

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)

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Abstract. Small carnivore scats collected over a two-year period in the southwestern Central African Republic revealed an unusually high occurrence of shrews (23.3%). Analysis of skull fragments yielded 311 individuals of 16 species. Shrew occurrence varied significantly with season (highest in the dry season), but not with proximity to water. The unusually high diversity of the shrew community in comparison to others in west-central Africa is attributed to a thorough and efficient sampling effort, and to a wide variety of available microhabitats maintained through disturbance factors such as a high density of elephants and selective logging activities. In addition to the scat remains, four shrew species were collected live; one is new to science and is described here as *Sylvisorex konganensis*. The species belongs to a group in which a basal portion of the tail is covered by long bristles. It is most similar to a yet unnamed species of *Sylvisorex* from Cameroon, with which it apparently occurs in sympatry. Both share critical characters with *S. howelli* and *S. usambarensis*, species endemic to the Uluguru and Usambara Mts. respectively. Accepted 11. November 1995.

Key words: Mammals, shrews, mongooses, carnivores, community structure, biogeography, *Sylvisorex konganensis* n. sp., Central African Republic, Africa, tropics.

INTRODUCTION

Shrews and other insectivores are difficult to sample with traditional small mammal traps, and unless a concerted effort is made to capture them via other techniques such as pitfall traps, one can arrive at a distorted picture of their role in small mammal communities (Churchfield 1990, Kirkland & Sheppard 1994). A useful additional method for gaining insight into soricid communities is the study of avian predator food habits. This method has led to the discovery of several African taxa that did not appear in traps (e.g. Demeter 1981, Simonetta 1968, Vernon 1971). To date, analyses of mammalian carnivore scats have proven less useful. Insectivores occur in the scats rarely, and carnivores are thought to scorn shrews, perhaps because they are distasteful (Churchfield 1990, Ewer 1973, Korpimäki & Norrdahl 1989).

During a study of mongooses and other mammalian carnivores in the Dzanga-Sangha Reserve of southwestern Central African Republic, a collection of scats revealed an unusually high occurrence of shrews. A unique opportunity existed to use this large sample, identifiable through recovered skull fragments, to ex-

amine the structure of the shrew community in this poorly-known region of the Congo Basin. Shrews have been the subject of recent sampling efforts at several west-central African sites (Brosset 1988, Hutterer *et al.* 1992, Hutterer & Schlitter 1996, Lasso *et al.*, *in press*). These, in addition to the work of Heim de Balsac (1959, 1968a, 1968b), have broadened the knowledge of species diversity and biogeography of soricids in the region. The collection of shrews described here is the largest to date from the region, with respect to both the number of individuals and species, and contains several new records from Central Africa, including a species new to science.

MATERIALS AND METHODS

Study area. The 35 km² study area (Kongana) is located in the extreme southwestern corner of the Central African Republic, between the borders of Cameroon and Congo (Fig. 1). The base camp, in the Dzanga-Sangha Special Dense Forest Reserve and Dzanga-Ndoki National Park, was 35 km from the village of Bayanga (population c. 1000). Sections of the study area were selectively logged in the early 1980s (approximately one

stem per hectare) for several species of hardwoods. Human populations in the area are relatively low (one person/2 km²; Carroll 1988).

The study area was a mosaic of five principal habitat types: mixed-species semi-deciduous unlogged forest, selectively logged forest, second-growth forest along secondary logging roads, mono-dominant *Gilbertiodendron deweyi* forest, and a thin ribbon of swamp forest bordering the Kongana stream that bisected the study area.

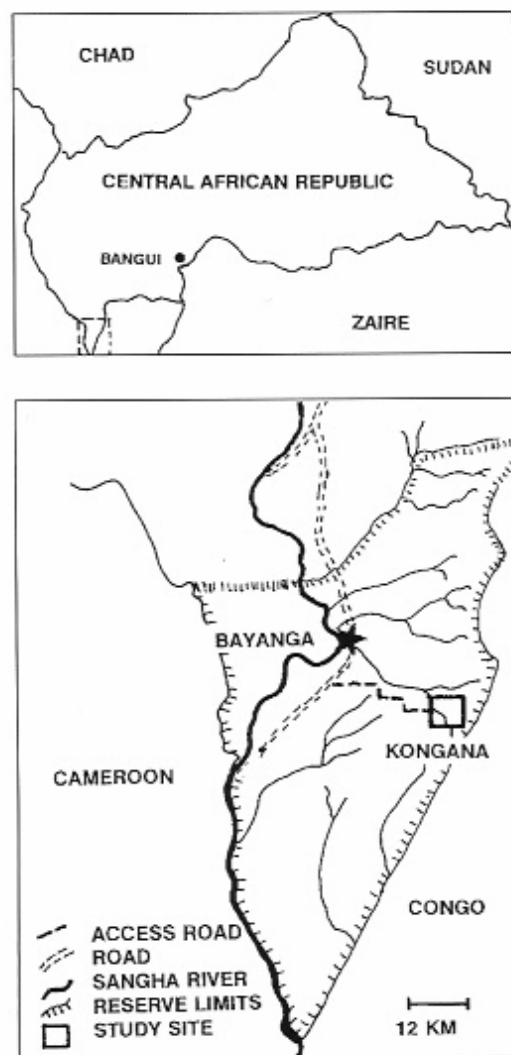


FIG. 1. The Central African Republic and Kongana Study Area, Dzanga-Sangha Reserve.

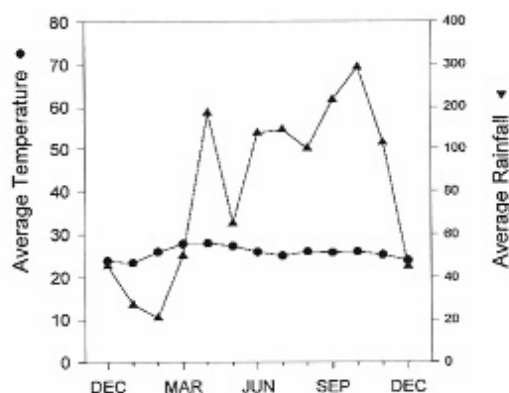


FIG. 2. Average monthly rainfall and temperature measured at Kongana Research Station, May, 1992-May, 1994.

The climate was highly seasonal, with rainfall over a two-year period averaging 1400 mm per year (Fig. 2). December through March was characterized by a marked dry season, with fewer than 200 mm of rain. Temperatures were likewise at their lowest during this period. Mean maximum daily temperatures throughout the study period were 32.3°C (range 23–45), and mean minimum daily temperatures were 19.5°C (range 12–22). Three seasons were defined *a priori*: “dry” (December–March), “early wet” (April–July), and “late wet” (August–November) (Fig. 2). Mean monthly rainfall in the dry season was 35.9 mm (range 2–52.3), in the early wet season was 136.4 mm (range 65.1–200.1), and in the late wet season was 181 mm (93.5–410.3).

Methods. Approximately 45 km of roads, trails and streambeds were walked regularly by one to four individuals during a 25-month period (May 1992–May 1994). Carnivore scats were collected opportunistically. The majority of scats (77.6%) were collected on the 26-km road that accessed the study area (Fig. 1). The mean number of scats collected per month was 36.2 (SE=4.61, $n=25$, range 2–81). Scat identifications were made based on diameter, field signs, hair ingested while grooming, and thin layer chromatography of bile acids. The latter technique was used to separate fecal bile acids, whereby patterns of bile acids in unknown samples were compared with those from known samples, using methods described in Ray (*in prep.*) and Johnson *et al.* (1981). In the present analysis, known leopard scats, and any scats that were not identified to species, but were larger than 2 cm in diameter were excluded. Thus, this analysis is based only on small carnivore scats.

Scats were washed in a fine-meshed sieve, dried in the sun or over a fire, and stored in plastic bags. An estimate of the relative volume of each major prey category (mammal, arthropod, fruit, bird, fish, and herpetofauna) to a scat was made by eye; foods that contributed the greatest volume of a scat were considered the "dominant" component. The presence of shrew remains in a scat was determined in most cases by recovery of teeth, and in a few cases by the microscopic examination of hair. Jaws and jaw fragments were identified and the minimum number of individuals tabulated by RH. When only hair was contained in the scat, one shrew was assumed to occur in the scat. The proximity of the collection site to water and the date the scat was collected were also recorded.

During extensive small mammal trapping conducted by JCR and Jay Malcolm (targeted at the rodent community), 29 shrews were captured and preserved as study skins or liquid specimens. These voucher specimens are deposited in the National Museum of Natural History, Washington, D.C. (USNM), and in the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Other specimens used for comparison with shrew skull fragments found in scats are housed in the American Museum of Natural History, New York, The Carnegie Museum Pittsburgh (CM), The Field Museum, Chicago, The University of Antwerp, and the Zoologisches Museum der Humboldt-Universität, Berlin (ZMB). Skull measurements were taken with an electronic calliper. All measurements are given in millimeters (mm) and body masses in grams (g). Names of authors and publication dates of species discussed in the text are listed in Hutterer (1993), where complete citations to species and type localities can be found.

RESULTS

Out of 904 small carnivore scats collected, 211 (23.3%) contained, in total, the remains of at least 344 shrews. The mean percent of scats per month that included shrew remains was 23.6 (SE=4.16, $n=25$, range 0-100%). Recovery of teeth allowed for 311 individuals of 16 species to be identified. One species, described in the appendix as *Sylvisorex konganensis*, was new to science. This list added 13 species to the known shrew fauna of the Central African Republic (Brosset et al. 1965, Hutterer 1986b, 1993). The species exhibited a wide range in body masses, from 1.5 to 85 g (Tab. 1, Fig. 3). Three species were numerically dominant: two accounted for over 60% of recovered re-

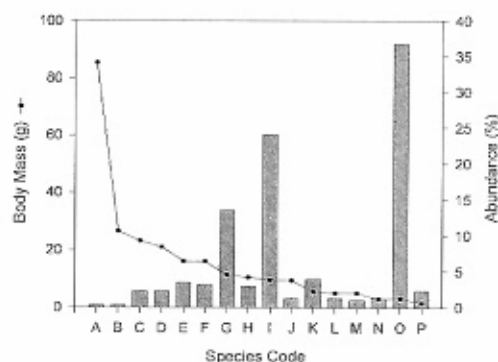


FIG 3. Mean body mass and proportional abundance in scats for 16 shrew species. Species Codes are defined in Table 1.

mains (*Sylvisorex johnstoni* at 36.7% and *Paracrocidura schoutedeni* at 24.1%) and *Crocidura nigrofusca* followed at 13.5%. All other species each represented less than 4% of the number of individuals found in the scats.

The identities of 37.4% of the scats that contained shrews were determined (Tab. 2). Of these, 84% were from the long-nosed mongoose (*Herpestes naso*), believed to be the numerically dominant carnivore in the Dzanga region (Ray 1995). The remainder were from genets (*Genetta* spp.), other species of mongoose (*Atalapha paludinosus* and *Bdeogale nigripes*), and one from a golden cat (*Felis aurata*). No shrew remains were found in 30 African civet (*Civettictis civetta*) or eight palm civet (*Nandinia binotata*) faeces.

The mean minimum number of individual (MNI) shrews per scat was 1.7. Most (93.3%) scats contained 3 or fewer shrew individuals; one scat had 11. Mammal remains were the dominant component of 71.6% of the scats with shrew remains; arthropods comprised the largest volume in 21.8%. However, arthropods were present in 92% of small carnivore scats that included shrews. The most prevalent arthropod groups were beetles (Coleoptera), termites (Isoptera), ants (Hymenoptera), and Orthoptera. A detailed analysis of 22 *Herpestes naso* scats by an entomologist revealed an invertebrate fauna characteristic of litter and soil environments (W.E. Steiner, pers. comm.).

The species accumulation curve presented in Fig. 4 shows a clear asymptote, indicating that the full complement of the shrew community sampled by small carnivores in the Dzanga area was attained. The curve rose steeply and steadily during the first 12 months of collection; after 355 scats (13 months), 15 shrew spe-

TABLE 1. Body mass (g) data from shrew species represented in the Dzanga-Sangha scat fauna and from common members of other communities in the region. Body mass data represent means of samples (n) of complete specimens from C.A.R., Cameroon and Zaire.

	Species Code	n	Body mass		Source	Abundance (n=311)	
			Mean	Range		MNI	%
Species:							
<i>Crocidura goliath</i>	A	6	85.3	51-102	1	1	0.3
<i>Crocidura olivieri</i>	B	34	26.6	13-38	1	1	0.3
<i>Crocidura mutesae</i>	C	4	23.2	19-25	3	7	2.3
<i>Crocidura littoralis</i>	D	5	21.0	20-24	2	7	2.3
<i>Sylvisorex ollula</i>	E	15	16.1	13-21	1	11	3.5
<i>Crocidura batesi</i>	F	1	16.0	-	1	10	3.2
<i>Crocidura nigrofusca</i>	G	7	11.4	7-14	3	42	13.5
<i>Crocidura denti</i>	H	8	10.5	8-12	1	9	2.9
<i>Paracrocidura schoutedeni</i>	I	8	9.6	7-12	1,4,5	75	24.1
<i>Crocidura hildegardeae</i>	J	20	9.4	9-16	2	4	1.3
<i>Crocidura dolichura</i>	K	11	5.6	4-7	1,4	12	3.9
<i>Crocidura ludia</i>	L	-	c.5.0	-	-	4	1.3
<i>Sylvisorex sp. A</i>	M	1	5.0	-	4	3	1.0
<i>Sylvisorex konganensis</i>	N	1	3.0	-	3	4	1.3
<i>Sylvisorex johnstoni</i>	O	23	3.1	2-5	1,4	114	36.7
<i>Suncus remyi</i>	P	1	1.5	-	1	7	2.3
Other Species:							
<i>Crocidura crenata</i>	-	9	8.5	6-10	1,4	-	-
<i>Crocidura grisei</i>	-	3	11.0	10-12	1	-	-
<i>Crocidura grandiceps</i>	-	1	25.0	-	4	-	-
<i>Crocidura lamottei</i>	-	1	15.0	-	4	-	-
<i>Crocidura poensis</i>	-	7	19.4	16-23	4	-	-

Sources: 1 Hutterer (*unpubl. data*); 2 Dieterlen & Heim de Balsac (1979); 3 Ray (*unpubl. data*); 4 Hutterer & Schlitter (*in press*); 5 Hutterer (1986b).

cies were recovered. However, all 16 shrew species were not obtained until the 697th scat was collected, 21 months after the study began.

Soricids occurred more frequently in scats collected during the dry season months (31% vs. 19% and 14% in the early wet and late wet seasons respectively). Log-linear analysis on each of the three most abundant taxa and on all shrews combined indicated that this seasonal effect was highly significant (Tab. 3).

The actual habitat where a given shrew was captured can obviously not be determined from the scat location, because defecation occurred after the shrew was eaten. Data from *Herpestes naso* trapping and radio-tracking revealed that although the species ranged primarily in upland habitats, streamside habitat was included in the range of every individual located within 500 m of the stream. Since home ranges of this species were found not to exceed 1 km² (Ray 1995) shrews

TABLE 2. Breakdown of small carnivore scat identifications (n=904), with and without shrew remains.

	Undet. small carnivore	<i>Herpestes naso</i>	<i>Atilax paludinosus</i>	<i>Bdeogale nigripes</i>	<i>Genetta sp.</i>	<i>Nandinia binotata</i>	<i>Civettictis civetta</i>	<i>Felis aurata</i>
Scats with shrews	131	66	3	4	6	0	0	1
Scats without shrews	269	280	46	17	29	7	30	15

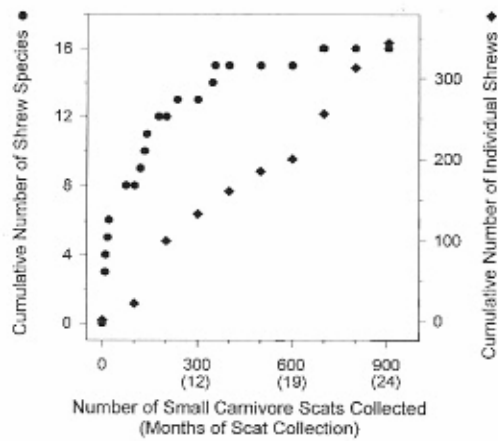


FIG 4. Cumulative number of species and cumulative number of individuals represented in 25 months of scat collection ($n=904$).

found in scats close (<500 m) to water may very well have been caught close to the water. When the prevalence of shrews in all small carnivore scats was compared as a function of distance to water, it was found that scats found closer to water were significantly less likely to contain shrews. In order to eliminate a possible carnivore species effect a second analysis was conducted, in which carnivore species least likely to eat shrews were eliminated from the analysis. The result was no longer significant; the ratios of scats found close to and far from water were about equal for scats with and without shrews (Tab. 4).

DISCUSSION

The present study fills a gap in the knowledge of insectivore communities of the Congo Basin. These data, coupled with data generated from recent trapping

TABLE 3. Percentage of shrew individuals by species, and all pooled, that appeared in scats during the dry, early wet, or late wet seasons. Note: Only the three most abundant species were included in this analysis.

Species	Season	MNI	Chi ² (df=2)	P-value
<i>Crocidura nigrofusca</i>	dry	35	15.22	$P<0.0005$
	early wet	6		
	late wet	1		
<i>Paracrocidura schoutedeni</i>	dry	61	30.14	$P<0.00001$
	early wet	8		
	late wet	6		
<i>Sylvisorex jolmstoni</i>	dry	77	19.01	$P<0.0001$
	early wet	19		
	late wet	18		
16 species pooled	dry	240	105.68	$P<0.00001$
	early wet	61		
	late wet	43		

TABLE 4. Proportions of all small carnivore scats and of scats containing shrews found near water (<500 m) and away from water (>500 m).

	Proximity to water			
	>500 m All Small Carnivore Scats ($n=904$)	<500 m	>500 m <i>Herpestes naso</i> and unid. small carnivore scats only ($n=730$)	<500 m
Scats with shrews	490 (70.7%)	203 (29.3%)	422 (78.4%)	116 (21.6%)
Scats without shrews	167 (79.1%)	44 (20.9%)	152 (79.2%)	40 (20.8%)
Chi ² (df=1), P-value	5.802, $P<0.02$		0.45, $P=0.833$	

efforts on the eastern and western rim of the basin (Lasso *et al.*, *in press*, Hutterer & Schlitter 1996, Kerbis-Peterhans & Hutterer, *unpubl. data*), demonstrate that many shrew species enjoy more widespread distributions than previously assumed. The Dzanga community is the most speciose community in the region sampled to date (Tab. 5), but it is also the numerically largest collection.

The unusually high occurrence of shrews in the diet of Dzanga-Sangha small carnivores is a fascinating result. It seems clear that predation on shrews was not a community-wide phenomenon, and only certain species, particularly *Herpestes naso*, ate insectivores on more than an occasional basis. The preponderance of soil and leaf litter arthropods in the scats, as well as the frequent presence of *Deomys ferrugineus*, a rodent that specializes on termites (Rahm 1972, Duplantier 1982)

and is found in areas with a high density of fallen timber, suggests that these carnivores were foraging in microhabitats where the encounter rate with shrews was high.

It is often difficult to assess how closely a sampled community reflects the real community of interest, and to what degree the results are simply an artifact of the sampling method. It is reasonable to suggest that the opportunistic nature with respect to food habits (Ray, *in prep.*) of the Dzanga carnivores most likely to consume shrews (*Herpestes naso*, *Bdeogale nigripes*, and *Genetta* spp.) would result in the taking of shrews in approximate accordance with their abundance. Moreover, the diurnal activity pattern of the former, and the nocturnal tendencies of the latter two (Ray 1995, and *unpubl.*) ensures complete coverage of shrew activity periods. The dominance patterns of ro-

TABLE 5. A comparison of shrew communities inhabiting the lowland forest at Dzanga-Sangha (C.A.R.), Monte Alen N.P. (Equatorial Guinea), Belinga-Makokou (Gabon), Korup National Park, Yaoundé plateau, and mixed lowland and montane forests of Mount Cameroon (all Cameroon). Based on the present paper, Brosset (1988), Lasso *et al.* (*in press*), Heim de Balsac (1957, 1968a, 1968b), Hutterer *et al.* (1992), Hutterer (1993), Hutterer & Schlitter (1996) and unpublished data.

Species Recorded	Dzanga	Mt. Alen	Belinga	Korup	Yaounde	Mt. Cameroon
<i>Suncus remyi</i>	X		X			
<i>Crocidura graesei</i>		X	X		X	
<i>Crocidura batesi</i>	X	X	X		X	
<i>Crocidura crenata</i>			X	X		
<i>Crocidura grandiceps</i>				X		
<i>Crocidura lamottei</i>				X		
<i>Sylvioirex konganensis</i>	X					
<i>Sylvioirex sp. A</i>	X			X		
<i>Sylvioirex johnstoni</i>	X	X	X	X		X
<i>Sylvioirex ollula</i>	X	X	X	X	X	X
<i>Paracrocidura schoutedeni</i>	X	X	X	X	X	X
<i>Crocidura dolichura</i>	X	X	X	X		X
<i>Crocidura poensis</i>			X	X	X	X
<i>Crocidura goliath</i>	X	X	X		X	X
<i>Crocidura olivieri</i>	X	X	X		X	X
<i>Crocidura nigrofusca</i>	X					
<i>Crocidura mutesae</i>	X					
<i>Crocidura littoralis</i>	X					
<i>Crocidura ludia</i>	X					
<i>Crocidura jousenetae</i>						X
<i>Suncus infinitimus</i>						X
<i>Crocidura hildegardeae</i>	X					X
<i>Crocidura eisentrauti</i>						X
<i>Sylvioirex morio</i>						X
<i>Crocidura denti</i>	X				X	X
<i>Crocidura astila</i>					X	X
<i>Crocidura manengubae</i>					X	
Number of Taxa Recorded	16	8	11	9	10	14

TABLE 6. A comparison of the proportional abundances of soricids (expressed as the percentage of collected specimens) in Dzanga-Sangha, Central African Republic (this study), Belinga-Makokou, Gabon (Brosset 1988), Korup, Cameroon (Hutterer & Schlitter, *in press*), and Mt. Alen, Equatorial Guinea (Lasso *et al. in press*). In addition to total number of individuals sampled, the duration of each study in months is indicated.

Species	Body mass (g)	C.A.R. n=311 25 month	GABON n=160 11 month	CAMEROON n=59 2 month	EQ. GUINEA n=43 6 month
<i>Crocidura goliath</i>	85.3	0.3	1.9	-	1.1
<i>Crocidura olivieri</i>	26.6	0.3	3.1	-	1.1
<i>Crocidura grandiceps</i>	25	-	-	1.7	-
<i>Crocidura mutaeae</i>	23.2	2.3	-	-	-
<i>Crocidura littoralis</i>	21	2.3	-	-	-
<i>Crocidura poensis</i>	19.4	-	48.1	16.9	-
<i>Sylvioorex ollula</i>	16.1	3.5	5.0	8.5	4.4
<i>Crocidura batesi</i>	16	3.2	1.2	-	11.2
<i>Crocidura lamottei</i>	15	-	-	1.7	-
<i>Crocidura nigrofusca</i>	11.4	13.5	-	-	-
<i>Crocidura grisei</i>	11.0	-	3.1	-	1.1
<i>Crocidura denti</i>	10.5	2.9	-	-	-
<i>Paracrocidura schoutedeni</i>	9.6	24.1	8.7	3.4	8.9
<i>Crocidura bidegardeae</i>	9.4	1.3	-	-	-
<i>Crocidura crenata</i>	8.5	-	1.2	15.2	-
<i>Crocidura dolichura</i>	5.6	3.9	7.5	8.5	1.1
<i>Crocidura ludia</i>	5.0	1.3	-	-	-
<i>Sylvioorex sp. A</i>	5.0	1.0	-	1.7	-
<i>Sylvioorex konganensis</i>	3.0	1.3	-	-	-
<i>Sylvioorex johnstoni</i>	3.1	36.7	15.0	42.4	60.0
<i>Suncus remyi</i>	1.5	2.3	5.0	-	-

dent taxa recovered in small carnivore scats was similar to that derived during 2 years of rodent trapping (Ray & Malcolm, *unpubl. data*).

The pattern of species dominance in the Dzanga assemblage is typical of that found in other multispecies communities of shrews: 1-3 abundant taxa and the rest being relatively rare (Churchfield 1990, Churchfield & Sheftel 1994; Tab. 6). A similar result was obtained for the rodent community in Dzanga (Ray & Malcolm, *unpubl.*). *Sylvioorex johnstoni* was consistently dominant in the west-central African communities examined in Tab. 6. Otherwise, species that were common representatives in one community were often rare in others, a pattern similar to that found across North American forest shrew communities (Kirkland 1991). With the exception of *Crocidura goliath*, body weights of Dzanga shrews were more or less continuously distributed, rather than falling into size classes spread apart from each other, as in less speciose assemblages (Kirkland 1991, Fox & Kirkland 1992). As many as 3 species have more-or-less equal body weights, which may speak for the great potential for niche differentiation in tropical environments. Species-

rich shrew communities may be structured by different assembly rules than simpler communities. One should recall that 16 species of shrews were found in the 35 km² Kongana study area while only 17 species are known from all of Europe (Niethammer & Krapp 1990). It must be noted, however, that most weight estimates were derived from areas outside Dzanga, and that syntopic members of the Dzanga assemblage may be characterized by weight distributions that are more limited and thus discrete from each other. This may be further reflected in CI length which has been found to be non-overlapping among members of a species-rich shrew community in Gabon (Brosset 1988).

The unusually high diversity of the Dzanga community may partly reflect the relatively large sampling effort. The sampling period of 25 months was over twice as long as the longest other effort (11 months) in the region, and yielded almost twice as many individuals. The importance of an intensive sampling effort in attempts to describe the full community is highlighted by the fact that it took 21 months for the full 16 species to be collected. Although the sampling effort from the various other studies cannot be quantified exactly,

it is clear that the area covered by the scat collection in our study was much greater than in any of the other sampling schemes. Furthermore, the mongoose as a "moving trap" has a far wider sampling area than an immobile pitfall trap, and a greater potential to sample a variety of microhabitats. A collection effort that does not cover a large enough area is unlikely to sample the full range of microhabitats frequented by shrews. This point is illustrated by 5 independent trapping sessions that were conducted over a 20-year period in one forest in Rwanda: in no one effort were all 9 species of shrews captured (the accumulated number of species), and each effort obtained different species compositions. This result was probably explained by traplines set in different areas of the forest (Hutterer *et al.* 1987). In contrast, capture localities from a study in Gabon did not give any indication of differential habitat use among 11 soricid species (Brosset 1988). Microhabitat preferences are often too subtle to be detected without extensive measuring (Churchfield 1990, Neet & Hausser 1990).

Although the collection method in this study probably maximized the chance of sampling the full spectrum of microhabitats exploited by shrews, it is also possible that the availability of these habitats was quite high. The partitioning of microhabitats has been used to explain the maintenance of diversity in temperate insectivore communities (Terry 1981, Dickman 1988, Churchfield 1990, Neet & Hausser 1990, Fox & Kirkland 1992, Sheftel 1994). When diets in syntopic shrews are examined, it is common for trophic niches to be broad and overlapping, a reflection of the opportunistic nature of these insectivores (Churchfield 1991, Churchfield & Sheftel 1994; Kirkland 1991). Ecological separation in diverse multispecies communities is often expressed in differences in prey size arising from differential microhabitat exploitation (Dickman 1988, Churchfield 1993, Churchfield & Sheftel 1994). Several studies have found evidence of "vertical" stratification, with species found principally in either the leaf litter, ground surface, or the soil environments (see Churchfield 1990, 1993; Churchfield & Sheftel 1994, Terry 1981). Different body forms have also been used to explain the potential variety in exploitation of trophic niches (Brosset 1988). As in many animal communities, this one is probably composed of a mixture of habitat generalists and specialists (Kirkland 1991, Sheftel 1994) and the ecological segregation between the most abundant species is likely to be the most critical (Churchfield & Sheftel 1994, Dokuchaev 1989).

Southwestern C.A.R. has among the highest densities of forest elephants remaining in Africa (Carroll 1988, Western 1986). Since the establishment of legal protection in 1990, poaching has decreased significantly, and relatively undisturbed populations of large herbivores exist in the area (Fay 1991, pers. obs.). The role that large herbivores play in contributing towards a forest mosaic is well-known in East Africa (Kortlandt 1984). The constant modifications of vegetation, which generate a mosaic of disturbance regimes, as well as the dense network of trails generated by elephant movements in the Dzanga area are obvious at any scale (pers. observ.). In addition, logging activities in the region since the early 1980s created gaps and roads. All of these activities contribute to a shifting mosaic of edge and gap habitats, perhaps creating many microhabitats potentially available for shrews. Further evidence of a high opportunity for niche differentiation in the Dzanga shrew community may be that two of the three most abundant species, *Crocidura nigrofusca* and *Paracrocidura schoutedeni*, are quite similar in body mass. Elsewhere, trapping records have demonstrated that the numerically dominant members of species-rich assemblages (Brosset 1988, Churchfield & Sheftel 1994, Hutterer & Schlitter 1996, Lasso *et al.*, *in press*), as well as the members of less diverse communities (Kirkland 1991), have markedly different body masses.

A surprising result of this study is the significantly higher occurrence of shrews in scats collected during the dry season. Moisture has been found to be a primary factor in determining local abundance and diversity of temperate insectivores, due in part to the fact that invertebrates are themselves influenced by moisture (Churchfield 1990, Kirkland 1991, Wrigley *et al.* 1979). In Equatorial Guinea, for example, the lowest number of captures was achieved during the dry season (Lasso *et al.*, *in press*), and in eastern Zaire shrews were most abundant in swamp areas (Dieterlen & Heim de Balsac 1979). Mongooses were apparently not responding to a decrease in the abundance of other small mammal prey in the dry season, since rodent densities were also at their highest at this time (Ray, *unpubl.*). A low availability of food and concomitant increased competition could result in increased ranging activity for shrews (Churchfield 1993); this combined with the desiccation of leaf litter can contribute to their increased visibility. Most scats that contained shrew remains were located far away from streams, thereby providing evidence that shrews are not restricted to well-watered habitats. Several species that are thought to be closely associated with water (e.g., *Paracrocidura schoutedeni*;

Hutterer 1986b) were captured by carnivores apparently travelling well away from these areas.

A great deal remains to be learned about the distributions, adaptations, and trophic relationships of the shrews of Africa. This is not only in the interest of science, but also for nature conservation. For example, the Central African Republic is hardly mentioned in the Action Plan for the conservation of African Insectivora (Nicoll & Rathbun 1990). Our results, however, indicate that the Dzanga-Sangha Special Dense Forest Reserve and Dzanga-Ndoki National Park constitute a key area for the conservation of small mammal diversity in the Afrotropics, and that this diversity may be related to the abundance of elephants in the same area.

APPENDIX: A NEW SPECIES OF SHREW

Sylvisorex konganensis, new species (Figs. 6, 8, 11)

Holotype. USNM 580655, young adult female preserved in fluid, skull extracted and cleaned; collected on 8 April 1994 by Justina C. Ray in unlogged mixed species forest near Kongana Camp (02°47'N, 16°25'E), Dzanga-Sangha Forest Reserve, SW Central African Republic. External measurements (mm): Total length, 100; tail, tip missing, (36); hindfoot, 12; ear, 8; body mass, 3 g. Field number, JCR 1736.

Etymology. The species epithet is derived from the type locality, Kongana Stream, a tributary of the Kenie River.

Diagnosis. A small lowland forest species of *Sylvisorex* in which a basal portion of the tail is covered by long bristles. Species slightly larger than *S. johnstoni* and most similar to *Sylvisorex* sp. A (Hutterer & Schlitter 1996), but with a shorter tail and hindfoot, darker ventral coloration, and smaller skull measurements.

Description. *Sylvisorex konganensis* is a small shrew, with a dark body and contrastingly paler hands, feet, outer ear, and tail. The dorsal pelage is brownish gray, and the ventral pelage is only faintly lighter. Hairs on the dorsum are about 3.6 mm in length, and on the venter 2.8 mm. Numerous facial vibrissae cover the snout, the longest of which measure 13 mm. Ear conch small, rounded, and covered by very short hairs (Fig. 7). Fore- and hindfeet with somewhat elongated digits as in *S. megalura*. The first toe of *S. konganensis* is unusually long, and the inner surface of the sole is smooth (Fig. 10). The tail is covered by short hairs and by a few longer bristles over 15 mm of the proximal portion of its length.

Skull (Fig. 5) flat and slender, much flatter than in *S. megalura* (illustrated by Brossier *et al.* 1965, Hutterer & Hapold 1983, Jenkins 1984), and in overall

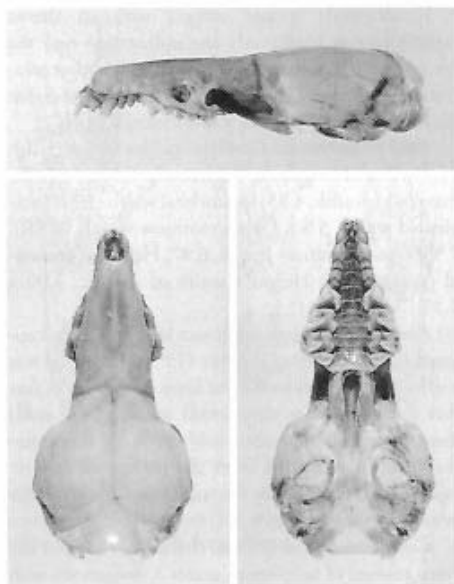


FIG. 5. Dorsal, ventral and lateral aspects of the cranium of *Sylvisorex konganensis*, new species (USNM 580655, holotype); length of skull is 16.95 mm.

configuration rather resembling that of *S. sp. A* (holotype CM 107950 illustrated by Hutterer & Schlitter 1996), *S. morio*, and *S. lunaris* (figured by Heim de Balsac 1968a and Jenkins 1984). The skull is wedge-shaped, with a large braincase and slender rostrum. The braincase is hexagonal in dorsal view and rather flat in lateral view. An interparietal bone is clearly visible, although its posterior margin is fused with the occipital bone. The same condition is found in *S. morio* and in some species of *Myosorex* (Heim de Balsac 1968a).

Upper teeth: First upper incisor small, with a small talon. First upper unicuspid large, its tip in straight line with the tip of the paracone of P4. Second and third unicuspid reach less than half and the fourth unicuspid a fifth of the height of the first unicuspid. P4 with a large angular parastyle and a prominent protocone, as is typical for the genus. M1-2 squarish, otherwise without special features. M3 large, as in *S. morio* and *S. megalura*.

Mandible: Very slender with a thin ramus. Foramen mentale below the root of lower P4. Condyle small and rounded, about as wide as high.

Lower teeth: Incisor straight with an almost smooth cutting blade; only one indentation near the tip is present. The shape of the lower P4 is almost symmetrical in occlusal view. Lower molars of normal shape; third lower molar with a small talonid basin.

Skull measurements. Condylar-incisive length (CIL), 16.95; Palatal length, 6.79; Greatest width, 7.97; Bimaxillary breadth, 4.85; Interorbital width, 3.72; Postglenoid width, 5.54; Upper toothrow length (UTR), 7.36; Lower toothrow length, 6.87; Height of coronoid process, 4.00; Height x width of condyle, 1.00 x 1.15.

Remarks. The single specimen was incidentally captured by hand during the day (13:30h) while it was scuffling around under the leaf litter. Fragments of further four specimens were found in mongoose scats; these fragments represent only 1.3% of the entire shrew fauna identified from the mongoose scat remains. This suggests that the population density of the new species is very low.

Comparisons. One external character, a low but obvious amount of tail pilosity, unites *S. konganensis* with three other species of its genus: *S. sp. A* (Hutterer & Schlitter 1996), *S. howelli* and *S. usambarensis* (Table 7). All other species of *Sylvisorex* (for a checklist, see Hutterer 1993) have an entirely 'naked' tail. We limit comparisons to the four pilose species. A full revision on the genus by the junior author is underway and will be published elsewhere.

S. sp. A (Hutterer & Schlitter 1996) from Cameroon is easily distinguished by its cream-white venter, and a larger skull (Tab. 7).

Sylvisorex howelli (Jenkins 1984) differs from the new species by an overall blackish coloration. The skull (figured by Jenkins 1984, and Hutterer 1986c) is similar in size but higher, the braincase is large and more ellipsoid in shape. The species is endemic to the Uluguru Mts. in Tanzania.

Sylvisorex usambarensis (Hutterer 1986a) was first described as a subspecies of *S. howelli* but recently collected material from the Usambara Mts. (Stanley, Goodman & Hutterer, *unpubl. data*) suggests that it deserves species rank. The species differs from *S. konganensis* by an overall deep brown coloration, and by smaller hindfoot and skull measurements.

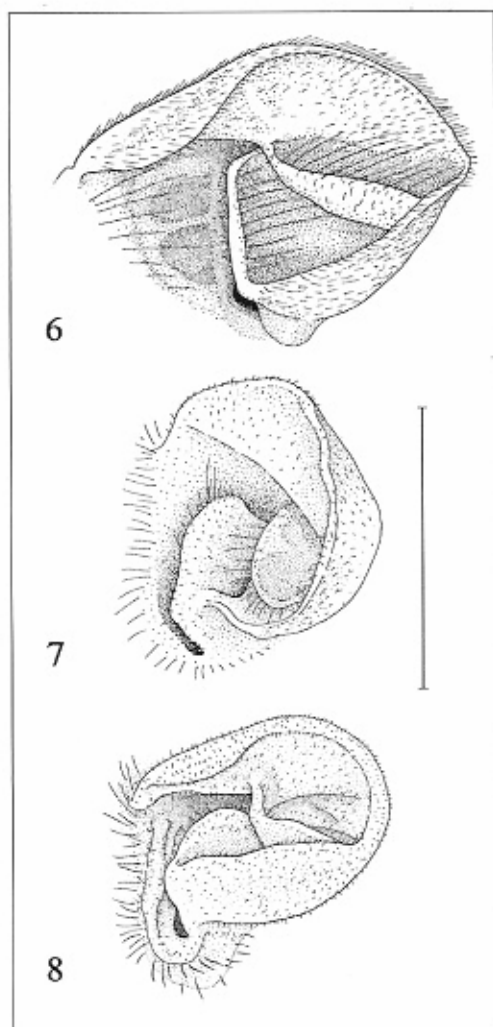
No attempts are made here to fix the position of the new species within a phylogenetic context. This is not possible at present and may be subject to a future revision. It is also not sure that the four species united by a certain degree of tail pilosity are closely related. Several papers dealing with phylogenetic aspects (Butler & Greenwood 1979, Hutterer 1993, Hutterer & Schlitter 1996, McLellan 1994, Maddalena 1990) suggest that *Sylvisorex* is not a monophyletic unit. However, no attempt has yet been made to analyse all species in a systematic manner.

It is striking that *S. konganensis* lacks the tubercles (Fig. 10) which cover the inner surface of the sole in other species such as *S. megalura* (Fig. 9) or the small *S. johnstoni* (Fig. 11). This feature recalls the foot of *Paracrocidura schoutedeni* (figured in Hutterer 1985), a species which is thought to forage on the ground under leaf litter (Hutterer 1986b, Hutterer & Duda 1990). On the other hand the long first toe of *S. kon-*

TABLE 7. Comparison of measurements and characters of *S. konganensis*, new species, with other pilose species of *Sylvisorex*.

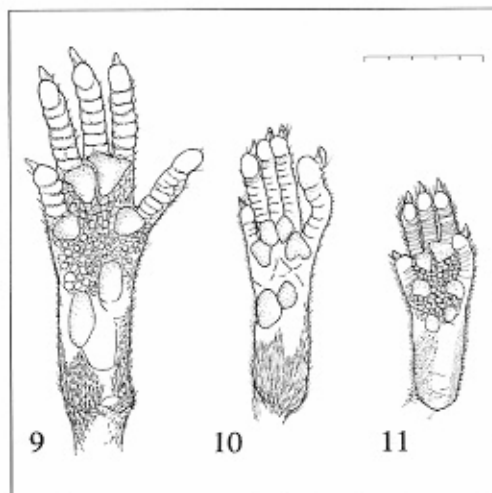
Character	<i>S. konganensis</i> ¹	<i>S. n. sp. A</i> ^{1,2}	<i>S. howelli</i> ³	<i>S. usambarensis</i> ^{1,3}
Body mass	3	5	-	-
Head and body length	64	74	51	56
Tail length	[36]	67	43.6	38.5
Tail as % of head and body	[56.2]	90.5	85.5	68.7
Pilosity (%)	[51]	40	45	45
Hindfoot length	11.3	14	11.0	10.0
Condylar-incisive length	16.9	19.3	16.9	16.1
Upper toothrow length	7.5	8.5	7.2	6.6
Upper M3 length	0.64	0.71	0.62	0.54
Skull profile	flat	flat	flat	flat
Dorsal color	gray	gray	black	deep brown
Ventral color	gray	cream	black	deep brown

¹holotype, ²Hutterer & Schlitter (*in press*), ³Hutterer (1986a & *unpubl. data*)



FIGS. 6-8. Left ear conch of *Sylvioorex megalura* (6, ZFMK 59.500), *S. konganensis* (7, holotype), and *S. johnstoni* (8, ZMB 92952a). Scale is 5 mm.

ganensis suggests that the species may be somehow adapted for climbing, as shown by Vogel (1974) for *S. megalura*. The shape of the ear conch, however, is that of a small terrestrial shrew such as *S. johnstoni* and not that of a scansorial shrew such as *S. megalura* (Figs. 6-8). Whatever the particular adaptation of *S. konganensis* may be, we do not know it yet. Only careful biological studies will uncover the secrets of this shrew and all the other unknown small mammals which occur in the forest mosaic of the Kongana area.



FIGS. 9-11. Ventral aspect of right hindfoot of *Sylvioorex megalura* (9), *S. konganensis* (10), and *S. johnstoni* (11). Same specimens as in Figs. 6-8. Scale is 5 mm.

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REFERENCES

- Brosset, A. 1988. Le peuplement de mammifères insectivores des forêts du nord-est du Gabon. *Revue d'Ecologie (Terre Vie)* 43: 23-46.

- Brosset, A., Dubost, G., & H. Heim de Balsac. 1965. Mammifères inédits recoltés au Gabon. *Biol. Gabon* 1: 147-174.
- Butler, P.M., & M. Greenwood. 1979. Soricidae (Mammalia) from the early Pleistocene of Olduvai Gorge, Tanzania. *Zool. J. Linn. Soc.* 67: 329-379.
- Carroll, R.W. 1988. Relative density, range extension, and conservation potential of the lowland gorilla (*Gorilla gorilla gorilla*) in the Dzanga-Sangha region of southwestern Central African Republic. *Mammalia* 52: 309-323.
- Churchfield, S. 1990. The natural history of shrews. Ithaca & New York.
- Churchfield, S. 1991. Niche dynamics, food resources, and feeding strategies in multispecies communities of shrews. Pp. 23-34 in Findley, J.S., & T.L. Yates (eds.). The biology of the Soricidae. The Museum of Southwestern Biology, University of Mexico, Albuquerque.
- Churchfield, S. 1993. Foraging strategies of shrews: interactions between small predators and their prey. *Symp. Zool. Soc. Lond.* 65: 235-252.
- Churchfield, S., & B.I. Sheftel. 1994. Food niche overlap and ecological separation in a multi-species community of shrews in the Siberian taiga. *J. Zool. Lond.* 234: 105-124.
- Demeter, A. 1981. Small mammals and the food of owls (*Tyto* and *Bubo*) in northern Nigeria. *Vert. Hung.* 20: 127-136.
- Dickman, C.R. 1988. Body size, prey size, and community structure in insectivorous mammals. *Ecology* 69: 569-580.
- Dieterlen, F., & H. Heim de Balsac. 1979. Zur Ökologie und Taxonomie der Spitzmäuse (Soricidae) des Kivu-Gebietes. *Säugetierk. Mitt.* 27: 241-287.
- Dokuchaev, N.E. 1989. Population ecology of *Sorex* shrews in north-east Siberia. *Ann. Zool. Fenn.* 26: 371-379.
- Duplantier, J.M. 1982. Les rongeurs myomorphes forestiers du nord-est du Gabon. Ph.D. Diss., Univ. Sci. Tech. Languedoc, France.
- Ewer, R.F. 1973. The carnivores. London.
- Fay, J.M. 1991. Forest elephant population in the Central African Republic. *Pachyderm* 14: 3-12.
- Fox, B.J., & G.L. Kirkland, Jr. 1992. An assembly rule for functional groups applied to North American soricid communities. *J. Mamm.* 73: 491-503.
- Heim de Balsac, H. 1959. Nouvelle contribution à l'étude des Insectivores Soricidae du Mont Cameroun. *Bonn. zool. Beitr.* 10: 198-217.
- Heim de Balsac, H. 1968a. Contribution à l'étude des Soricidae de Fernando Po et du Cameroun. *Bonn. zool. Beitr.* 19: 15-42.
- Heim de Balsac, H. 1968b. Contributions à la faune de la région de Yaoundé I. Premier aperçu sur la faune des Soricidae (Mammifères Insectivores). *Ann. Fac. Sci. Cameroun* 1968(2): 49-58.
- Hollister, N. 1916. Shrews collected by the Congo expedition of the American Museum. *Bull. Amer. Mus. Nat. Hist.* 35: 663-680.
- Hutterer, R. 1985. Anatomical adaptations in shrews. *Mammal Review* 15: 43-55.
- Hutterer, R. 1986a. Diagnosen neuer Spitzmäuse aus Tansania (Mammalia: Soricidae). *Bonn. zool. Beitr.* 37: 23-33.
- Hutterer, R. 1986b. Synopsis der Gattung *Paracrocidura* (Mammalia: Soricidae), mit Beschreibung einer neuen Art. *Bonn. zool. Beitr.* 37: 73-90.
- Hutterer, R. 1993. Order Insectivora. Pp. 69-130 in Wilson, D.W., & D.A. Reeder (eds.). *Mammal species of the world, a taxonomic and geographic reference*. Second edition. Washington, D. C.
- Hutterer, R., & A. Dudu. 1990. Redescription of *Crocridura caliginea*, a rare shrew from northeastern Zaire. *J. Afr. Zool.* 104: 305-311.
- Hutterer, R., & D.C.D. Happold. 1983. The shrews of Nigeria (Mammalia: Soricidae). *Bonn. zool. Monogr.* 18: 1-79.
- Hutterer, R., Dieterlen, F., & G. Nikolaus. 1992. Small mammals from forest islands of eastern Nigeria and adjacent Cameroon, systematical and biogeographical notes. *Bonn. zool. Beitr.* 43: 393-414.
- Hutterer, R., & D.A. Schlitter. *In press*. Shrews of the Korup National Park, Cameroon, with the description of a new *Sylvioorex* (Mammalia: Soricidae). *Spec. Publ. Mus. Texas Tech Univ.*
- Hutterer, R., Van der Straeten, E., & W.N. Verheyen. 1987. A checklist of the shrews of Rwanda and biogeographical considerations on African Soricidae. *Bonn. zool. Beitr.* 38: 155-172.
- Jenkins, P.D. 1984. Description of a new species of *Sylvioorex* (Insectivora: Soricidae) from Tanzania. *Bull. Brit. Mus. (Nat. Hist.), Zool.* 47: 65-76.
- Johnson, M.K., Aldred, D.R., Clinite, E.W., & M.J. Kutilek. 1981. Biochemical identification of bobcat scats. *Proc. Bobcat Res. Conf. Nat. Wildl. Fed. Sci. and Tech. Ser.* 6: 92-96.
- Kirkland, G.L., Jr. 1991. Competition and coexistence in shrews (Insectivora: Soricidae). Pp. 15-22 in Findley, J.S., & T.L. Yates (eds.). The biology of the Soricidae. The Museum of Southwestern Biology, University of New Mexico, Albuquerque.
- Kirkland, G.L., Jr., & P.K. Sheppard. 1994. Proposed standard protocol for sampling small mammal communities. Pp. 277-284 in Merritt, J.F., G.L. Kirkland, Jr., & R.K. Rose (eds.). *Advances in the biology of shrews*. Carnegie Mus. Nat. Hist. Spec. Publ. No. 18.
- Korpimäki, E., & K. Norrdahl. 1989. Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. *Ann. Zool. Fenn.* 26: 389-400.
- Kortlandt, A. 1984. Vegetation research and the 'bulldozer' herbivores in tropical Africa. Pp. 205-226 in Chadwick, A., & C. Sutton (eds.). *Tropical rainforest*. Leeds.

- Lasso, C., Hutterer, R., & A. Rial. *In press*. Records of shrews from Equatorial Guinea. *Mammalia*.
- Maddalena, T. 1990. Systematics and biogeography of Afrotropical and Palearctic shrews of the genus *Crocidura* (Insectivora: Soricidae): an electrophoretic approach. Pp. 297-308 in Peters, G., & R. Hutterer (eds.). *Vertebrates in the tropics*. Bonn.
- McLellan, L.J. 1994. Evolution and phylogenetic affinities of the African species of *Crocidura*, *Suncus*, and *Sylviovores* (Insectivora: Soricidae). Pp. 379-391 in Merritt, J.F., Kirkland, G.L., Jr., & Rose, R.K. (eds.). *Advances in the biology of shrews*. Carnegie Mus. Nat. Hist. Spec. Publ. No. 18.
- Neet, C.R., & J. Hausser. 1990. Habitat selection in zones of parapatric contact between the common shrew *Sorex araneus* and Miller's shrew *S. coronatus*. *J. Anim. Ecol.* 59: 235-250.
- Nicoll, M.E., & G.B. Rathbun. 1990. African Insectivora and elephant shrews, an action plan for their conservation. Gland.
- Niethammer, J., & F. Krapp (eds.). (1990): *Handbuch der Säugetiere Europas*, Band 3/1. Wiesbaden.
- Rahm, U. 1972. Zur Ökologie der Muriden im Regenwaldgebiet des östlichen Kongo (Zaire). *Rev. suisse Zool.* 79: 1121-1130.
- Ray, J.C. 1995. The life in sympatry of *Xenogale naso* and *Atilax paludinosus* in a central African forest. *Small Carnivore Conservation* 12: 1-4.
- Sheftel, B.I. 1994. Spatial distribution of nine species of shrews in the central Siberian taiga. Pp. 45-56 in Merritt, J.F., Kirkland, G.L., Jr., & Rose, R.K. (eds.). *Advances in the biology of shrews*. Carnegie Mus. Nat. Hist. Spec. Publ. No. 18.
- Simonetta, A.M. 1968. A new golden mole from Somalia with an appendix on the taxonomy of the family Chrysochloridae (Mammalia, Insectivora). *Monit. zool. ital. (N.S.)* 2 (suppl.): 27-55.
- Terry, C.J. 1981. Habitat differentiation among three species of *Sorex* and *Neurotrichus gibbsii* in Washington. *Amer. Midl. Nat.* 106: 118-125.
- Vernon, C.J. 1971. An analysis of owl pellets collected in southern Africa. *Ostrich* 43: 109-122.
- Vogel, P. 1974. Note sur le comportement arboricole de *Sylviovores megalura* (Soricidae, Insectivora). *Mammalia* 38: 171-176.
- Western, D. 1986. An African odyssey to save the elephant. *Discover*, pp. 56-70.
- Wrigley, R.E., Dubois, J.E., & H.W.R. Copland. 1979. Habitat, abundance and distribution of six species of shrews in Manitoba, Canada. *J. Mamm.* 60: 505-520.