FIRST APPROACH ON THE SKULL MORPHOLOGY OF THE BLACK RAT (RATTUS RATTUS) FROM TERCEIRA AND SÂO MIGUEL ISLANDS (AZORES ARCHIPELAGO)

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FIRST APPROACH ON THE SKULL MORPHOLOGY OF THE BLACK RAT (*RATTUS RATTUS*) FROM TERCEIRA AND SÃO MIGUEL ISLANDS (AZORES ARCHIPELAGO)

RAMALHINHO M.G.[(1)], *MATHIAS M.L.*[(1)], *SANTOS-REIS M.*[(1)], *LIBOIS R.*[(2)], *FONS R.*[(3)], *PETRUCCI-FONSECA F.*[(1)], *OOM M.M.*[(1)] *& COLLARES-PEREIRA M.*[(4)]

[(1)] *Centro de Biologia Ambiental da Universidade de Lisboa, Campo Grande, Edifício* C_2*, 1700 Lisboa, Portugal*
[(2)] *Institut de Zoologie, Université de Liège, quai Van Beneden, 22 B 4020 Liège, Belgique*
[(3)] *Laboratoire Arago, Université P.-et-M.-Curie (Paris 6), CNRS URA 2156, F 66650 Banyuls-sur-Mer, France*
[(4)] *Laboratório de Leptospiras, Instituto de Higiene e Medicina Tropical, Rua da Junqueira 96, 1300 Lisboa, Portugal*

SKULL MORPHOLOGY
SIZE INCREASE
BLACK RAT
AÇORES ARCHIPELAGO

ABSTRACT. – The present paper deals with an analysis of metric (cranial measurements) and non-metric (epigenetic cranial characters) variation in black rat populations from S. Miguel and Terceira islands compared to a continental sample. Assuming the Azorean rats originate from the European continent, we tested the similarity between the samples, considering only adult and subadult animals. Having verified that there was no sexual dimorphism in the characters studied, we computed discriminant functions and made a PCA with the most discriminant variables. The three samples are clearly separated by these functions, the Azorean rats showing a larger general skull size and differing between the two islands. The Mean Measure of Divergence (MMD), based on non-metric cranial traits frequencies, was also used to express the interpopulational differences : the rats of Terceira differ significantly either from the continental ones or from those of S. Miguel. Finally, the possible origin of these differences is discussed.

MORPHOLOGIE CRÂNIENNE
AUGMENTATION DE LA TAILLE
RAT NOIR
AÇORES

RÉSUMÉ. – Ce travail traite de la variation des caractères métriques (mensurations crâniennes) et non-métriques (caractères épigénétiques du crâne) de populations de Rat noir des îles de San Miguel et de Terceira, comparées à un échantillon d'origine continentale. En considérant que les Rats des Açores proviennent du continent Européen, la similarité entre échantillons a été testée en ne prenant seulement en compte que les individus adultes et sub-adultes. Après avoir vérifié qu'il n'y avait pas de dimorphisme sexuel dans les caractères étudiés, nous avons mesuré les fonctions discriminantes et fait une ACP avec les variables les plus discriminantes. Les trois échantillons sont nettement separés par ces fonctions, les Rats des Açores montrent une taille générale du crâne plus grande et des différences entre les deux îles. La MMD, basée sur les caractères non-métriques du crâne a également été utilisée pour exprimer les différences interpopulationelles : les Rats de Terceira diffèrent de façon significative des Rats du continent ou des Rats de San Miguel. Finalement, l'origine de ces différences est discutée.

INTRODUCTION

According to historical records, the black rat (*Rattus rattus*) was introduced into the Azores archipelago when the first two islands (Santa Maria and São Miguel) were officially discovered around 1427 by Portuguese navigators. In fact, due to their privileged location in mid-North Atlantic, these islands had long before been visited not only by the Portuguese but as well by Carthaginians, Spanish and Greek sailors (e.g. Chaves, 1911 ; Frutuoso, 1978).

When the first settlers arrived to São Miguel, they found a reasonable number of sheep and cattle bones, which confirms a previous human presence on the island. So, although the available data on the introduction of terrestrial mammal species, reports them as essentially proceeding from Portugal and probably from northern Europe under the influence of Flemish colonizers (e.g.

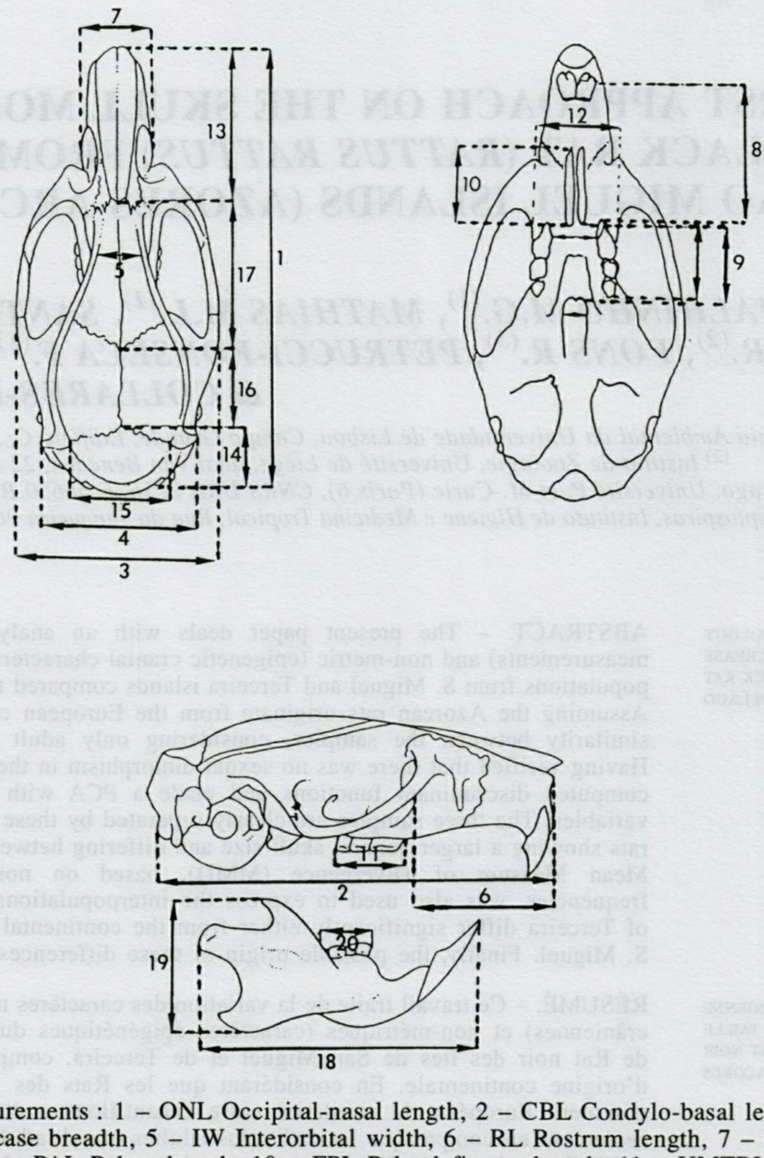

Fig. 1. – Cranial measurements : 1 – ONL Occipital-nasal length, 2 – CBL Condylo-basal length, 3 – ZB Zygomatic breadth, 4 – BB Braincase breadth, 5 – IW Interorbital width, 6 – RL Rostrum length, 7 – RW Rostrum width, 8 – DL Diastema length, 9 – PAL Palate length, 10 – FPL Palatal fissure length, 11 – UMTRL Length of upper molar tooth row, 12 – MW Width across upper molars, 13 – NL Nasal length, 14 – IPL Interparietal length, 15 – IPW Interparietal width, 16 – PL Parietal length, 17 – FL Frontal length, 18 – GML Greatest length of mandible, 19 – HML Mandible height, 20 – LMTRL Length of lower mandibular tooth row.

Drouet, 1861), we may wonder if black rats have or not been introduced earlier than suspected.

Assuming an European origin for the founder *R. rattus* population we here report the findings of a preliminary study on the morphological evolutionary trend of Azorean black rats (Libois *et al.*, 1996). The hypothesis tested is the theoretical assumption of similarity between neighboring insular populations (from the islands of São Miguel and Terceira), presumably with similar ancestors and date of origin and the greater distinctiveness of a mainland Portugal population, farther apart from which they may have originated (Patton *et al.*, 1975).

STUDY AREA

The Azores archipelago lies in the middle of the North Atlantic, roughly between the coordinates 37° to 40 °N and 25° to 31 °W. The distance from the Azores to mainland is about 1 390 km, calculated from Cabo da Roca in Portugal, the most western cape of the European continent.

The nine islands of the archipelago, all of volcanic origin, are aligned on a WNW-ESE trend and accordingly to their relative location are included in three groups : the western group (Corvo and Flores), the central group (Faial, Pico, Graciosa, São Jorge and Terceira) and the eastern group, which is the nearest from Portugal (São Miguel and Santa Maria). São Mi-

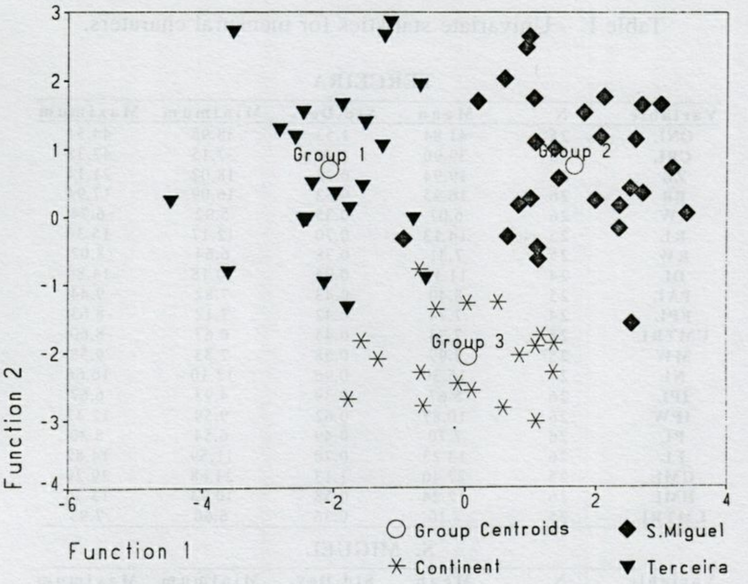

Fig. 2. – Canonical discriminant analysis of all samples.

guel is the largest island in the whole archipelago (750 km^2) and, as mentioned before, one of the first to be discovered. Terceira, lying 140 km NW of São Miguel and 1 764 km from mainland Portugal, has an area of about 450 km^2 and, as indicated by its name (Terceira means 'third') was the third island found, about five years later than São Miguel.

For more details and a map of the Azorean Archipelago see Mathias *et al.* (in prep.).

MATERIAL AND METHODS

The specimens studied, a total of 84 adult or subadult black rats, were organized in 3 samples in accordance to their geographic origin : Terceira (N = 26), São Miguel (N = 33) and mainland Portugal (N = 25, scattered on the central and southern regions). Age was defined on the basis of the skull strengthening and tooth wear.

Assessment of morphological intergroup divergence was based on two sets of cranial variables : mensural and 'epigenetic' or non-metrical variables.

Accordingly, from each specimen 20 skull measurements were taken, as shown in Figure 1. All measurements were made with a Mitutoyo dial caliper, to the nearest 0.01 mm, always from the right side of the skull and by the same person. The non-metrical variation was tested using frequency of occurrence of foraminal variants proposed by Berry & Searle (1963). The following 13 'epigenetic' traits also scored on the right side of each skull were coded as present or absent : 1 – Frontal foramen double ; 2 – Accessory maxillary foramen ; 3 – Foramen palatinum majus double ; 4 – Foramen hypoglossi double ; 5 – Accessory mental foramen ; 6 – Accessory foramen incisivum ; 7 – Foramen incisivum ; 8 – Preorbital foramen double ; 9 – Lacrimal foramen ; 10 – Foramen oval double ; 11 – Foramen oval open ; 12 – Fenestra flocculi ; 13 – Mandibular foramen.

Statistics which are used to analyse the metric variability included several tests performed (SPSS software, Norusis, 1992) in accordance with the following sequence and objectives :

i) a two-way ANOVA, on a character-by-character basis to assess the effects of sex and local on the divergence among samples ;

ii) discriminant analyses to maximize the divergence among samples separately computed using the metric and non-metric characters ;

iii) a Principal Component Analyses based on a correlation matrix of those variables denoting a higher discriminating power.

To estimate genetic divergence among samples, the frequencies of occurrence of epigenetic variants were used according to the formulas proposed by Berry (1964) :

$$MMD = (\theta_1 - \theta_2)^2 - (1/n_1 + 1/n_2)$$

for any character

where θ is the angular transformation in radians of relative frequency of variants p [$\theta = \arcsin(1-2p)$] and n_i is the sample size. The standard deviation of MMD, expressed by the equation $SD_{MMD} = \sqrt{2R}\ V^2$, where V is the correlation making allowance for different sample size ($V = 1/n_1 + 1/2 + 1/n_2 + 1/2$) and R is the number of variants examined, allowed to estimate the significance of the differences observed (Sikorski, 1982). If the MMD value is greater than the double value of SD_{MMD}, then the difference between the populations can be considered as statistically significant. The measure of Uniqueness of each sample was calculated as the sum the MMD values relatively to the others (Sikorski, 1982).

RESULTS

Univariate statistics of the metric characters are summarized in Table I.

Table I. – Univariate statistics for mensural charaters.

TERCEIRA

Variable	N	Mean	Std.Dev.	Minimum	Maximum
ONL	25	41.84	1.53	38.95	44.34
CBL	26	39.90	1.40	37.15	42.38
ZB	26	19.94	0.72	18.02	21.14
BB	26	16.95	0.43	16.09	17.94
IW	26	6.07	0.35	5.02	6.74
RL	25	14.13	0.70	12.17	15.30
RW	25	7.31	0.38	6.64	8.02
DL	24	11.18	0.95	10.18	14.80
PAL	25	8.40	0.43	7.82	9.44
FPL	24	7.74	0.42	7.12	8.63
UMTRL	25	7.34	0.45	6.67	8.60
MW	25	7.99	0.58	7.33	9.58
NL	25	15.30	0.96	12.10	16.66
IPL	26	5.67	0.39	4.93	6.67
IPW	26	10.87	0.62	9.59	12.42
PL	26	7.70	0.49	6.54	8.30
FL	26	13.23	0.70	11.59	14.82
GML	25	27.40	1.13	24.68	29.29
HML	26	12.24	0.58	10.94	13.36
LMTRL	25	7.10	0.36	6.60	7.93

S. MIGUEL

Variable	N	Mean	Std.Dev.	Minimum	Maximum
ONL	33	42.30	1.36	39.36	45.20
CBL	33	40.29	1.28	37.65	42.90
ZB	32	20.11	0.59	18.98	21.32
BB	32	17.35	0.48	16.52	18.83
IW	33	6.26	0.30	5.73	6.97
RL	33	14.49	0.54	13.70	15.67
RW	32	7.47	0.37	6.75	8.22
DL	33	11.12	0.52	10.10	11.99
PAL	32	8.28	0.32	7.70	8.78
FPL	33	7.76	0.43	7.04	8.66
UMTRL	32	7.29	0.31	6.57	7.87
MW	33	8.28	0.66	6.17	9.80
NL	33	16.20	0.99	12.44	17.46
IPL	33	6.32	0.42	5.23	6.98
IPW	33	11.35	0.52	10.21	12.26
PL	33	7.41	0.41	6.59	8.72
FL	33	13.26	0.52	12.28	14.40
GML	33	27.52	1.06	25.15	30.04
HML	30	12.60	0.60	11.35	13.81
LMTRL	32	7.29	0.31	6.57	7.87

MAINLAND

Variable	N	Mean	Std.Dev.	Minimum	Maximum
ONL	21	40.22	1.44	38.07	44.04
CBL	23	38.36	1.57	36.00	42.60
ZB	25	19.98	0.95	18.64	23.04
BB	25	17.13	0.43	16.01	18.16
IW	25	5.95	0.23	5.58	6.41
RL	25	13.96	0.74	13.04	15.73
RW	24	6.98	0.42	6.00	7.75
DL	25	10.45	0.52	9.69	11.64
PAL	23	7.93	0.38	7.49	8.97
FPL	25	7.35	0.44	6.56	8.23
UMTRL	25	7.14	0.28	6.66	7.66
MW	25	7.63	0.54	5.83	9.00
NL	22	14.84	0.80	13.44	16.45
IPL	22	5.71	0.44	5.01	6.42
IPW	24	10.64	0.46	9.70	11.94
PL	23	7.61	0.48	6.91	8.51
FL	25	13.38	0.62	12.00	14.77
GML	25	26.52	1.24	24.96	29.79
HML	22	12.11	0.79	10.84	13.90
LMTRL	25	7.14	0.28	6.66	7.66

Results of the two way Anova to test the effects of sex and locality groups on the samples variation indicate the absence of sexual dimorphism but a significant effect of locality (Table II A). In fact, the locality has a highly significant effect on the variability of all the variables except five. In no case, the observed variability is due to the sex or to the interaction between sex and locality.

Consequently, skulls of both sexes were pooled to yield a larger sample, and a discriminant analysis was performed to maximize the differences previously found.

We verified that 95.7 % of the skulls were correctly classified and three clusters, corresponding to each of the samples, were individualized (Fig. 2).

Table II. – A, Signification levels of the F values from two-way (sex-local) analysis of variance. B, Standardized canonical discriminant function coefficients.

A

VARIABLES	SOURCE OF VARIATION Local	Sex	Interaction
BB	0.006*	0.572	0.590
CBL	<0.001*	0.449	0.508
FL	0.920	0.054	0.051
IPL	<0.001*	0.516	0.648
IPW	<0.005*	0.059	0.242
IW	0.001*	0.209	0.538
MW	<0.001*	0.914	0.428
NL	<0.001*	0.511	0.805
ONL	<0.001*	0.281	0.457
PL	0.077	0.875	0.869
DL	<0.001*	0.623	0.315
PFL	0.002*	0.169	0.408
GML	0.005*	0.574	0.341
HML	0.052	0.878	0.134
RL	0.013*	0.417	0.226
MTRL	0.087	0.555	0.879
PAL	<0.001*	0.944	0.876
UMTRL	0.034*	0.679	0.992
RW	<0.001*	0.868	0.195
ZB	0.595	0.628	0.366

* Values highly significant

B

VARIABLES	FUNC1	FUNC2
BB	0.368	- 0.183
CBL	0.307	0.046
FL	0.469	- 0.065
IPL	**1.054**	- 0.108
IPW	0.113	0.062
IW	- 0.174	- 0.024
MW	0.233	0.483
NL	**1.031**	0.433
ONL	**- 0.859**	**0.712**
PL	- 0.165	**- 0.521**
DL	- 0.118	0.445
FPL	**- 0.562**	0.288
GML	- 0.333	**0.913**
HML	0.075	- 0.124
RL	0.478	**- 0.790**
LMTRL	**0.683**	0.190
PAL	**- 1.085**	0.276
UMTRL	**0.612**	- 0.468
RW	- 0.452	- 0.265
ZB	- 0.235	**- 0.988**

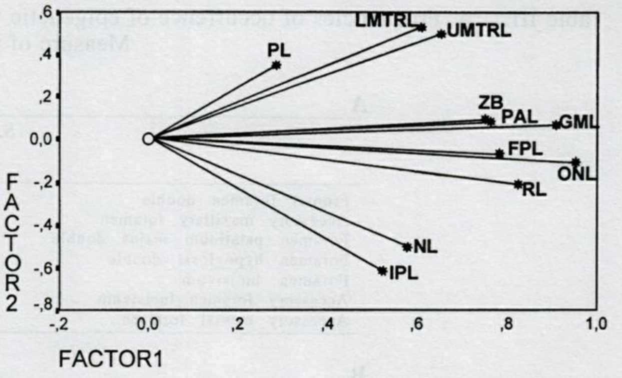

Fig. 4. – Factor loading of the skull dimension on the two first PC axis.

To understand the relationships between samples, a principal component analysis was performed using the eleven cranial variables that showed a higher discriminating power (Table II B). The first three eigenvectors accounted for 73.3 % of the total variability. The first component (51.7 %) is related to skull size once it is positively correlated with all the variables (Fig. 3), namely with those referring to the most anterior part of the skull (PAL, RL, FPL). The second axis (12.4 %) is a shape axis opposing the skulls with longer tooth rows to those with longer nasals and interparietals.

Figure 4 shows the Azorean animals are bigger than the continental ones and the rats of S. Miguel differ from those of Terceira having longer tooth rows and smaller nasals on the one side and a braincase with longer parietals and smaller interparietal bones on the other side.

In what concerns epigenetic (non-metrical) traits : from the thirteen scored, only those variables that show a different distribution between at least two of the samples were further analysed in this study. So frequencies of occurrence of seven non-metrical cranial variants were calculated

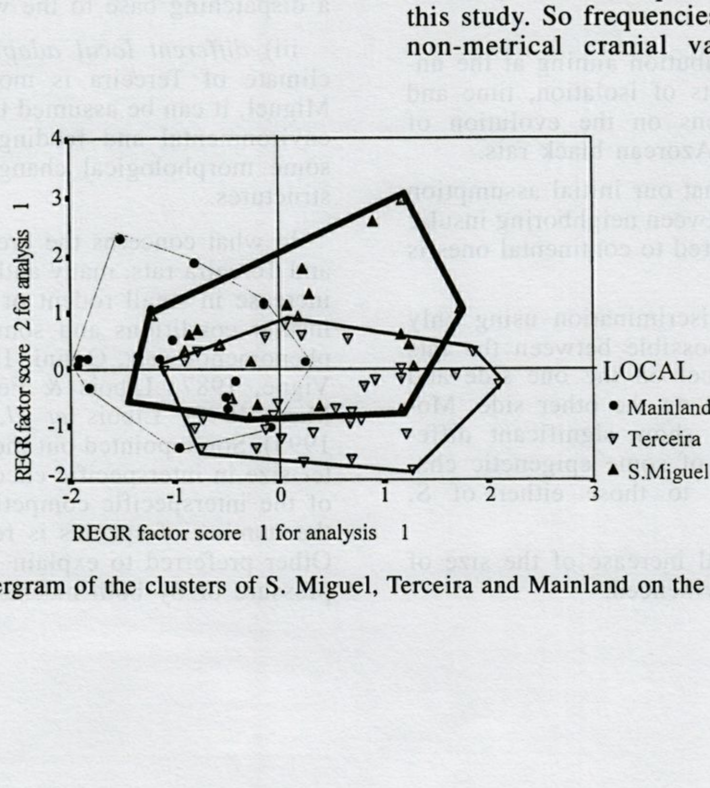

Fig. 3. – Scattergram of the clusters of S. Miguel, Terceira and Mainland on the two first PC axis.

Table III. – A, Frequencies of occurrence of epigenetic variants. B, Mean Measure of Divergence (MMD) in bold and Measure of Uniqueness (MU).

A

	S. MIGUEL N=32 %	TERCEIRA N=27 %	MAINLAND N=30 %
Frontal foramen double	66.5	88.9	53.3
Accessory maxillary foramen	18.75	33.3	10.0
Foramen palatinum majus double	12.5	33.3	16.7
Foramen hypoglossi double	6.2	11.1	7.7
Foramen incisivum	90.6	70.4	90.0
Accessory foramen incisivum	34.4	37.0	26.7
Accessory mental foramen	6.2	0.0	3.3

B

	MU	MMD TERCEIRA	MMD S. MIGUEL
MAINLAND	**-0.004**	**0.016** (0.0017)	**0.02** (0.0014)
S. MIGUEL	**-0.005**	**0.015** (0.0013)	
TERCEIRA	**0.031**		

(Table III A). The discriminant analysis performed with these seven variables revealed a relatively lower percentage of cases correctly classified : 46.4 %, denoting a higher epigenetic similarity between samples comparing overall morphometric similarity.

The Mean Measure of Divergence reveals significant differences between the pairs S. Miguel/Terceira and Terceira/Mainland. No significant differences were observed between the groups S. Miguel/Mainland. The highest value of the Measure of Uniqueness was found between Terceira and the other samples (Table III B).

DISCUSSION

This is the first contribution aiming at the understanding of the effects of isolation, time and new ecological conditions on the evolution of phenotyic characters in Azorean black rats.

The results indicate that our initial assumption of a greater similarity between neighboring insular populations when compared to continental ones is not verified.

Indeed, a complete discrimination using only metrical characters, is possible between the rats of Terceira and S. Miguel on the one side and those from the continent on the other side. Moreover, rats of Terceira show significant differences in the frequency of some epigenetic characters when compared to those either of S. Miguel or of mainland.

Additionally, a general increase of the size of the insular samples is evidenced.

To explain the observed morphological differences between S. Miguel and Terceira black rats, several hypotheses can be drawn :

i) *a founder effect* : the populations of these islands could have been originated from different European pools due to the fact that both Portuguese and Flemish colonized Terceira while S. Miguel was initially occupied only by Portuguese settlers ;

ii) *differences in the gene flow* : a greater gene flow between S. Miguel and the continent than between the two islands or between Terceira and mainland. S. Miguel, besides the fact of its previous knowledge, due to a greater proximity to mainland always had very close commercial links with continental Portugal. The ship traffic was always very intense and the island was serving as a dispatching base to the whole archipelago ;

iii) *different local adaptations* : as far as the climate of Terceira is more humid than on S. Miguel, it can be assumed that rats faced different environmental and feeding conditions involving some morphological changes in the masticatory structures.

In what concerns the greater size of S. Miguel and Terceira rats, many authors did observe a size increase in small rodent or insectivore species in insular conditions and some have discussed that phenomenon (e.g. Orsini, 1982 ; Lomolino, 1985 ; Vigne, 1987 ; Libois & Fons, 1990 ; Mathias & Mira, 1992 ; Libois *et al*, 1993 ; Vigne *et al.*, 1993). Some pointed out the advantages of a greater size in interspecific encounters and the release of the interspecific competition on islands where the number of species is reduced (Foster, 1964). Other preferred to explain it by a lower predator pressure or by both mechanisms (Thaler, 1973).

Our results do not allow to pay more attention to one of these hypotheses but it is worth mention that the observed metrical modifications concern mainly the anterior part of the skull namely those characters related to food processing. That fact is also evidenced in other insular rodent populations (e.g. *Apodemus sylvaticus* : Libois & Fons, 1990, *Mus musculus* : Orsini & Cheylan, 1988 and Mathias & Mira, 1992) and it is probably a good adaptive character, assuming as Lawlor (1982) and Angerbjorn (1985), that generalist species on islands, due to the reduced interspecific competition can expand its range of food sources, and therefore the size of the structure related with exploitation of these food sources. In this cases, the third hypopthesis (different local adaptations) would best explain the differences observed between the rats of both islands.

This study is included in a project "The mammals of Azores Islands and their relevance as zoonotic reservoirs : an insular syndrome?" supported by JNICT (STRDA/C/CEN/447/92).

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