The Rusty-spotted genets as a group with three species in Southern Africa (Carnivora: Viverridae)

João Crawford-Cabral
Carlos Alberto Fernandes

Introduction

In Southern Africa, defined by ELLERMAN *et al.* (1953) as the whole of Africa south of the Democratic Republic of Congo and Tanzania, four species of *Genetta* G. Cuvier, 1816, were accepted in the second edition of the reference book *Mammal Species of the World*: *Genetta angolensis* Bocage, 1882, *Genetta genetta* (Linnaeus, 1758), *Genetta maculata* (Gray, 1830), and *Genetta tigrina* (Schreber, 1776) (WOZENCRAFT, 1993). With the exception of the Small-spotted genet (*G. genetta*), which is easily recognizable, among other features, by its white tipped tail, all other species had been mixed up and their systematics is far from settled.

The present paper concerns the Rusty-spotted genets, a group of forms that inhabits tropical Africa from the Volta River to Zululand, and which are considered subspecies of *G. maculata* by WOZENCRAFT (1993). They generally present rows of more rusty than black spots and stripes on each side of a median dorsal line, the spots being smaller and the stripes narrower than in *G. tigrina* (ROBERTS, 1951) and the hair length shorter than in *G. angolensis* (CRAWFORD-CABRAL, 1969). However, as result of a significant amount of individual and ecological variation, it is sometimes difficult to identify them, as their characteristics sometimes fall into those typical of other species. Moreover, since there is no proof that these several forms are all conspecific, the colloquial name Rusty-spotted genet is used herein, instead of a scientific species name, until a conclusion can be drawn about the taxonomy and nomenclature of these animals. They were classified by SCHWARZ (1930) within *G. tigrina* (commonly mentioned under the colloquial name Large-spotted genet) as subspecies, a classification maintained by several authors until a very recent date (ANSELL, 1960; SMITHERS, 1971; WENZEL and HALTENORTH, 1972; COETZEE, 1977; KINGDON, 1977; SMITHERS, 1983; MEESTER *et al.*, 1986; KINGDON, 1997). For instance, PRINGLE (1977), based on the analysis of pelage coloration pattern of specimens from KwaZulu-Natal, stated that within this area hybridisation occurred between *G. tigrina* and a Rusty-spotted genet. However, *G. tigrina* has been regarded as specifically distinct from the Rusty-spotted genets by some other authors (ROBERTS, 1951; ELLERMAN *et al.*, 1953; CORBETT and HILL, 1980; CRAWFORD-CABRAL, 1980-81; HONACKI *et al.*, 1982; ANSELL and DOWSETT, 1988). Indeed, CRAWFORD-CABRAL and PACHECO (1992), using multivariate analysis of cranial measures, also concluded that the Rusty-spotted and the Large-spotted genets are separate species.

Meanwhile, two alternatives to the species name *G. tigrina* for the Rusty-spotted genets arose. One was to consider the forms of this group as conspecific with the Pardine genet. In this way, they were classified as subspecies of *Genetta pardina* I. Geoffroy, 1832 (CRAWFORD-CABRAL, 1969, 1970, 1973; ANSELL, 1978) or as subspecies of *G. maculata* (SCHLAWE, 1980, 1981; WOZENCRAFT, 1993), a difference that has only to do with the scientific name assigned to the Pardine genet. However, the sympatry that apparently occurs, at least in Nigeria (POWELL et VAN ROMPAEY, 1998), between *poensis* Waterhouse, 1838, a form generally considered as a morph of the Pardine genet and whose type locality is Fernando Po (= Bioko, Equatorial Guinea) (but see POCOCK, 1907 and ROSEVEAR, 1974) and a Rusty-spotted genet (possibly *fieldiana* Du Chaillu, 1860), seems to imply a non-conspecificity (CRAWFORD-CABRAL, 1980-81). The other alternative was to accept the Rusty-spotted genets as a separate species either from the Large-spotted or the Pardine genets and, following various authors (BOCAGE, 1882, 1889; HILL and CARTER, 1941; ROBERTS, 1951; ELLERMAN *et al.*,

1953) to name the Rusty-spotted genets *Genetta rubiginosa* Pucheran, 1855 (CRAWFORD-CABRAL, 1966, 1981; ANSELL and DOWSETT, 1988). Nevertheless, having in view that *G. rubiginosa* is the senior synonym of *Genetta thierryi* Matschie, 1902, as SCHLAWE (1981) ascertained, we have serious doubts in maintaining the name *rubiginosa* for the Rusty-spotted genet (CRAWFORD-CABRAL and FERNANDES, 1999).

With regard to the Southern African forms of this complex, ROBERTS (1951), on the basis of material in the Transvaal Museum, recognized five subspecies within the *G. rubiginosa* complex: the nominate *rubiginosa*, in Rustenberg and Zoutpansberg districts of North West Province – on the incorrect supposition that Pucheran's type came from southern « Bechuanaland », an area presently corresponding to northern Cape Province, when in fact that specimen came from Senegal and represents *G. thierryi* (SCHLAWE, 1981; CRAWFORD-CABRAL and FERNANDES, 1999); *letabae* Thomas and Schwann, 1906, in Mpumalanga Province; *zuluensis* Roberts, 1924, in Kwazulu-Natal; *zambesiana* Matschie, 1902, in Malawi (a form described from Boror, Mozambique); and *albiventris* Roberts, 1932, in northern Botswana and northern Namibia. In addition to considering *G. rubiginosa* a valid species, ROBERTS (1951), on the basis of specimens from Boror, Mozambique, also accepted *Genetta mossambica* Matschie, 1902, a form described from Mossimboa, northern Mozambique. The taxonomic position of G. *mossambica* has been controversial and it is still unresolved. It was regarded in some classifications (ELLERMAN *et al*, 1953; ANSELL, 1960; COETZEE, 1977) as more closely related to the forms described by ROBERTS (1951) in *G. rubiginosa*. Later, *G. mossambica* was considered by other authors (WENZELL and HALTERNOTH, 1972; SCHLAWE, 1980, 1981; WOZENCRAFT, 1993) as a synonym or subspecies of *G. angolensis*. However, a principal component analysis (PCA) by CRAWFORD-CABRAL and PACHECO (1992), that included the two specimens from Boror recognized by ROBERTS (1951) as *G. mossambica*, found that *mossambica* (but not *angolensis*) falls, at least craniometrically, within the phenotypic profile typical of the Rusty-spotted genets. In view of this result, which also supports the older classifications grouping *mossambica* with the *rubiginosa* forms (i.e. with the traditionally called Rusty-spotted genets), *mossambica* is included *a priori* in the present study as a Rusty-spotted genet.

Material and methods

The material upon which this study was based, is composed of ninety four specimens of *Genetta* from several parts of Southern Africa, housed in different museums, namely the Transvaal Museum, Pretoria, South Africa (TM); the Natural History Museum, London, England (BM); the Centro de Estudos of the former Instituto de Investigação Científica de Angola, at Lubango, today the Instituto Superior de Ciências e Educação, Angola (ISCED), and the Centro de Zoologia of the Instituto de Investigação Científica Tropical, Lisbon, Portugal (CZ). These specimens were examined many years ago, their skulls measured and the resulting measurements published (CRAWFORD-CABRAL, 1981). Sixty-six of these specimens represent forms regarded here as Rusty-spotted genets, therefore including, besides sixty-three « *rubiginosa* » specimens, three representatives of *G. mossambica*, and served to establish relationships between them; the remaining were seventeen specimens of *G. tigrina* and eleven specimens of *G. angolensis* used for comparison and to position these two species in regard to the forms of Rusty-spotted genets.

The following twelve cranial measurements were taken on the specimens with a dial calliper: x_1 – Condylo-basal length; x_2 – Braincase breadth; x_3 – Zygomatic breadth; x_4 – Intertemporal constriction; x_5 – Rostrum breadth; x_6 – Basion-inion height; x_7 – Greatest diameter of bullae; x_8 – Interpterygoid width; x_9 – Palate length; x_{10} – M^1- M^1 outside breadth; x_{11} – Upper tooth row C-M^2; x_{12} – Greatest diameter of P^4. All the cranial measurements that form the raw data of the present analyses are listed in a table (Quadro I) in CRAWFORD-CABRAL (1981), with the exception of a specimen of group MOZ (CZ n° 48.00941), the data of which were taken from CRAWFORD-CABRAL (1973).

With the purpose of performing a multiple group discriminant analysis (canonical analysis), the specimens were organized in groups, in accordance with their identification and geographical origin. The groups were defined in such a way as to produce taxonomic units with a level of geographic scale that seemed sensible and suitable for the questions that the study tries to address. The groups considered for the statistical analysis are described in table 1. The approximate

Group name	Group size	Geographical area	Identification and Type Locality	Museum
TRV	16	Mpumalanga Province, South Africa	*G. rubiginosa letabae (a); Klein Letaba, eastern Transvaal*	Transvaal
ZUL	8	KwaZulu-Natal Province, South Africa	*G. rubiginosa zuluensis (a); White Umfolozi, Zululand*	Transvaal
KAL	3	North West Province, South Africa; Botswana	*G. rubiginosa rubiginosa (a)*	Transvaal
NAM	4	North East Namibia	*G. rubiginosa albiventris (a); Maun, northern Botswana*	Transvaal
ZIM	9	Mt. Selinda and Salisbury, Zimbabwe		British; ISCED; Transvaal
ZAM	5	Southwestern Zambia	*G. rubiginosa albiventris (b); Maun, northern Botswana*	British
MOZ	8	Central Mozambique	*G. rubiginosa zambesiana (c); Boror, Mozambique*	British; CZ
ANG	10	Southwestern Angola	*G. rubiginosa gleimi (c); Luanda, Angola*	ISCED
BOR	3	Boror, Mozambique	*G. mossambica (a); Mossimboa, Mozambique*	Transvaal
KNY	17	Knysna, Cape Province, South Africa	*G. tigrina tigrina (a); Cape of Good Hope*	British; Transvaal
MUL	11	Mulundo, Angola	*G. angolensis angolensis (c); Caconda, Angola*	ISCED

I Table 1
Arrangement of the groups for canonical analysis according to the geographical origin and identification of the specimens. *The identification is founded on* (a) Roberts, 1951, (b) Ansell, 1978, and (c) Crawford-Cabral, 1980-81.

locations for the groups of specimens and the geographical areas under study are displayed in figure 1.

For all the analyses we used *Statistica* version 5 software. For the discriminant function analysis the "forward stepwise with casewise deleted" (i.e. without missing values) method was used. The results, in the form of scatter plots of canonical scores for the two most

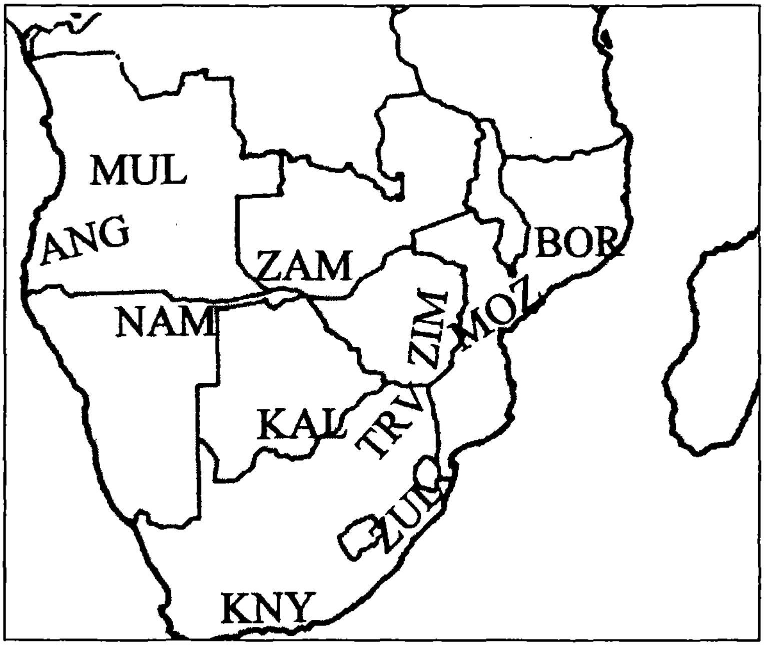

Figure 1
Map of Africa indicating the areas from where the groups considered in the present study originate

discriminant functions or canonical roots, were studied in order to screen those which were most informative and with the greatest statistical robustness. With this purpose the canonical roots were tested for significance using the Chi-Square test. The size of the Wilk's Lambda and the cumulative proportion of explained variance accounted for by each root were also taken into account.

Results

We present here only the results of the analyses, among all those which were undertaken, that allow a clear and synthetic description of the suggested taxonomic arrangement of the Rusty-spotted genets in Southern Africa, and their relationships with other genet species occurring in the same area.

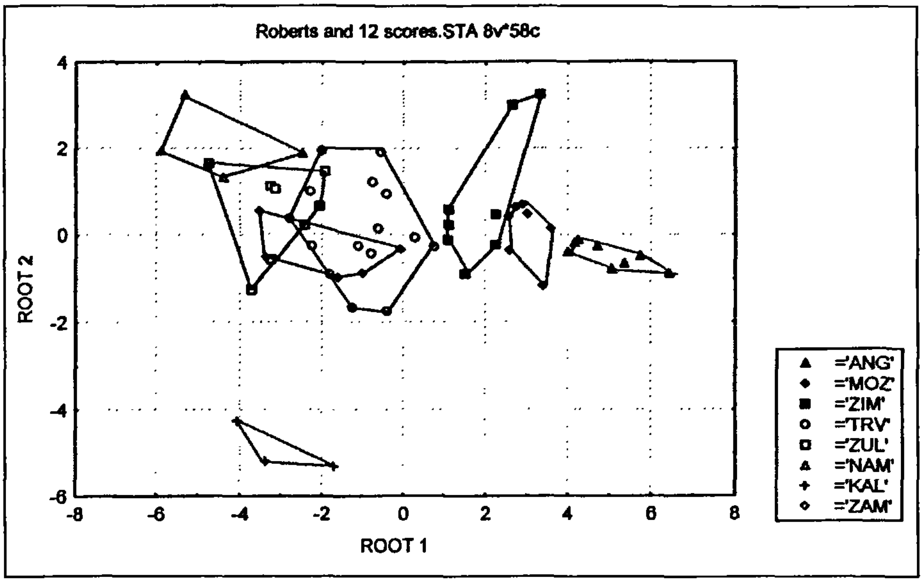

Figure 2

First analysis: projections of the groups ANG, MOZ, ZIM, TRV, ZUL, NAM, KAL and ZAM onto the plan of the first two canonical roots.

The purpose of the first analysis performed was to examine the taxonomic relationships of all the Southern African forms classically regarded as Rusty-spotted genets. It dealt not only with the forms accepted by ROBERTS (1951) as subspecies of *G. rubiginosa*, i.e. *letabae*, *zuluensis*, *albiventris*, *zambesiana* and the form of Botswana and western Transvaal considered by him as the topotypical *rubiginosa*, but also with a genet of southwestern Angola, that CRAWFORD-CABRAL (1969) regarded as a subspecies akin to *gleimi* Matschie, from Luanda. These forms were respectively represented by the groups TRV, ZUL, NAM, MOZ, KAL and ANG; the groups ZAM and ZIM were also included, the first one to test the statement of ANSELL (1960, 1978) that the population from SW Zambia would represent or incline towards *albiventris*, and the group ZIM to get an insight of the taxonomic relationships of populations in eastern Zimbabwe, which until now have been vaguely defined.

The graphic of the projections onto the plan of the first two canonical roots (fig. 2) reveals a fair separation of the groups, in spite of

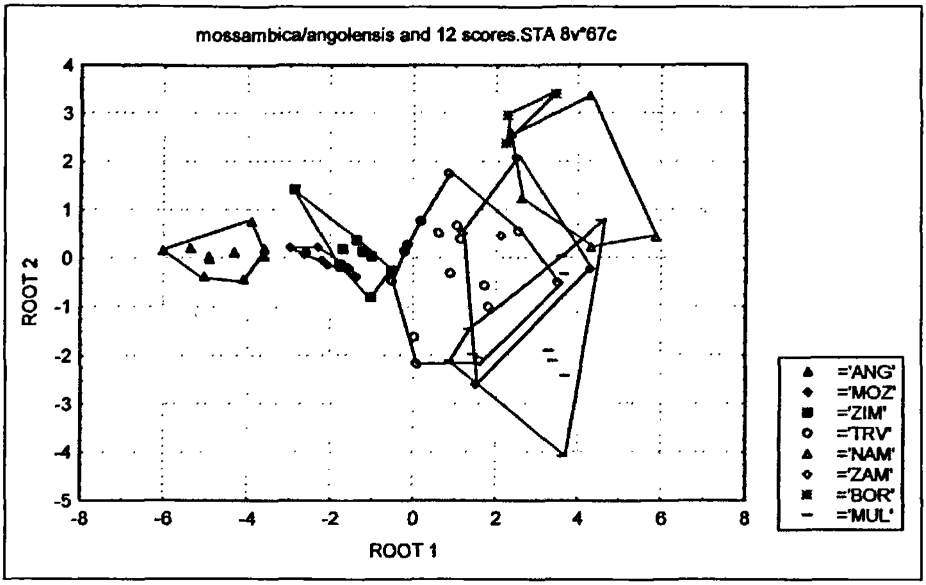

Figure 3
Second analysis: projections of the groups ANG, MOZ, ZIM, TRV, NAM, ZAM, BOR and MUL onto the plan of the first canonical roots.

some overlap that occurs between the groups NAM and ZAM, in the second case even more pronounced, with ZUL and TRV. It is possible to observe a clear separation between the groups ZIM, MOZ and ANG, which are projected on the positive side of the first canonical axis, and all other groups, which, with the only exception of two TRV specimens, are projected on the negative side of the same axis. The importance of skull size in the position of the groups along the first axis is obvious and reflected in the extreme positions of the small-sized *gleimi* (ANG) and the large-sized *albiventris* (NAM).

The aim of the second analysis was to evaluate the status of *mossambica* (BOR) as a Rusty-spotted genet, as suggested by PCA data (CRAWFORD-CABRAL and PACHECO, 1992), but now through the use of canonical analysis. As this form was already also regarded as conspecific with *angolensis* (WENZELL and HALTERNOTH, 1972; SCHLAWE, 1981; ANSELL and DOWSETT, 1988), the group MUL, which represents this species, was also included in the analysis. In

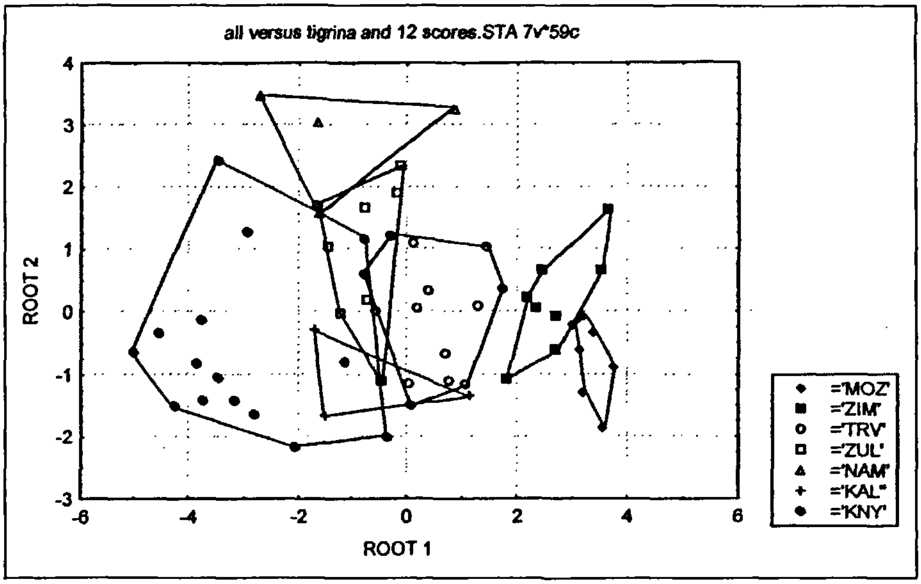

Figure 4
Third analysis: projections of the groups MOZ, ZIM, TRV, ZUL, NAM, KAL and KNY onto the plan of the first two canonical roots.

order to avoid the noise resulting from the redundant presence of too many groups giving the same kind of information that is not essential to understand the status of *mossambica*, the geographical range of the Rusty-spotted genet groups was restricted by the exclusion of the southernmost ones, i.e. KAL and ZUL.

In the scatter plot of canonical scores for the two first canonical roots that resulted from the analysis (fig. 3), it is possible to observe again a fairly clear separation between sets of groups along the first canonical axis. The groups BOR and MUL, both with positive scores in regard to the first root, have their projections distant from one another, BOR with positive scores and MUL mostly with negative scores in the second root.

The objective of the third analysis was to compare forms of Rusty-spotted genets with *G. tigrina* (represented by the group KNY), in order to evaluate the taxonomic relationships between them. In the resulting scatter plot (fig. 4) it is possible to observe that, in spite of

	Standardised Coefficients for Canonical Variables								
	First Analysis			Second Analysis			Third Analysis		
	Variable	Root 1	Root 2	Variable	Root 1	Root 2	Variable	Root 1	Root 2
	x1	- 0,96265	- 0,168368	x1	0,690000	0,420688	x1	- 0,736656	0,037981
	x11	0,05659	0,651040	x3	0,147741	- 0,695789	x4	- 0,567026	- 0,407739
	x3	- 0,26770	- 0,537422	x2	0,439402	- 0,393540	x8	0,107203	0,679333
	x8	0,13123	0,214076	x8	0,240528	0,056656	x12	- 0,184447	0,436636
	x4	- 0,56776	- 0,062913	x7	0,139792	0,081600	x9	- 0,262580	0,423312
	x2	- 0,38943	0,532763	x5	0,422499	0,323198	x2	- 0,372115	0,385000
	x12	- 0,27435	0,209025	x4	0,413720	- 0,265507	x11	- 0,159149	0,260220
	x10	0,20244	0,663861	x9	0,354046	0,427182	x10	- 0,279512	- 0,174369
	x5	- 0,52388	0,571895	x10	0,311606	- 0,252658	x3	- 0,179228	- 0,038186
	x6	- 0,138393	0,260378	x11	- 0,174002	- 0,003242			
Eigenvalue		10,00727	2,109977		8,822047	1,068085		5,254144	1,117620
Cumm. Prop. Variance		77%	93%		78%	88%		72%	87%

Table 2
Standardized coefficients for canonical variables, eigenvalues and cumulative proportions of explained variance for the two canonical roots.

a slight overlap of KNY with both KAL and ZUL, most of the *G. tigrina* specimens are projected as a well detached cloud onto the negative side of both canonical axes.

Table 2 lists, for all three analyses, the standardized coefficients for canonical variables, the eigenvalues and the cumulative proportion of explained variance accounted for by each root. In table 3, the Chi-Square tests and Wilks' Lambda are presented for the canonical roots for the three analyses. It is possible to observe, for any of the three analyses, a total variance of around 90% explained by the two first roots. The roots are significant in accordance with the Chi-Square tests, and the small Wilks' Lambda values indicate that they have a strong discriminatory power.

	Chi-Square Tests with Successive Roots Removed											
	First Analysis				Second Analysis				Third Analysis			
Roots Removed	Wilks' Lambda	Chi-Square	DF	p-level	Wilks' Lambda	Chi-Square	DF	p-level	Wilks' Lambda	Chi-Square	DF	p-level
0	0,012922	197,8712	63	0,000000	0,01545	235,6188	77	0,000000	0,034794	157,84120	54	0,000000
1	0,142237	88,7369	48	0,000321	0,151736	106,5372	60	0,000208	0,217604	71,67880	40	0,001555
2	0,442353	37,1119	35	0,371971	0,313803	65,4830	45	0,024761	0,460802	36,415	28	0,132474

Table 3
Chi-quare tests with successive roots removed for the three canonical analyses.

Discussion

All the analyses seem to indicate a clear separation between the forms represented by the groups ANG, MOZ and ZIM, i.e. *gleimi* and *zambesiana*, and those represented by TRV, ZUL, ZAM and NAM, i.e. *letabae*, *zuluensis* and *albiventris*. This is particularly visible in the scatter plot of canonical scores derived from the first analysis (fig. 2). Certainly, the position of these forms in different clusters is not a reason in itself to accept them as non-conspecific. The fact that ZIM has an intermediate position between MOZ and TRV could even be interpreted as the result of an intergradation between the two groups. However, all specimens in CZ (including flat skins examined for this study) collected in Mozambique from Mambone, south of the Save River, represent *letabae* (*zuluensis* in CRAWFORD-CABRAL, 1973), whereas those from localities from the Manica and Sofala Province, just north of the Save River, represent *zambesiana* (*rubiginosa* in CRAWFORD-CABRAL, 1973). In fact, *zambesiana* specimens are generally smaller, and with smaller and more numerous spots in the coat, than *letabae* individuals (CRAWFORD-CABRAL, 1973). But, even if we accept the presence of a continuous series of forms merging gradually into each others on the eastern part of the range of the southern African Rusty-spotted genet and then the hypothesis of a single species, the situation on the western part of the range is quite different. Indeed, both the largest-sized *albiventris* and the smallest-sized *gleimi* occur in southern Angola, probably separated by the Cunene River as suggested by the examination of flat skins from both sides of this river, and without any signal of intergradation. So, the presence of geographical barriers like rivers separating populations from the two sets of groups opens the possibility that *G. rubiginosa* in Southern Africa might not be one but two separate taxa, possibly species.

This case seems to be an example of a "circle of species", where the intermediate forms appear as representing different stages of a polytypic species, but the extreme forms behave as separate species. In fact, circles of species are superspecies (MAYR and ASHLOCK, 1991), and most likely when referring to the forms included by Roberts (1951) in *rubiginosa* we are dealing not with a single species, but with a superspecies. If this is the case here, then *zambesiana* and *gleimi* may represent the same allospecies, to which the proposed name in the present paper is *G. zambesiana*, with *letabae, zuluensis* and *albiventris* being another allospecies, the name of which, according to the priority rule, should be *G. letabae.*

More difficult to interpret is the form represented by KAL, projected far from all other groups on the second canonical root, but with similar regression coefficients for the first root to TRV, ZAM, ZUL and NAM. It may represent a small population of southern Botswana, northern Cape Province and western Transvaal, to which the closest neighbour seems to be the eastern Transvaal (TRV) population. The most moderate taxonomic procedure would be to regard such a form as a subspecies of *G. letabae*, yet still innominate, in view that the name *rubiginosa*, as ascribed by ROBERTS (1951) to that form, should not be used for any Rusty-spotted genet (CRAWFORD-CABRAL and FERNANDES, 1999).

The second analysis suggests, considering the separate positions of their projections, that *mossambica* and *angolensis* are different species. Moreover, the projection of BOR is very far from MOZ and ZIM, which are their nearest geographical neighbours, which means, agreeing with ROBERTS' (1951) opinion, that *mossambica* and *zambesiana* are two quite different forms. On the other hand, the projection of *mossambica* near to *albiventris*, two forms with quite different external traits, may only reflect craniometrical similarity without taxonomic value. The same can be said of the projection of *angolensis* near to *letabae* and *albiventris.*

By observing the scatter plot of canonical scores for the third analysis (fig. 4) where the majority of the projections of KNY are fairly isolated, in spite of some overlap with ZUL and KAL, no reasons are found to support *G. tigrina* and *G. letabae* as conspecific. The opinion that they are separate species is therefore maintained.

Conclusion

We can conclude that in Southern Africa there are three species of *Genetta* that can be considered under the colloquial name Rusty-spotted genets. The three species are: *G. letabae*, G. *zambesiana* and *G. mossambica.* The first two are parapatric and most likely constitute a superspecies, comprising all the forms placed by ROBERTS (1951) in *G. rubiginosa. Genetta mossambica* and *G. angolensis* are allopatric in relation to each other and both are sympatric with *G. zambesiana. Genetta tigrina* has an isolated distribution in the Cape Province and a plausible contact with *G. letabae* in Natal and Orange Free State.

Considering the overall picture in Southern Africa, it is quite probable that these five species of *Genetta,* all of them characterised by three to five longitudinal rows of rusty, black with rusty hairs or even deep black spots on each side of a mid-dorsal line and by 6 to 9 black tail rings, confluent to the always black tail tip, form a species-group (MAYR and ASHLOCK, 1991). It is also possible that the remaining forms, from other parts of Africa, normally accepted as Rusty-spotted genets, and even *G. pardina,* are part of such species-group.

Although consistent with the results obtained in this study, and also with accumulated evidence in the literature, it is clear that the conclusions that we draw here are still quite speculative and exploratory. For instance, and considering that the range of the Rusty-spotted genets is larger than the geographic scope of this study, it is necessary to perform a study concerning the entire area of the distribution before definite taxonomic conclusions may be put forward. Regarding the urgency of studying such a problematic group as the Rusty-spotted genets with modern tools of taxonomic research, one of us (F. C.) has begun to investigate the internal structure of this complex of forms and its relationships with akin species, as part of a PhD on the phylogeny of cryptic species complexes within the genus *Genetta*, using molecular markers. Besides data coming from sequencing of specific mtDNA regions, it is obvious that information resulting from other kinds of molecular research, such as cytogenetical and biochemical ones, are also most welcome in the production of a more robust Rusty-spotted genets' taxonomy.

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