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MORPHOMETRIC EVIDENCE OF THE MONOTYPIC STATUS OF THE AFRICAN LONG-NOSED MONGOOSE *XENOGALE NASO* (CARNIVORA, HERPESTIDAE)

by

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SUMMARY

Xenogale naso has a discontinuous distribution between three nominal subspecies : *X. n. naso, X. n. almodovari* and *X. n. microdon*. Examination of extant specimens shows that *X. naso* occurs throughout forested areas of Central Africa, including the « South Central » faunal region. A morphometric analysis of 122 skulls, indicates that the three nominal subspecies cannot be distinguished cranially, nor any specimens originating from the « South Central » region. *X. naso* should be regarded as a monotypic species and evolved in an area close to the three faunal regions, « West Central » (WC), « South Central » (SC), and « East Central » (EC). We believe it dispersed in a centrifugal manner. Indeed, if *X. naso* had originated from isolated peripheral refuges in mountain areas, centripetal dispersal would have favoured subspeciation in other faunal regions. These data support the theory that, during the dry climatic period of the Late Pleistocene, the lowland forests of the Central Zaire Basin constituted areas of refuge.

Keywords : morphometrics, refuges, dispersion, Zaire, Herpestidae, *Xenogale*.

INTRODUCTION

The rare long-nosed mongoose, *Xenogale naso* (DE WINTON, 1901) is known from only about 40 museum specimens, originating primarily from the rain forests of Central Africa (ALLEN, 1919 ; CABRERA, 1902 ; COETZEE, 1977 ; HALTENORTH and DILLER, 1980 ; ORTS, 1970 ; ROSEVEAR, 1974 ; SCHOUTEDEN, 1947 ; Fig. 1). In the northwest part of the region, *X. n. naso* inhabits the forests between the Cross River (Nigeria) and the north bank of the Sanaga River in Cameroon. South of this river, *X. n. almodovari* is limited to the coastal regions of Cameroon, Equatorial Guinea, and Gabon. In the east, *X. n. microdon* is distributed over a large area on the right bank of the Zaire River, including the gallery forests of the upper reaches of the

Fig. 1. — Long-nosed mongoose (*Xenogale naso*) from the Niger Delta, Nigeria. *Photo : A. P. Leventis.*

Zaire/Lualaba River and the Bas-Zaire region, as well as of areas south of the Zaire River (area around Lake Tumba and Lake Mai-Ndombe areas, and the upper reaches of the Sankuru River). According to these data, *X. naso* has a discontinuous distribution, and the three « subspecies » are separated either by a fluvial barrier (Sanaga River), or by a gap of several hundred kilometers (Fig. 2).

Recently a specimen was caught near Yenagoa in the Niger Delta, Nigeria, approximately 200 km west of the Cross River, thus extending the species' range of distribution to the Niger River (C. B. Powell, in litt.).

The distribution described above could result from a scarcity of specimens, taxonomic confusion, or both. Confusion exists at the generic and specific levels and is based on similarities of morphological characters.

Long nosed mongooses, first described as *Herpestes naso* (De Winton, 1901), were alternately named *Mungos* (Cabrera, 1912 ; Thomas, 1912) for specimens from Equatorial Guinea and Cameroon, respectively and *Xenogale* (J. A. Allen, 1919) for specimens from NE Zaire. Later these three genera were considered to be synonyms and regrouped into the genus *Atilax* (Allen, 1939). Monard (1951) pointed out that the specimen of *Herpestes galera*, described by Jeannin (1936) from South Cameroon, was actually *Xenogale naso*. *X. naso* has 40 teeth, while *H. galera* (= *Atilax paludinosus*) has only 36 teeth. The genus *Xenogale* has also been considered a subgenus of *Herpestes* (Petter, 1969).

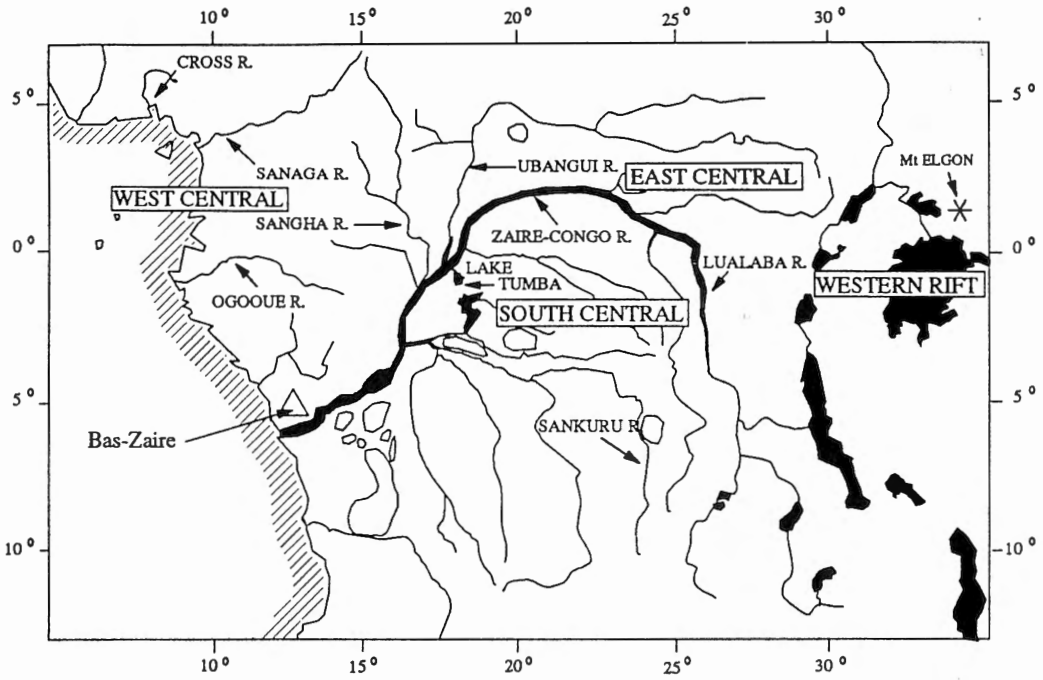

Fig. 2. — Principal faunal regions and rivers of Central Africa : West Central (WC), East Central (EC), South Central (SC); after MISONNE (1963), KINGDON (1980), GRUBB (1978, 1982), and COLYN (1988, 1991).

ORTS (1970) underlined the difficulty in distinguishing between *Xenogale, Atilax*, and the black-tailed variety of *Ichneumia*, all of which are almost identical in coat color. These similarities in external characters had been previously noted by many authors (J. A. ALLEN, 1919, 1924 ; CABRERA, 1903 ; DE WINTON, 1901 ; LÖNNBERG, 1917 ; SANDERSON, 1940 ; THOMAS, 1915) and ORTS (1970) pointed out that having similar external markings has led to incorrect identifications. For example, he found that ten specimens were misidentified as either *Atilax* or *Ichneumia*, and three specimens were mislabelled as *Xenogale* in SCHOUTÈDEN's (1947) list. On the basis of cranial analyses of *Xenogale* from Zaire and *Herpestes ichneumon* from Central Africa, ORTS (1970) retained the two genera. ROSEVEAR (1974) confirmed this distinction. In summary, while many authors agree with the name *Herpestes naso* (COETZEE, 1977 ; CORBET and HILL, 1991 ; HAPPOLD, 1987 ; HINTON and DUNN, 1967 ; PERRET and AELLEN, 1956 ; KINGDON, 1977 ; WILSON and REEDER, 1993 ; WOZENCRAFT, 1989), others use the name *Xenogale naso* (ANSELL, 1960, 1978 ; DEKEYSER, 1955 ; EISENTRAUT, 1963 ; GREGORY and HELLMAN, 1939 ; MALBRANT and MACLATCHY, 1949 ; MONARD, 1951 ; SIMPSON, 1945).

Confusion has been greater at the specific and subspecific levels. The best example is given by CABRERA (1902, 1903, 1908, 1912) who describes a new long-nosed mongoose from Equatorial Guinea that he named successively *Herpestes*

almodovari (1902), *H. albicauda* var. *almodovari* (1903), *Mungos albicaudus almodovari* (1908, 1912b), and *H. almodovari* (1912a). Each original description of a 'subspecies' (*naso, almodovari*, and *microdon*) was done without any knowledge of the existence of the other(s). Each author thought he was describing a new species, that is, *Herpestes naso, Herpestes almodovari*, and *Xenogale microdon*. So no comparisons were made, only ROSEVEAR (1974) remarked that *almodovari* skulls are in general larger than *naso* skulls.

In this study, we retain the classification of ORTS (1970) at the generic level, based on cranial differences, and discuss only the validity of the subspecies classification.

genus
Xenogale J. A. ALLEN, 1919
species
X. naso (DE WINTON, 1901)
subspecies
X. n. naso (DE WINTON, 1901)
= *Mungos naso nigerianus* THOMAS, 1912
X. n. almodovari (CABRERA, 1902)
X. n. microdon J. A. ALLEN, 1919

This study is based on a re-examination of all extant museum material, as well as an analysis of newly-collected material. It examines the taxonomic relationships of long-nosed mongooses based on cranial differences and their patterns of distribution. Biogeographic considerations arising from these results allow us to hypothesize how evolution of these taxa occurred.

MATERIAL AND METHODS

Material. All known specimens of *Xenogale, Atilax*, and *Ichneumia* in museums and 46 newly-collected specimens from Zaire (COLYN *et al.*, 1988) were examined. From this sample, a total of 122 adult specimens showing permanent dentition and fusion of the basioccipital and basisphenoid were considered to belong to the genus *Xenogale*. Because there exists no external morphological character that allows the differentiation of specimens of *Xenogale* at the subspecific level and, because skins of all three described subspecies exhibit marked color polymorphism, only cranial material was used (Appendices 1, 2). Institutions housing the specimens examined are listed in Appendix 3.

Skull measurements. Measurements were taken with calipers and recorded to the nearest 0.1 mm (Appendix 4). Seventeen cranial measurements as defined by GOLDMAN (1984) were used : GSL : greatest skull length, from the anterior edge of I^1 to posterior edge of occipital bone ; CBL : condylobasal length of the skull, from anterior edge of of I^1 alveolus to posterior edge of occipital condyle ; ROL : length of rostrum, from lateral base of hamular process of lacrimal to anterior most edge of premaxillae ; PAL : length of palate, from posterior edge of alveolus of I^1 to posterior edge of palatine ; MAX : greatest crown length of maxillary toothrow ; TYM :

greatest length of tympanic bulla, not along longitudinal axis of skull ; CAN : breadth of canines, distance between labial crown edges of C^1-C^1 ; ROB : breadth of rostrum, distance between lateral base of hamular process of lacrimals ; IOB : least interorbital breadth ; PAB : breadth of palate, distance between labial crown edges of M^1-M^1 ; ZYG : greatest zygomatic breadth ; BRB : greatest breadth of braincase at the right angle to longitudinal axis of skull ; MAS : mastoid breadth ; BRH : height of braincase, distance from occipital bone between bullae to parietal, excluding sagittal crest ; MAL : mandible length from anterior edge of I_1 alveolus to posterior surface of mandibular condyle ; MAN : greatest crown length of mandibular toothrow ; CMH : mandible height, perpendicular distance from dorsal edge of coronoid process to line from angular process to ramus.

Data analysis. Of the 122 skulls examined, only the 103 intact skulls were used for multivariate analyses to reduce missing data (Appendices 1, 4). On the basis of taxonomic and biogeographic criteria, four operational taxonomic units (OTU's) were made (Fig. 3). These include the four principal populations comprising the three nominal subspecies, and also the specimens originating from the left bank of the Zaire River.

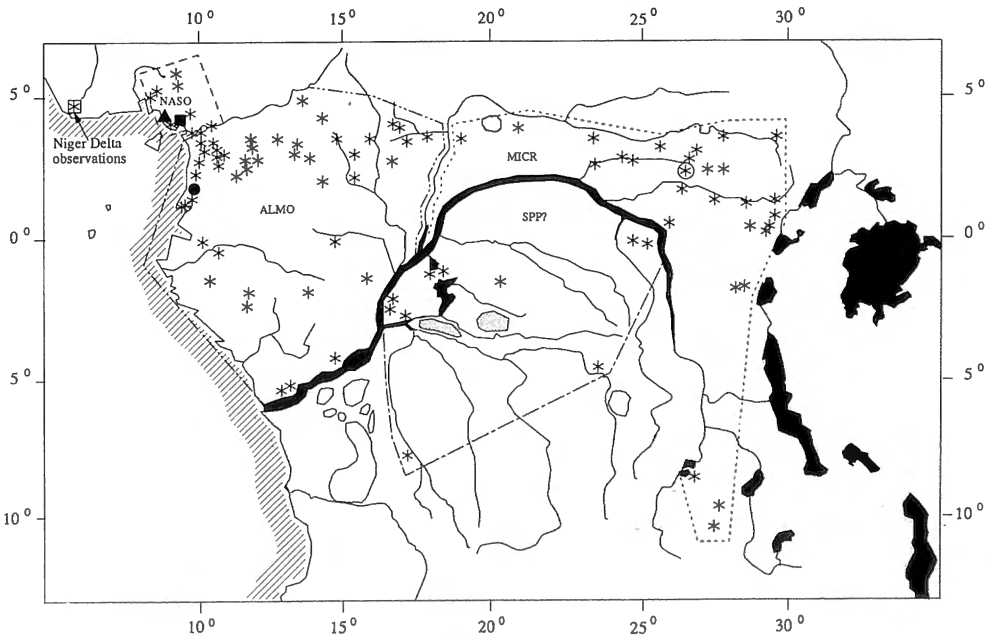

Fig. 3. — Distribution of *Xenogale naso* in Central Africa based on data from museum material (stars). Holotypes: triangle, *X. n. naso*; square, *Mungos naso nigerianus*; full circle, *X. n. almodovari*; star in circle, *X. n. microdon*. The unshaded areas represent rain forest areas.

OTU « NASO » : *X. n. naso* from the « West Central » region : 21 specimens from Nigeria and North Cameroon.

OTU « ALMO » : *X. n. almodovari* from the « West Central » region : 51 specimens from South Cameroon, Equatorial Guinea, Gabon, Central African Republic, Congo, and Zaire (coastal region).

OTU « MICR » : *X. n. microdon* from the « East Central » region : 21 specimens from the right bank of the Zaire River (Zaire).

OTU « SSP ? » : *X. naso* ssp. from the « South Central » region : 29 specimens from the left bank of the Zaire River (Zaire).

We conducted several multivariate analyses to differentiate these populations. Principal component analysis was undertaken on the basis of the nine most significant skull measurements (ROL, PAL, MAX, CAN, ROB, BRB, MAL, MAN, and CMH) chosen by the CASEL program from the 17 cranial measurements. Results were then tested by canonical dispersal analysis, using the method of SEAL (1964) further adapted by HERBRANT (1974). This analysis maximizes the variation between groups in relation to the variation within groups. The original variables (skull measurements) are transformed into a new set of canonical variables. Each original variable is multiplied by its corresponding coefficient of the calculated eigenvector and the resulting values are added up. Each specimen can be plotted in a diagram of canonical variates represented as an abscissa or an ordinate. The OTUs are represented by the contour of the most extreme values and by the canonical means (= centroids).

In order to identify phenetic affinities between the four populations on the basis of the same cranial variables, discriminant analyses were conducted and phenograms drawn from the matrices of generalized Mahalanobis distances using the UPGMA method (SNEATH and SOKAL, 1973 ; Table 2).

TABLE 1

Eigenvectors of the nine variables for the first two Canonic Variables (CVs).

Variable	CV I	CV II
ROL	1.9276	−2.8297
PAL	−4.0460	−4.4084
MAX	0.8531	−1.9804
CAN	−3.3020	−4.9126
ROB	0.2845	0.8985
BRB	4.2293	0.5718
MAL	2.4999	1.0345
MAN	5.3790	2.4980
CMB	1.4564	6.8908

TABLE 2

Matrices of the generalized Mahalanobis distances (D^2m ; lower triangle) and possibility of a faulty determination (% ; upper triangle). OTU's = NASO, ALMO, MICR and SSP ?

	NASO	ALMO	MICR	SSP ?
NASO		29.62	14.82	1.42
ALMO	1.15		16.83	3.84
MICR	4.35	3.66		7.82
SSP ?	19.22	12.52	8.51	

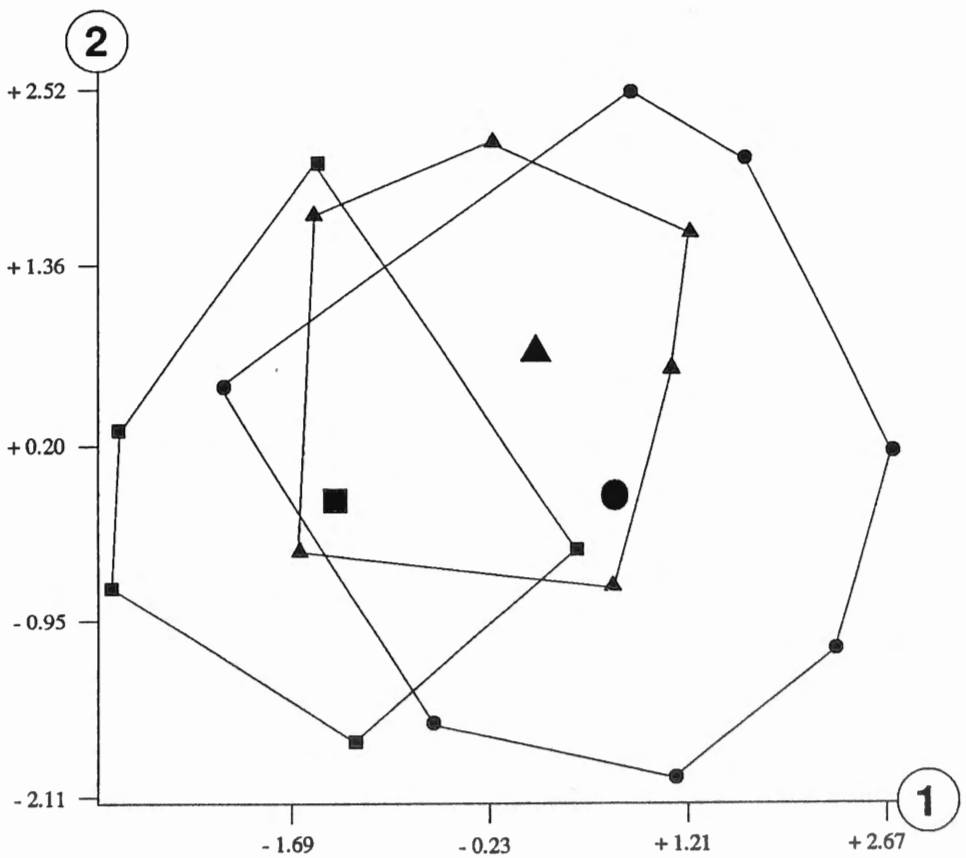

Fig. 4. — Results of the Canonical Variate Analysis of nine cranial characters of three OTU's of *Xenogale naso*. Dispersion of the three OTU's: triangles = *X. n. naso* (NASO), circles = *X. n. almodovari* (ALMO), and squares = *X. n. microdon* (MICR).

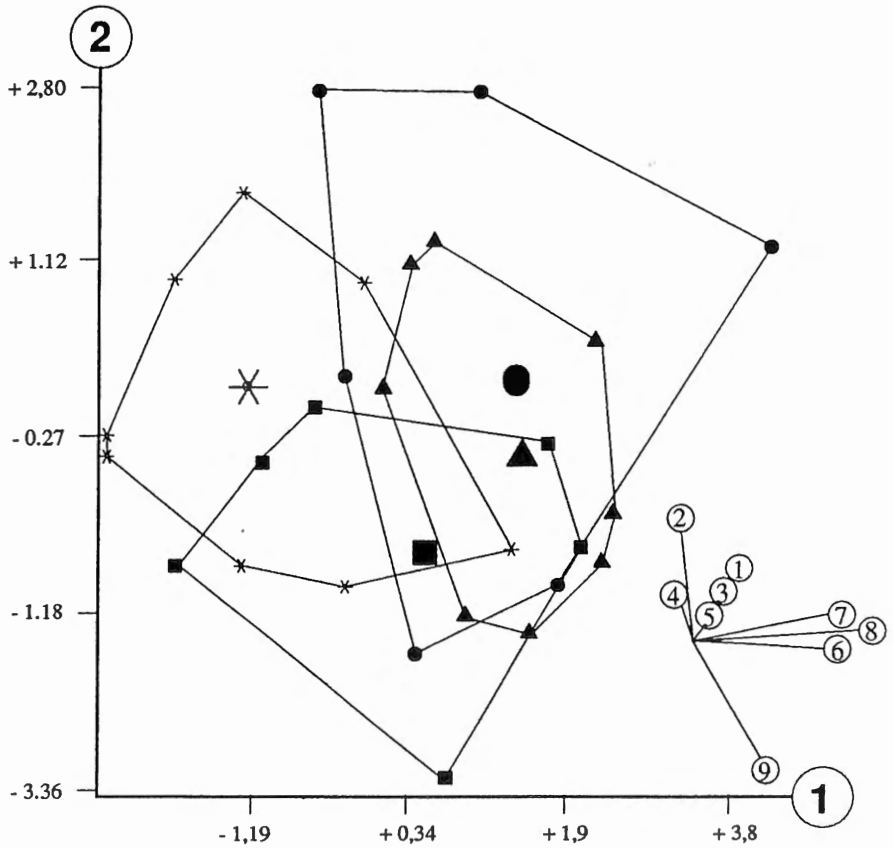

Fig. 5. — Results of the Canonical Variate Analysis of nine cranial characters of four OTU's of *Xenogale naso*. Dispersion of the four OTU's: triangles = *X. n. naso* (NASO); circles = *X. n. almodovari* (ALMO); squares = *X. n. microdon* (MICR), and stars = *X. naso* ssp? (SSP?) specimens from the « South Central » faunal region.

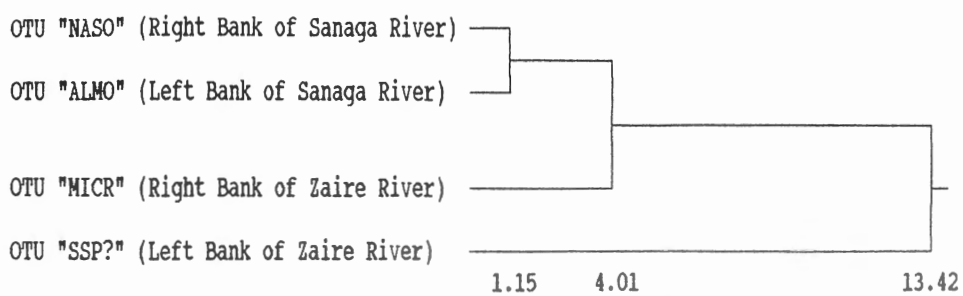

Fig. 6. — Phenogram based on the Discriminant Analysis of nine cranial variables, schematically representing the morphological distances between the four principal population aggregates of *Xenogale naso*.

RESULTS

Patterns of distribution of the genus Xenogale. — The present number of specimens allows a refinement of the distributional data on long-nosed mongooses. Results show that genus *Xenogale* is more evenly distributed than previously thought (Fig. 3). Long-nosed mongooses are present in the entire forested area north of the Zaire River and without any obvious gaps between the western and eastern areas. The species is also present south of the Zaire River to ca. 10°30'S.

Taxonomic relationships. — The first canonical dispersal analysis does not distinguish the three nominal subspecies ($P=0.8454$), in spite of the large size of the skull in *X. n. almodovari.* The diagram based on the eigenvectors of the nine significant variables shows that the three OTUs overlap considerably and that the centers of dispersion are all located within the contour of points representing *X. naso* (Table 1, Fig. 4).

The second analysis includes the four populations and gives similar results. The first axis of the canonical analysis contains 81.3 % of the total variation, the second axis 15.2 %. On the diagram derived from the eigenvectors (Table 1), the three OTUs, *X. n. naso, X. n. almodovari,* and *X. n. microdon* overlap considerably so that the dispersion centres are nearly all located within the OTU NASO (Fig. 5). The OTU SSP, although slightly distinguished on Axis 1, does overlap considerably with the three other OTUs.

The projection of the nine cranial variables, regrouped near the centroid of the two CVs, does not allow the identification of any cranial character that is specific to populations from the SC region.

Phenetic affinities were searched for by a discriminant analysis. The phenogram (Fig. 6) represents the morphological distances between the four population aggregates. The results show that :

1. — *X. naso* ssp. from the left bank of the Zaire River is the most differentiated of all the populations ; 2. — *X. n. microdon* from eastern Zaire closely resembles *X. n.naso* and *X. n. almodovari* from western Africa ; and 3. — *X. n. naso* and X. n. almodovari are phenetically very close to each other.

DISCUSSION

Although there is a range of variation of skull dimensions in the four populations studied, there is also a large degree of overlap between them, and none of the populations can be characterized by any specific cranial character. The least distinct populations are those from the WC faunal region (*X. n. naso* and *X. n. almodovari*) and which clearly belong to the same subspecies. Differences are more obvious for the EC population, and especially for the SC population. However, without more additional data, the erection of a new subspecies for the SC population does not seem justifiable. We tentatively propose that the long-nosed mongooses of Central Africa belong to the monotypic *Xenogale naso*, however, we cannot exclude the

possibility that the relatively small sample size, which originates from a large geographic area could mask geographical variation.

The distribution pattern of *Xenogale naso* in western Cameroon and northeastern Zaire described previously largely agrees with the long-standing biogeographical theory which recognises only two main faunal regions : the EC and the WC (GRUBB, 1978, 1982 ; KINGDON, 1980 ; MISONNE, 1963 ; MOREAU, 1966 ; PRIGOGINE, 1988 ; RAHM, 1966), and accords a minor role to the SC area (GRUBB, 1978, 1982 ; KINGDON, 1977, 1980 ; MISONNE, 1963 ; RAHM, 1966). According to this scenario, the main Quaternary refugia would have been in the proximity of montane forests at the foot of the Central Rift in eastern Zaire, and at the periphery of Mt Cameroon in the west.
Dispersal would have occurred from these peripheral refugia, and would have been limited by fluvial barriers, thus favouring subspeciation.

The actual distribution of *X. naso* shown by this study suggests that the main fluvial barriers (either the Sanaga River, the Ubangui River, or the huge Zaire River) did not, however, play an important role in the subspeciation of *Xenogale*. The fact that long-nosed mongooses have colonized the whole of Central Africa's forests but without showing any clear differentiation does not support centripetal dispersion from the peripheral montane refugia Mt. Cameroon and the Central Rift. We propose that the species originated from a refugium in the lowland forests, situated at the centre of the three faunal regions, and that dispersal occurred in a centrifugal manner. Such a hypothesis supports the existence of lowland forest refugia within the whole drainage area of the Central Basin and particularly of the Zaire River, as previously suggested by studies on African primates (COLYN, 1987, 1988, 1991, 1993 ; COLYN *et al.*, 1991).

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APPENDIX 1

List of known material : specimens used in the statistical analyses are shown in bold type ; FO : field observation

CAMEROON : Ajos Höhe, 1 (**MNHU-31442**) ; Akak, 1 (**MHNC-37021117**) ; Akonangi, 1 (**MNHU-82942**) ; Balaga, between Dingi and, 1 (MNHU-83134) ; Balingekore, between Balasane and, 1 (**MNHU-82945**) ; Bange Forest, 1 (**SMF-4615**) ; Basho, 4 (**MNHU : 82925, 83035**, 83136, 83137) ; Batouri District, 1 (PCM-no No.) ; Bipindi, 17 (BMNH-1171 ; **MNHU :** 18727, 82909, **82941, 82944,** 82946, 82950, **82963, 82966, 82967,** 83139, 83142, **91380, 92604**, no No., no No., no No.) ; Cameroon River, estuary, 1 (**BMNH-0751**) ; Debundscha, 2 (**NRST : A580173, A582404**) ; Dendeng, 1 (**MNHU-18461**) ; Djaposten, 1 (AMNH-85194) ; Douala, 1 (**MNHU-18392**) ; Edea region, 9 (MNHU : 18541, 18542/43, 18545/44, 18547/46, 18548, 18549, 18550, 18551, 18553) ; Efulen, 2 (**BMNH : 22131, 552320**) ; Ekom, Dja Faunal Reserve, FO ; Idenau, 1 (**BMNH-68335**) ; Koto-Barombi Lake, 1 (**SMNS-6389**) ; Kribi, 1 (**ZSM-1903/1545**) ; Lolodorf, 1, (**MNHU-82959**) ; Lomie District, 1 (P-CM-M552) ; Longji, 2 (MNHU : 83099, 83141) ; Mainju Bridge, Mamfe, 1 (**BMNH-48838**) ; Mamfe, 2 (**BMNH : 48836, 36103011**) ; Metet, 1 (**MCZ-42019**) ; Minkan, near Kiango, 1 (**PCM-ZIV21**) ; Moloundou, 2 (**MNHU-82939, SMF-4614**) ; Muele, 1 (**ZFMK-61396**) ; Mundame, 1 (**MNHU-82957**) ; Niede River, 1 (**PCM-ZII2**) ; Nkalla, between Njong River and, 1 (**MNHU-31319**) ; Obala, 1 (**PCM-M692**) ; Okoiyono, 1 (BMNH-48837) ; Sakbayemé, 7, (FMNH : 25308, 43737, 43738, 43739, **MCZ : 18620, 23199**, MNHU-48393) ; Sanaga River, between Ossa Lake and, 1 (**MNHU-82586**) ; Sanga-Dja, 1 (**ZSM-1913/1169**) ; Sangmelima, 7 (**MNHU : 18355, 18356,** 18363, **19097, 19099, 35209, 35212**) ; South Cameroon, 1 (**MNHU-82954**) ; Victoria, 10 (**MNHU : 82912, 82940, 82943,** 83138, no No., no No., **ZSM :** 1902/3004, 1902/3005, **1902/3006, 1902/30À07**) ; Yaoundé, 8 (AMNH-236489, PCM-CAMI193, **MNHU :** 11429, **82969, 82970, 82980**, no No., no No.) ; Yem, near Efulen, 1 (**MCZ-26836**).

CENTRAL AFRICAN REPUBLIC : Balondo, N'Gotto Forest, FO ; Bambio, N'Gotto Forest, FO ; Bomboko Forest, 1 (**MNHU-17073**) ; Kongana, Dzanga-Sangha Reserve (Ray, 1994) ; La Maboké, 1 (**MNHN-1970/20**) ; Londo, N'Gotto Forest, FO ; Salo2, Dzanga-Sangha Reserve, FO.

CONGO : Etoumbi, 1 (PCM-273) ; Karagoua River, near Souanké, 1 (**AMNH-54339**) ; Kinkala, 1 (AMNH-118823) ; Makoua, 3 (AMNH : 119897, 119941, 119942).

EQUATORIAL GUINEA : Bata, 2 (MNHU : 31443, **31444**) ; Benito River, 3, (**BMNH : 111218, 111219, 112715**).

GABON : Franceville region, FO (Carpaneto, in litt.) ; Ngori, 1 (**NMNH-220398**) ; Kango, 1 (**AMNH-119938**) ; M'bigou, 1 (**FMNH-73796**) ; N'djolé region, 1 (**AMNH-119937**) ; Ngori, 1 (**NMNH-220398**) ; Yombi (FMNH-73797).

NIGERIA : Niaji, 1 (**BMNH-106114**) ; Otuopoti, near Yenagoa (C. B. Powell, in litt.)

ZAIRE : Akenge, 5 (RMCA-12306, **AMNH :** 51617, 51620, **51621, 51625**) ; Amadjabe, 42 (**MC : ZX4312, ZX4313, ZX4315, ZX4339, ZX4517, ZX4654, ZX4655, ZX4734, ZX4881 to ZX4883, ZX4943, ZX4960, RMCA** : 88047M68, 88047M69, **89023M77,** 90042M43, **90042M44,** 90042M45, 90042M46, **90042M48,** 90042M49, **90042M50 to 90042M52, 90042M53,** 90042M54, **90042M55,** 90042M56 to 90042M59, **90042M60**, 90042M61, **90042M62,** 90042M63, **90042M64, 90042M65,** 90042M66, 90042M67, **90042M68, 90042M69**) ; Avakubi, 2 (AMNH-51604, 51605) ; Bambesa, 1 (RMCA-23990) ; Batiakuya, 5 (**MC : Z1093, Z2204, Z2770, RMCA : 90042M40**, 90042M41) ; Beni, 1 (**RMCA-3250**) ; Bokuma, 1 (RMCA-20552) ; Bolobo, 3 (RMCA : 15795, 15796, 15797) ; Buta, 4 (RMCA : **10433bis,** 10434, **11582, 18692**) ; Dali, 1 (**RMCA-1904**) ; Faradje, 1 (AMNH-51093) ; Go, 1

(ZSM-1912/1555); Ibembo, 5 (RMCA : **19600, 19621,** 20235, **20236, 21712**); Inkongo, 1 **(RMCA-7834)**; Ituri River, 80 km SW of Irumu, 1 (BMNH : 301111225); Kasongo Lunda Falls, 1 (RMCA-15063); Koteli, 1 **(RMCA-16577)**; Kundulungu, 1 (RMCA-4995); Kunungu, 1 (RMCA-8150); Lesse, 1 (RMCA-3249); Lukafu, 1 (RMCA-11097); Mabwe, 2 (IRSNB : 11862, 11864); Makaia, 1 (RMCA-5848); Manguredjipa, 1 (RMCA-18391); Medje, 5 (AMNH-51007, 51088, 51089, 51091, 51609); Molegbe St. Antoine, 1 (RMCA-10345); Mushie, 1 (RMCA-17593); Niangara, 1 (AMNH-51092); Niapu, 3 **(AMNH : 51624, 51637**, 51673); Panga, 1 **(RMCA-3409)**; Poko Welle, 1 **(BMNH-195831)**; Sambo River, right bank of, 1 **(RMCA-9724)**; Temvo, 1 (RMCA-5847).

APPENDIX 2

Gazetteer

The distributional localities cited are listed alphabetically below. Abbreviations are as follows : CM, Cameroon ; CAR, Central African Republic ; C, Congo ; EG, Equatorial Guinea ; G, Gabon ; N, Nigeria ; Z, Zaire.

Ajos Höhe (Ayos Heights), CM, 03°54′N, 12°31′E ; Akak, CM, 02°25′N, 10°E ; Akenge, Z, 02°54′N, 26°48′E ; Akonangi, CM, 02°12′N, 11°21′E ; Amadjabe, Z, 00°04′N, 25°17′E ; Avakubi, Z,01°20′N, 27°35′E ; Balondo, CAR, 03°58′N, 16°45′E ; Bambesa, Z, 03°28′N, 25°43′E ; Bambio, CAR, 03°57′N, 16°58′E ; Basho, CM, 06°08′N, 09°26′E ; Bata, EG, 01°51′N, 09°49′E ; Batiakuya, Z, 00°36′N, 23°59′E ; Beni, Z, 00°30′N, 29°28′E ; Benito R., estuary, EG, 1°35′N, 9°37′E ; Bipindi, CM, 03° 05′N, 10° 25′E ; Bokuma, Z, 02°26′N, 27°57′E ; Bolobo, Z, 02°10′S, 16°17′E ; Bomboko, CAR, 03°54′N, 18°35′E ; Buta, Z, 02°48′N, 24°47′E ; Butuhe, Z, 00°13′N, 29°16′E ; Cameroon River, estuary, CM, 03°56′N, 09°33′E ; Dali, Z, 03°49′N, 23°40′E ; Debundsha, Cape, CM, 04°07′N, 08°58′E ; Deng Deng, CM, 05°10′N, 13°30′E ; Djaposten, CM, 03°25′N, 13°32′E ; Douala, CM, 04°04′N, 09°43′E ; Edea, CM, 03°48′N, 10°08′E ; Efoulan, CM, 03°00′N, 10°55′E ; Ekom, CM, 03°20′N, 13°02′E ; Etoumbi, C, 00°01′N, 14°57′E ; Faradje, Z, 03°44′N, 29°42′E ; Fougamou, G, 01°16′S, 10°30′E ; Gamangui, Z, 02°10′N, 27°45′E ; Ibembo, Z, 02°38′N, 23°41′E ; Impfondo, C, 01°36′N, 18°00′E, Idenau, CM, 04°14′N, 08°59′E ; Inkongo, Z, 04°53′S, 23°15′E ; Irangi, Z, 01°55′S, 28°27′E ; Irumu, Z, 01°15′N, 29°40′E ; Ituri River, 80 km SW of Irumu, Z, 01°15′N, 29°40′E ; Kango, G., 0°09′N, 10°08′E ; Kasongo Lunga Falls-Tembo Falls, Z, 07°34′S, 17°17′E ; Kinkala, C, 04°18′S, 14°49′E ; Kisangani, Z, 00°33′N, 25°14′E ; Kongana, CAR, 02°47′N, 16°25′E ; Koteli, Z, 02°52′N, 24°33′E ; Kotto-Barambi, CM, 04°28′N, 09°15′E ; Kribi, CM, 02°56′N, 09°56′E ; Kundelungu, Z, 09°50′S, 27°47′E ; Kunungu, Z, 02°06′S, 16°26′E ; Lac Tumba, Z, 01°05′S, 18°09′E ; La Maboké, CAR, 03°54′N, 17°53′E ; Lesse, Z, 00°45′N, 29°48′E ; Lolodorf, CM, 03°14′N, 10°44′E ; Lomie Distr., CM, 03°30′N, 13°30′E ; Londo, CAR, 03°37′N, 17°04′E ; Longji, CM, 03°04′N, 09°59′E ; Lukafu, Z, 10°31′S, 27°33′E ; Mabwe, Upemba NP, Z, 08°41′S, 26°31′E ; Mainyu Bridge, Mamfe, CM, 05°46′N, 09°17′E ; Makaia N'Tete, Z, 05°37′S, 13°05′E ; Makoua, C, 00°15′S, 15°40′E ; Mamfe, CM, 05°46′N, 09°17′E ; Manguredjipa, Z, 00°21′N, 28°44′E ; Mankaketi, near Bolobo, Z, 02°11′S, 16°20′E ; Mawambi, Z, 01°05′N, 28°35′E ; M'Bigou, G, 01°53′S, 11°56′E ; Medje, Z, 02°25′N, 27°18′E ; Metet, CM, 03°26′N, 11°45′E ; Minkan, near Kiango, CM, 03°01′N, 10°55′E ; Molegbwe, Z, 04°12′N, 20°53′E ; Moloundou, CM, 02°03′N, 15°14′E ; Mueli, CM, 04°23′N, 09°07′E ; Mundame, CM, 04°35′N, 09°31′E ; Mushi (or Muschie), Z, 03°01′S, 16°55′E ; N'Djole, G, 00°07′S, 10°45′E ; Niaji, N, 05°19′N, 08°34′E ; Niapu, Z, 02°25′N, 26°31′E ; Ndiki, CM, N'Djolé, G, 0°11′S, 10°45′E ; Niangara, Z, 03°42′N, 27°52′E ; Niede River, near Nkali, CM, 02°40′N, 11°50′E ; Nkolefong, N. W. of Sangmelima, CM, 02°56′N, 11°58′E ; Obala, Betouri Distr., CM,

04°15′N, 14°15′E ; Oban, N, 05°17′N, 08°33′E ; Okoiyongo, CM, Ossa Lake, between Sanaga and, CM, ca 03°49′N, 10°08′E ; Panga, Z, 01°51′N, 26°25′E ; Pemba Nyambi, G, 01°54′S, 09°27′E ; Poko Welle, Z, 03°09′N, 26°53′E ; Sakbayémé, CM, 04°02′N, 10°34′E ; Salo2, CAR, 03°10′N, 16°03′E ; Sangmelima, CM, 02°56′N, 11°59′E ; Souanké, C, 02°05′N, 14°03′E ; Temvo, Z, 05°30′S, 13°01′E ; Victoria, CM, 04°10′N, 09°10′E ; Yaoundé, CM, 03°52′N, 11°31′E ; Yaoundé District, CM, ca 03°45N, 11°30′E ; Yenagoa, N, 04°55′N, 06°15′E ; Yombi, G, 02°14′S, 11°56′E.

APPENDIX 3

Institutions housing study specimens

AMNH American Museum of Natural History, New York, NY, USA
BMNH The Natural History Museum, London, UK
MC Marc Colyn Collection, Paimpont, France
FMNH Field Museum of Natural History, Chicago, IL., USA
IRSNB Royal Institute of Natural Sciences, Brussels, Belgium
MCZ Museum of Comparative Zoology, Cambridge, MA, USA
MHNC Musée d'Histoire naturelle, La Chaux-de-Fonds, Switzerland
MHNG Muséum d'Histoire naturelle, Genève, Switzerland
MNHN Musée National d'Histoire naturelle, Paris, France
MNHU Museum für Naturkunde der Humboldt-Universität Berlin, Berlin, Germany
NMNH National Museum of Natural History, Washington, D.C., USA
NRST Riksmuseet Stockholm, Stockholm, Sweden
PCM The Powell-Cotton Museum, Birchington, UK
RMCA Royal Museum for Central Africa, Tervuren, Belgium
SMF Forschungsinstitut & Naturmuseum Senckenberg, Frankfurt, Germany
SMNS Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
ZFMK Zoologisches Forschungsinstitut & Museum A. Koenig, Bonn, Germany
ZSM Zoologische Staatssammlung, München, Germany

APPENDIX 4A

Basic statistics (in mm) of 17 skull characteristics of Xenogale naso.

	X. n. naso (« NASO »)						*X. n. almodovari* (« ALMO »)					
VAR	N	MIN	MAX	MEAN	SD	SE	N	MIN	MAX	MEAN	SD	SE
GSL	15	104.7	115.4	109.6	3.57	0.92	47	104.2	122.4	111.3	4.27	0.62
CBL	14	100.8	111.0	106.0	3.45	0.92	45	100.0	118.6	107.5	3.81	0.57
ROL	21	39.4	40.3	37.8	1.73	0.38	50	34.7	42.5	37.7	1.74	0.25
PAL	19	51.8	60.9	56.0	2.78	0.64	49	52.7	63.6	56.7	2.49	0.36
MAX	21	36.3	41.6	38.7	1.61	0.35	51	35.0	41.6	38.4	1.23	0.17
TYM	15	18.4	21.7	19.8	0.95	0.24	47	18.1	22.7	20.6	1.02	0.15
CAN	19	19.0	24.2	21.8	1.30	0.30	51	19.7	25.6	22.3	1.37	0.19
ROB	17	25.2	29.8	27.1	1.45	0.35	51	24.2	31.7	27.3	1.54	0.22
IOB	17	19.3	23.5	21.2	1.22	0.30	50	18.1	24.8	21.6	1.48	0.21
PAB	21	27.9	34.8	30.9	1.52	0.33	51	26.4	34.8	30.6	1.69	0.24
ZYG	16	48.5	60.4	55.6	3.16	0.79	48	48.5	66.4	56.6	3.62	0.52
BRB	16	34.1	38.5	35.7	1.11	0.28	50	32.9	38.4	35.6	1.29	0.18
MAS	14	38.3	44.1	40.6	1.61	0.43	47	38.0	46.8	41.6	2.27	0.33
BRH	15	28,2	31.4	29.9	0.91	0.24	48	27.3	31.7	29.7	1.11	0.16
MAL	21	68.8	79.0	73.4	2.89	0.63	50	68.6	78.8	73.2	2.40	0.34
MAN	21	42.2	48.0	44.5	1.65	0.36	50	41.3	48.0	44.5	1.55	0.22
CMH	19	27.3	32.0	29.6	1.39	0.32	50	27.3	34.6	30.0	1.55	0.22

APPENDIX 4B

	X. n. microdon (« MICR »)						*X. naso* ssp. (« SSP ? »)					
VAR	N	MIN	MAX	MEAN	SD	SE	N	MIN	MAX	MEAN	SD	SE
GSL	18	97.2	115.0	106.5	4.73	1.12	27	96.7	115.7	103.4	4.58	0.88
CBL	15	97.0	110.8	104.3	4.28	1.11	26	94.0	106.9	100.8	3.44	0.68
ROL	21	32.0	39.4	35.6	1.95	0.43	29	27.5	36.8	34.2	1.75	0.33
PAL	21	49.3	60.4	53.9	2.77	0.60	29	47.9	58.6	53.2	2.35	0.44
MAX	21	33.5	39.8	37.0	1.66	0.36	29	33.8	38.6	35.7	1.22	0.12
TYM	16	19.4	21.6	20.3	0.57	0.14	26	18.0	21.4	19.8	0.87	0.17
CAN	21	18.4	24.6	21.3	1.88	0.41	29	17.4	23.2	20.3	1.67	0.31
ROB	18	24.0	27.7	25.8	1.17	0.28	29	21.7	28.3	25.2	1.53	0.28
IOB	17	18.2	22.9	20.4	1.48	0.36	29	17.3	22.6	19.6	1.45	0.27
PAB	22	28.4	33.0	30.7	1.35	0.29	29	27.7	32.1	29.9	1.17	0.22
ZYG	19	49.1	60.2	54.0	4.79	0.87	29	46.5	60.1	51.5	3.69	0.68
BRB	20	31.5	36.1	34.5	1.29	0.29	29	31.6	36.0	33.2	0.94	0.18
MAS	14	38.2	43.0	39.9	1.25	0.33	26	34.5	41.9	37.8	1.83	0.36
BRH	17	27.8	33.0	29.9	1.27	0.31	28	26.3	30.3	28.1	1.11	0.21
MAL	21	64.7	75.1	70.5	3.30	0.72	29	61.6	72.8	67.7	2.68	0.50
MAN	21	38.7	46.5	43.0	2.06	0.45	29	37.6	44.2	41.0	1.39	0.26
CMH	21	26.6	33.0	29.7	1.87	0.41	29	23.5	30.9	27.2	1.72	0.32