S. (2001). Intérêts et limites de l'approche moléculaire pour aborder la biogéographie et la spéciation :

quelques exemples chez les mammifères d'Afrique tropicale. *Ph.D. thesis*, University of Rennes 1, France : 310 pp.

QUÉROUIL, S., R. HUTTERER, P. BARRIÈRE, M. COLYN, J.C. KERBIS PETERHANS & E. VERHEYEN (2001). Phylogeny and evolution of African Shrews (Mammalia : Soricidae) inferred from 16s rRNA sequences, *Mol. Phylogenet. Evol.,* 20(2) : 185-195.

QUÉROUIL, S., M. COLYN, E. VERHEYEN & P. DELEPORTE (2002). De la phylogéographie comparée à la biogéographie historique : l'exemple de quelques mammifères forestiers d'Afrique centrale. *Biosystema* 20, Systématique et Biogéographie : 131-140.

QUÉROUIL, S., E. VERHEYEN, M. DILLEN & M. COLYN (2003). Patterns of diversication in two African forest shrews : *Sylvisorex johnstoni* and *Sylvisorex ollula* (Soricidae, Insectivora) in relation to paleo-environmental changes. *Mol. Phylogenet. Evol.,* 28 : 24-37.

QUÉROUIL, S., P. BARRIÈRE, M. COLYN, R. HUTTERER, A. DUDU, M. DILLEN & E. VERHEYEN (in press). A molecular insight into the systematics of African *Crocidura* (Crocidurinae, Soricidae) using 16s rRNA sequences. In : MERRITT, CHURCHFIELD, HUTTERER & SHEFTEL (eds), *The Biology of the Soricidae II*, Carnegie Museum of Natural History Special Publication.

RAY, J.C. & R. HUTTERER (1996). Structure of a shrew community in the Central African Republic based on the analysis of carnivore scats, with the description of a new *Sylvisorex* (Mammalia : Soricidae). *Ecotropica,* 1 : 85-97.

SYMONDS, M.R.E. (1999). Life histories of the Insectivora : the role of phylogeny, metabolism and sex differences. *J. Zool. London,* 249 : 315-337.

TÉLLO, J.L. (2000). Inquiétante recrudescence du braconnage des éléphants dans le nord de la centrafrique. *Canopée, Bulletin sur l'Environnement en Afrique Centrale,* 17 : 11-12.

VOGEL, P., M. GENOUD & H. FREY (1981). Rythme journalier d'activité chez quelques Crocidurinae africains et européens (Soricidae, Insectivora). *Rev. Ecol. (Terre Vie),* 35 : 97-108.