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Morphological and morphometrical analyses of three cryptic species of *Tatera* Lataste, 1882 (Rodentia : Muridae) from West Africa

Laurent Granjon

Laboratoire de Mammalogie (CBGP, UR 022), IRD, BP 2528, Bamako, Mali & UMR "Origine, Structure et Evolution de la Biodiversité", Dept "Systématique et Evolution", Museum National d'Histoire Naturelle, 55 rue Buffon, 75005 Paris, France

Corresponding author : Laurent Granjon, e-mail : granjon@ird.fr

ABSTRACT. Three chromosomally well-differentiated but morphologically similar species of the Gerbilline rodent genus *Tatera* occur in West Africa, namely *T. gambiana*, *T. guineae* and *T. kempi*. In order to find reliable diagnostic characters, morphological and morphometrical analyses were performed on samples of these three species from Mali, the only country where they are known to occur sympatrically. Body measurement comparisons show that *T. guineae* has a longer tail and hindfoot, and *T. gambiana* a shorter ear, relative to the two other species. Skull measurements are less variable between species as only a larger upper tooth row characterizes *T. kempi*, and a shorter tympanic bulla length *T. guineae*. Conversely, geographically distant samples of *T. kempi* from Mali and Chad differ mainly for skull measurements. There is a wide overlap between the ranges of values recorded in the three species. Principal Component and Discriminant Analyses of skull measurements highlight the distinctiveness of *T. guineae*, whose sample is clearly separated from those of *T. kempi* and *T. gambiana*. All these results validate the status of morphologically cryptic species for *T. kempi* and *T. gambiana*, long treated as synonymous. *Tatera guineae* is the most differentiated, but the diagnosis of an individual specimen may prove difficult due to the observed interspecific overlap in all the characters considered.

KEY WORDS : Gerbilline rodents, *Tatera,* skull measurements, multivariate analyses, phenetic similarity.

INTRODUCTION

The Gerbilline rodent genus *Tatera* Lataste, 1882 is widely distributed in all sub-Saharan Africa, occupying a variety of habitats in northern and southern savannas to the margins of the rainforest. MUSSER & CARLETON (1993) recognized twelve species in the genus, the majority of which occur in southern or eastern Africa. Only two of these can be considered as having an exclusive West African range, namely *T. guineae* Thomas, 1910 and *T. kempi* Wroughton, 1906. The first one is characteristic of the Sudan savannas from Senegal, Guinea and Sierra Leone to Burkina Faso and Togo, whereas the second ranges from Sudan to Guinean savannas and from Sierra Leone to eastern Chad and northern Central African Republic. A third species, *T. gambiana* Thomas, 1910, should now be re-evaluated as present in West Africa : Long treated as synonym of *T. kempi*, *T. gambiana* has proven to be a distinct biological species, which main range covers Sahel savannas of Senegal and Mali (MATTHEY & PETTER, 1970; VOLOBOUEV et al., in prep.), with a proposed eastward extension to eastern Niger (DOBIGNY et al., 2002a). On the other hand, the presence of *T. robusta* (Cretzschmar, 1830) in West Africa should still be considered doubtful, as it only relies on one single specimen from Burkina Faso (BATES, 1985).

Tatera taxonomy and systematics has always been a matter of debate. As early as 1906, WROUGHTON highlighted the difficulty in finding and using unambiguously diagnostic morphological characters to recognize species in the genus. This problem has been repetitively mentioned by those who tried to organize the variability observed in *Tatera* into a coherent taxonomic arrangement (PIRLOT, 1955; DAVIS, 1966; ROSEVEAR, 1969; MATTHEY & PETTER, 1970; TRANIER, 1974; BATES, 1985 & 1988). Since the first karyotypic data obtained by MATTHEY (1954), cytogenetics has proven to be of great help in species identification, and chromosome data have accumulated for this genus (see QUMSIYEH & SCHLITTER, 1991 for a review until 1990; COLANGELO et al., 2001; VOLOBOUEV et al., in prep.). As for West African species, there is now a general agreement on karyotypic characteristics of *T. gambiana* (2n=52), *T. guineae* (2n=50) and *T. kempi* (2n=48; COLANGELO et al., 2001; VOLOBOUEV et al., in prep.).

These three species have been found in southern Mali, which as such represents a unique crossroads for this genus in West Africa. Based on series of karyotyped and therefore unambiguously determined specimens, we try here to find morphological and/or morphometrical characteristics enabling their determination in the field or from museum specimens. Interspecific variability of the characters used was assessed in *T. kempi* through the comparative study with a sample from Chad, i.e. the eastern extreme of the species range.

MATERIALS AND METHODS

All the specimens used in this study were karyotyped following standard procedures (see GRANJON & DOBIGNY, 2003 for instance). They are currently deposited as skin and skull specimens in the small mammal collection of the Institut de Recherche pour le Dévelopement, Bamako and will ultimately be housed at the Museum National d'Histoire Naturelle, Paris. The samples from Mali are as follows : 7 *T. kempi* (M177, M178, M179, M180, M196, M197, M198) from Founé (12°50'N - 4°42'W); 15 *T. gambiana* from various localities of west (Sekokoto : 13°31'N – 10°45'W, N=1 : M4178; Maréna : 14°38'N - 10°36'W, N=2 : M4183, M4190) and central south (Katibougou : 12°30'N – 8°6'W, N=1 : M4412; Samanko : 12°32'N – 8°5'W, N=7 : M4909, M4912, M4916, M4918, M4954, M4955, M4978; Samaya : 12°34'N – 8°4'W, N=4 : M194, M195, M199, M202); and 24 *T. guineae* from various localities along the Guinean border, mainly in the Mts Mandingues region (Kolobo : 13°15'N – 11°31'W, N=1 : M4170; Gainsoa : 12°27'N – 10°15'W, N=1 : M4723; Balamansala : 12°11'N – 8°48'W, N=8 : M4670, M4694, M4709, M4753, M4796, M4858, M4864, M4902; Kigniélendo : 12°20'N – 8°32'W, N=1 : M4664; Kangaba : 11°58'N – 8°25'W, N=1 : M188), in the central south (Niamana : 13°01'N – 8°14'W, N=4 : M4015, M4019, M4093, M4111; Kalifabougou : 12°57'N – 8°11'W, N=7 : M4037, M4044, M4048, M4099, M4104, M4107, M4114) and near the border with Burkina Faso in the south east (Mamouroubougou : 11°12'N – 5°29'W, N=1 : M4879). Additionnally, 23 specimens of *T. kempi* from the Zakouma National Park in south eastern Chad (10°41'N – 19°29'E) were included (I16, H2, O2, O5, O9, O26, O27, O28, O29, O38, O45, O46, P'3, Q10, Q17, Q19, Q20, Q27, Q43, R6, R7, R8, R13). All specimens were adult, most (60 of 67) belonging to age classes 2 or 3 following the 4-class system of BATES (1985) based on dental wear.

The following classical body measurements were taken, to the nearest gram or millimetre : Weight (Wt), head and body length (HB), tail length (T), ear length (E) and hindfoot lenth, excluding claw (HF). A selection of 11 skull measurements was made, based on their presumptive usefulness as revealed by previous studies, especially those of BATES (1985, 1988) and COLANGELO et al. (2001) : Greatest length of skull (GLS), condylobasal length (CBL), greatest width of skull (GWS), breadth of braincase (BB), interorbital constriction (IC), rostral width (RW), rostral length (RL), trans molar width (TMW), tympanic bulla length (TBL), mandible length (ML) and upper toothrow length (UTR). They were taken as described in BATES (1988), to the nearest 0.1mm. Skulls were examined for possible diagnostic characters. Special attention was paid to the first lower molar, the first lamina of which was characterized following the patterns illustrated in BATES (1988).

Measurements were compared by means of student t tests. Eight skull measurements were used to run Principal Component (PCA) and Discriminant (DA) analyses, using SYSTAT 8.0 (1998). GLS, RL and ML were abandoned because they could not be taken in a number of specimens and/or they were highly correlated with other characters. PCA was run using the covariance matrix on log-transformed data, whereas DA gave better results based on non-transformed data.

RESULTS

The mean and standard deviation values, as well as ranges of all measurements taken on the 4 *Tatera* samples, are summarized in Table 1. Distributions of individual dental wear data were compared between samples, prior to other statistical tests : None of the differences observed was found significant via non parametric Wilcoxon tests (P=0.083 between *T. kempi* from Mali and from Chad, P=0.194 between *T. kempi* and *T. gambiana* from Mali, P=0.059 between *T. kempi* and *T. guineae* from Mali, and P=0.924 between *T. gambiana* and *T. guineae*). Based on the hypothesis that age is one of the important determinants of dental wear in rodents, this suggests that the samples compared can be considered of similar age, which makes the following comparisons more relevant. Sexual dimorphism was tested for all body and skull measurements in the three largest samples (*T. kempi* from Chad, *T. gambiana* and *T. guineae* from Mali), using Mann-Whitney U test. Significant differences ($0.01<P<0.05$) were found in only 5 (of 48) instances, males being in all cases larger : Wt, HB and T in *T. kempi* from Chad, Wt and IC in *T. gambiana* from Mali. According to these results, sexual dimorphism was considered negligible in the samples here used and males and females were pooled in subsequent analyses.

Given the relatively small sample sizes, the differences recorded by student t tests were conservatively quoted as significant only when $P<0.01$. *T. gambiana* and *T. kempi* from Mali are the two samples showing the fewer number of differences (n=3), whereas *T. gambiana* and *T. guineae* on the one hand, *T. kempi* from Mali and *T. kempi* from Chad on the other hand, display significant differences for 7 measurements each. Regarding body measurements in the Malian samples, *T. guineae* is characterized by a longer tail and longer hindfoot than both *T. gambiana* and *T. kempi*, the latter sharing a long ear with *T. guineae* relative to *T. gambiana*. Skull measurements do not show many significant differences between species. The main one concerns UTR, significantly longer in *T. kempi* than in the two other species, and TBL, significantly shorter in *T. guineae* than in the two other species. Overlap between ranges of values is the rule, with the exception of tail length in the sample of *T. guineae* when compared with the samples of the two other species from Mali. Differences between the two geographically distinct samples of *T. kempi* often concern measurements that are not significantly variable between species in Malian samples, and are mainly skull ones.

The distribution of individuals of the four study samples according to the morphology of their first lower molar first lamina is summarized in Table 2. Most of the *T. gambiana* and *T. kempi* specimens are characterized by a M_1 first lamina opening posteriorly, *vs* only half of the *T. guineae* specimens, the other half having their first lamina divided into 2 islands.

TABLE 1

Body and skull measurements (in mm) of 4 samples of *Tatera*, and associated student t tests results (*p<0.01; **p<0.001; ***p<0.0001)

		Wt	HB	TL	H	E	GLS	CBL	GWS	BB	IC	RW	RL	TMW	TBL	ML	UTR
	N	15	15	11	15	15	12	14	12	15	15	14	11	13	15	15	14
T. gambiana Mali	Mean	114.47	153.33	144.82	30.83	19.70	38.20	34.63	19.10	15.70	6.35	5.27	13.14	8.16	10.17	24.29	5.79
	St. Deviation	30.208	13.819	8.542	1.397	1.207	1.523	1.388	0.998	0.400	0.302	0.289	0.905	0.312	0.415	1.413	0.164
	Range	78-180	139-188	128-160	29-35	18-22	36.5-41.2	31.8-36.7	17.5-20.7	15.1-16.5	6.0-7.0	4.9-5.9	11.8-14.7	7.8-8.7	9.2-10.7	20.9-26.4	5.4-6
	N	24	24	5	23	24	20	24	19	24	24	24	19	24	24	20	23
T. guineae Mali	Mean	87.13	143.00	173.20	34.87	21.21	37.85	33.87	18.56	15.50	6.55	5.56	14.28	7.94	9.68	22.93	5.65
	St. Deviation	22.046	12.857	6.496	1.236	0.871	1.864	1.737	1.175	0.434	0.308	0.399	1.122	0.395	0.593	1.215	0.178
	Range	50-136	116-164	163-179	32-37	20-23.5	33.5-40.6	30.4-36.4	16.7-21.2	14.9-16.3	6-7.3	4.9-6.9	11.5-15.8	7.1-8.5	9-11.6	20.3-25.6	5.3-5.9
	N	7	7	5	7	7	5	6	6	6	7	7	6	6	6	6	6
T. kempi Mali	Mean	77.71	138.14	138.20	32.57	21.86	39.22	35.90	19.83	15.92	6.39	5.33	13.68	8.25	10.67	23.95	6.03
	St. Deviation	12.134	12.522	12.696	1.512	1.069	0.712	0.626	0.680	0.392	0.344	0.111	0.325	0.226	0.216	0.243	0.175
	Range	56-90	120-155	120-150	31-34	20-23	38.1-40	35-36.7	18.6-20.3	15.4-16.4	5.9-6.7	5.1-5.4	13.3-14.2	8-8.5	10.4-10.9	23.6-24.3	5.7-6.2
	N	23	23	19	23	23	19	23	22	23	23	23	17	23	23	21	23
T. kempi Chad	Mean	71.96	138.96	149.26	31.87	20.07	36.79	34.00	18.37	15.65	6.32	5.03	12.59	7.73	10.50	23.44	5.89
	St. Deviation	12.517	9.883	8.937	1.245	1.237	1.422	1.331	0.672	0.413	0.223	0.260	0.604	0.268	0.389	0.931	0.183
	Range	51-101	114-159	127-170	28-33.5	17-21.5	33.1-40	30.4-37.2	16.9-20.5	14.7-16.4	6-6.9	4.5-5.7	11.5-14.1	7.3-8.6	9.6-11.2	21.1-25.8	5.3-6.1
gambiana vs guineae		*	NS	***	***	***	NS	NS	NS	NS	NS	NS	*	NS	*	*	NS
gambiana vs kempi		*	NS	NS	NS	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*
guineae vs kempi		NS	NS	**	**	NS	NS	*	NS	NS	NS	NS	NS	NS	**	NS	***
kempi Mali *vs kempi* Chad		NS	NS	NS	NS	*	*	*	***	NS	NS	*	**	**	NS	NS	NS

TABLE 2

Morphology of the first lower molar first lamina (see Bates, 1988 for an illustration)

	T. gambiana	*T. guineae*	*T. kempi* (Mali)	*T. kempi* (Chad)
1st lamina open posteriorly	12	8	5	22
1st lamina open anteriorly	0	0	0	0
1st lamina divided into 2 islands	1	8	1	0
Other	0	0	1	1

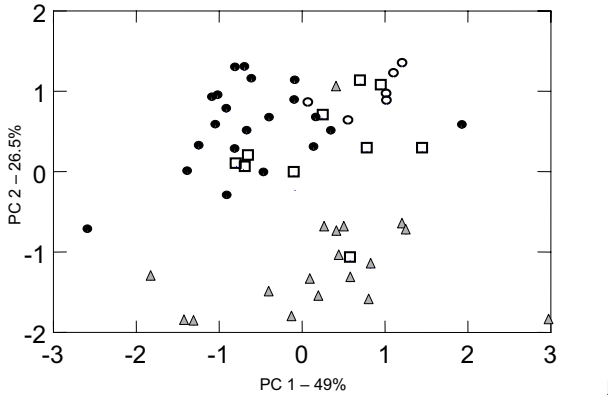

Fig. 1. – Scatter plot of the first two Principal Components (F1 x F2) of the PCA run on 8 log-transformed skull measurements of the four samples of *Tatera* from Mali (*T. gambiana* - squares, *T. guineae* - triangles & *T. kempi* – open circles) and Chad (*T. kempi* – black circles).

The scatter plot of the first two principal components is represented in Fig. 1 (representing more than 75% of the total variance of the original matrix). All the characters correlate positively with PC 1, which thus represents an overall size axis. The main loadings on this axis are from RW, GWS, CBL, TMW and IC. The dispersion of individuals of the four study samples along this factor matches quite well the age-related differences in size observed within each sample. Most of the inter-samples differentiation occurs along PC 2, which mainly separates *T. guineae* from the other three samples. The variables which contribute the most to this discrimination are TBL (positive loading) and RW (negative loading). Overlap between the two *T. kempi* and the *T. gambiana* samples is important, and stay so along PC 3 or 4 (not shown).

The scatter plot of the first two discriminant vectors represents more than 95% of the total dispersion among the study samples (Fig. 2). The associated classification matrix indicates that all *T. guineae* (14/14) and *T. kempi* from Mali (6/6) are correctly classified by the analysis, *vs* only 9 of 10 *T. gambiana* and 19 of 21 *T. kempi* from Chad, yielding an overall value of 94% of well-classified individuals.

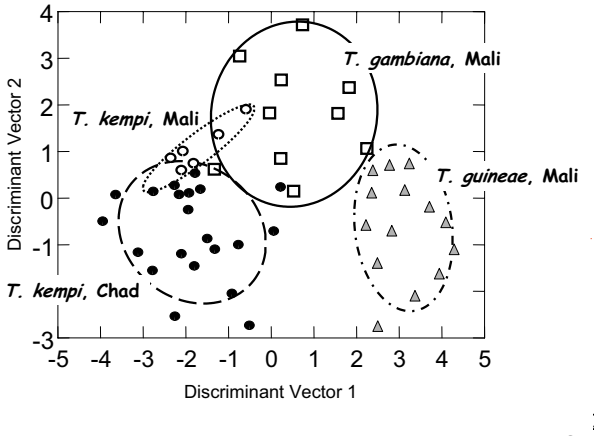

Fig. 2. – Scatter plot of the first two Discriminant Vectors from the DA of 8 raw skull measurements of the four samples of *Tatera* from Mali (*T. gambiana*, *T. guineae* & *T. kempi*) and Chad (*T. kempi*). Confidence ellipses drawn using "Sample" option with *P*=0.683.

The hierarchical classification (Single Linkage Method) based on Mahalanobis distances between group means (Fig. 3) shows that the two *T. kempi* samples are phenetically the most similar, *T. guineae* being the most divergent. When both *T. kempi* samples are pooled in DA, the overall percentage of well-classified individuals remains 94%, (2 *T. kempi* and 1 *T. gambiana* misclassified). When only samples from Mali are considered, this value raises to 97%, only one *T. gambiana* being mistaken for a *T. kempi*.

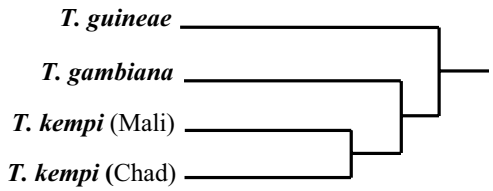

Fig. 3. – Hierarchical classification (single linkage method) based on Mahalanobis distances between the four samples of *Tatera* studied in DA (cf Fig. 2).

DISCUSSION

The validity of the various characters that have been used to distinguishing between species and species groups in *Tatera* has been critically discussed by DAVIS (1966) and ROSEVEAR (1969). DAVIS (1966) distinguished an *afra* and a *robusta* group based on a series of characters showing a relatively large degree of overlap. Among the 3 species studied here, *T. kempi* and *T. gambiana* are considered to belong to the *afra* group, and *T. guineae* to the *robusta* one. As a matter of fact, the general coloration of *T. kempi* and *T. gambiana* is usually quite dull, their pelage is rather harsh and their tail shorter or subequal than head and body, without a densely haired terminal pencil while the pelage of *T. guineae* is more silky with a brighter coloration, and its tail is usually much longer than head and body, with a marked terminal pencil of

hairs. These tail characteristics appear to be reliable whenever the tail is complete, while pelage aspect is more subject to individual variation.

Similarly, skull characters are difficult to associate to one or another species. No one has been found to unambiguously characterize any of the three species here studied. Even the morphology of the zygomatic plate, said to project less forward in *T. guineae* than in other West African species by ROSEVEAR (1969), can be of ambiguous interpretation. The morphology of the M_1 first lamina used by BATES (1988) to distinguish between *T. valida valida* and *T. valida kempi* also diplayed variability within each sample. However, it proved to be less variable in both the *T. kempi* samples studied here than in the one, mainly from Benin, analysed by COLANGELO et al. (2001). Here, and as in *T. gambiana*, the first lamina opens posteriorly in the vast majority of individuals, as supposed to be the rule in *T. kempi* according to BATES (1988).

Measurements give useful information on species characteristics, but they can hardly be used on an individual basis to identify a given specimen unambiguously, as the range of values overlap widely in most cases. The same was observed by BATES (1985) in his comparative analysis of cryptic species from East Africa, namely *T. robusta*, *T. nigricauda* (Peters, 1878) and *T. phillipsi* (de Winton, 1898). This casts doubt on the absolute diagnostic value of some of the criteria proposed by ROSEVEAR (1969) and resumed by MATTHEY & PETTER (1970) to distinguish between *Tatera* species in West and Central Africa (e.g. molar row length or bullae length, but see hereunder). As said above, tail length is especially helpful in discriminating *T. guineae* from the other species, as is hind foot length. Combining these two measurements, in bivariate plots, clearly separate *T. guineae* from the two other species (not shown here due to scarcity of data on tail length). As for skull measurements, the short bullae of *T. guineae* and the long molar row of *T. kempi* were already used by ROSEVEAR (1969) in his determination key for West African species of *Tatera*. The large maxillary tooth row in *T. kempi* was also mentioned by COLANGELO et al. (2001) in their sample from Benin, when compared with data on *T. nigrita* WROUGHTON, 1906 (= *T. valida* Bocage, 1890 in MUSSER & CARLETON, 1993) from Chad published by TRANIER (1974). However, comparing skull measurement data of *T. kempi* from Mali or Chad with those on *T. kempi* from Benin presented by COLANGELO et al. (2001) shows that the latter are systematically larger. This trend is not associated with an older mean age of the sample from Benin, as the differences of dental wear distribution between this sample and the two *T. kempi* ones of our study are not significant (Wilcoxon non parametric test, P=0.339 with Malian sample, P=0.837 with Chadian sample). Conversely, it could be linked with the way in which the measurements were taken (experimental bias), but may also illustrate a true geographical variation. The latter interpretation is reinforced by the differences observed here between the samples from Chad and Mali. It has also to be underlined that none of the variables used in bivariate representations by BATES (1985, 1988) to separate between East African species proved to be of use here (GLS vs RW or BB; RW vs RL), showing again the great similarity between the skulls of the samples under study.

Multivariate analyses confirmed the distinctiveness of *T. guineae*, which even appeared well distinct in PCA ordination. Conversely, *T. gambiana* and *T. kempi* still show some overlap in the distribution of their individuals in the DA space. This confirms the validity for West African species of the distinction between the *afra* and *robusta* groups made by DAVIS (1966). Within the species of the *afra* group, the percentage of misclassified individuals between *T. kempi* and *T. gambiana* was weak, which makes it possible to envisage successful assignation of unknown individuals with rather great confidence based on this kind of analyses. For that purpose, sample sizes of unambiguously determined individuals should be enlarged, so that age-related (and possibly sex-related) variation can be taken into account more precisely. But even with such precautions, one should keep in mind that this kind of use should be restrained to geographically well-defined regions : Geographical variation, here illustrated between samples of *T. kempi* from Mali and Chad, is always important and counfounding in such groups of cryptic species, a qualifier that certainly applies to these West African *Tatera*, as it does for East African ones (BATES, 1985) or for the related genus *Taterillus* Thomas, 1910 (DOBIGNY et al., 2002b).

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