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1 **Regular article: Genetic differentiation and structuration of the Gobra zebu**
2 **cattle breeds reared in Senegal**

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28 **Abstract**

29 The Gobra zebu genetic breeding programme has resulted in a population with genetic
30 characteristics that differ from other cattle populations exploited in Senegal. These differences
31 seem to be due to the reproductive isolation and selection to which this population of the "Centre
32 de Recherches Zootechniques" of Dahra has been subjected since the 1950s. The objective of
33 this study is to evaluate the genetic differentiation and structuration of this population in relation
34 to the main cattle breeds used in Senegal. A sample of 180 individuals from the Gobra selection
35 nucleus and six other bovine populations from the four main breeds exploited in Senegal was
36 thus constituted. The genotyping of these individuals was done with 21 microsatellite markers
37 recommended by the Food and Agriculture Organization. The basic parameters of
38 differentiation and structuration genetic were calculated using various bioinformatics software.
39 The results of this study, notably the degrees of genetic differentiation (F_{st}), the coefficient of
40 genetic homogeneity (G_{st}) and the gene flow (N_m), show a significant genetic differentiation
41 of the Gobra from the station compared to the other populations studied. The analysis of genetic
42 structuring reveals a micro-structuring within the Gobra population. This micro-structuring
43 clearly identifies the centrally-bred Gobra individuals from the other Gobra populations
44 studied. The main causes of these observations would be reproductive isolation and the
45 selection pressure exerted on this population for several decades.

46 **Keywords:** genetic characterization; Gobra zebu; local cattle breeds; microsatellites; Senegal.

47 **Introduction**

48 Indigenous animal genetic resources are known for heat and draught tolerance, disease
49 resistance and subsistence on poor feed, opening scope for allele mining for these traits (Sharma
50 et al., 2013). However, usually in animals breeding program, many traits of local breeds are
51 neglected at the expense of productivity traits of exotic breeds. This leads in some countries to
52 a continuous decline of the indigenous cattle population. As a result, the introduction of highly

53 productive breeds and population pressure contribute to the loss of valuable traits or to the
54 decline in the population of local breeds (Sharma et al., 2015). Description of cattle biodiversity
55 is important as an aid to conservation of animal genetic resources and national heritage (Mannen
56 et al. 2004). Indeed, genetic characterization (in particular elucidate genetic variability and
57 genetic relationship) of breeds has direct relevance with the issues of sustainable use of
58 domestic animal genetic resources (Mannen et al., 2004; Sodhi et al., 2005). Furthermore, such
59 information should contribute to the formulation of rational breeding programs with the goal of
60 increasing output in the production system (Mannen et al., 2004; Sodhi et al., 2005).

61 In Senegal, four local cattle breeds and one exotic breed are generally found on pastoral farms
62 (Missohou et al., 1997; Diack et al., 2016). The African breeds are the Gobra zebu in the
63 Sahelian area of the country (in the north and centre - sylvo-pastorale area), the N'dama taurine
64 in the Sudano-Sahelian area of the country (in the south and east), the Djakoré (resulting from
65 cross-breeding between Gobra zebras and N'dama taurines in transitional zones) and the
66 Moorish zebu in the north of the country (Missohou et al, 1997; Mbengue et al., 2007; Diack et
67 al., 2016; Wane et al., 2017). Among the exotic breeds, the Guzera zebu is the most commonly
68 encountered in pastoral farms, especially in the sylvo-pastoral area (Diack et al., 2016).

69 The Gobra zebu is, from a socio-economic point of view, one of the most important bovine
70 genetic resources in the country and the "Centre de Recherches Zootechniques" (CRZ) of Dahra
71 hosts the genetic breeding programme of this breed (Missohou et al., 1997; Sambe et al., 2019).
72 Its genetic selection programme aims to: conserve the Gobra breed *in vivo in situ* at the CRZ of
73 Dahra and to provide breeders in the sylvo-pastoral zone with animals that are better adapted
74 and perform better in this particular production environment. The genetic breeding programme
75 of this breed was carried out by an intra-racial closed-nucleus mass selection initiated in 1952
76 (Sow et al., 1988). Together with the maintenance of reproductive isolation, this desire to
77 preserve this breed within the CRZ of Dahra for so long has had an impact on the genetic

78 diversity within this population (Sambe et al., 2022). However, the impact on genetic
79 differentiation and structuration between these populations and the wild populations is not
80 documented. The objective of this study is to assess the impact of this selection and isolation
81 on the genetic differentiation and structuration of this population compared to mainly other
82 cattle populations exploited in Senegal.

83 **Materials and methods**

84 **Study areas**

85 The study involved 180 individuals randomly selected from the 7 study sites shown in Figure
86 1. The study areas other than the CRZ of Dahra were chosen either to obtain animals preserved
87 as much as possible from inter-racial crossings (CRZ of Kolda and EMAAP farm), or because
88 of the accessibility of the individuals (Dakar slaughterhouses), or because the foundation herd
89 would have been made up of cattle that notably came from these areas (Amaly, M'beuleukhé
90 and N'diané).

91 **Study population and blood collection**

92 The study population is made up of the venous blood of 4 breeds: N'dama taurines, Gobra zebus,
93 Guzera zebus and Moorish zebus. Thus, 41 samples of Gobra from the CRZ of Dahra were
94 compared to: 68 samples of Gobra from 3 villages located close to CRZ of Dahra (21 in Amaly,
95 22 in M'beuleukhé and 25 in N'diané); 29 samples of N'dama from the selection nucleus of the
96 CRZ of Kolda; 22 samples of Moorish zebu from the Dakar slaughterhouses; and 20 Guzera
97 individuals from the EMAAP industries farm in Thiès. The 41 animals from the CRZ of Dahra
98 are made up of: i) 29 animals from the genetic breeding programme (native); ii) and 12 animals
99 (from the 33 animals from villages close to CRZ of Dahra) introduced in 2017 to reinforce the
100 nucleus selection (acquired).

101 Blood collection was carried out between October 2016 and March 2017. On each of the
102 individuals sampled, blood was taken from the jugular vein of the animal in tubes with ethylene
103 diamine-tetra-acetic acid (EDTA) as an anticoagulant. The samples thus obtained are

104 centrifuged at 8,000 rpm during 10 minutes to collect the buffy coat. The buffy coat is then
105 placed in 1.5 ml Eppendorff tubes and stored at -20°C until the genomic DNA is extracted.

106 **DNA extraction and genotyping of individuals**

107 Genomic DNA was extracted from the buffy coat using the Zymo Research commercial kit
108 (Quick-DNATM Universalt Kit) following the protocol described by the manufacturer. The
109 extracted DNA was stored at -20°C until the individuals were genotyped. Individuals were
110 genotyped with 21 of the 30 microsatellite markers recommended by FAO (2011). The
111 genotyping protocol is described by Sambe et al. (2022).

112 **Data analysis**

113 **Impact of technical errors and linkage disequilibrium between loci**

114 The impact of technical errors during genotyping was assessed using MicroChecker software
115 version 2.2.3 (Oosterhooft et al., 2004). These analyses consisted of checking: dropout,
116 stuttering, and the presence and proportion of null alleles for each locus and each population.
117 Furthermore, the proportion of null alleles expected under the double null hypothesis of
118 panmixing and that null alleles explain the variance of the inbreeding coefficient deficit is
119 calculated according to the second method of Brookfield (1996). Microchecker analyses were
120 performed after 10,000 replicates and with a confidence level of 95%. A binomial test,
121 performed with R software, was used to compare the significance at the 5% level of the
122 differences between the proportions of null alleles observed and calculated by the second
123 method of Brookfield (1996).

124 Linkage disequilibrium (between pairs of loci) was assessed using Genepop version 4.2.2
125 (Rousset, 2008). The linkage disequilibrium signal was tested on R with a binomial test as
126 described by De Meeûs (2012). The significance level of the tests performed is set at 5%.

127 **Genetic differentiation**

128 For each locus, genetic differentiation was assessed using the Wright (1978) degree of genetic
129 differentiation reported by Weir and Cockerham (1984) (θ denoted F_{st} in the following) and

130 the Nei (1973) genetic homogeneity coefficient (G_{st}) reported by Nei and Chester (1983). These
131 analyses were carried out using SPAGeDi version 1.4 software (Hardy and Vakemans, 2002)
132 after 20,000 randomisations using the Jackknife resampling method.

133 Genetic differentiation was also assessed between the different populations by calculating: the
134 degree of genetic differentiation (F_{st} per population pair), gene flow (N_m) and genetic distances
135 (D_{cs}) according to the method of Cavalli-Sforza and Edwards (1964). The results of these
136 analyses were generated with the Genepop version 4.2.2 and Populations version 1.2.32
137 software (Langella et al., 1999). A significance level of 5% was retained for the tests performed.

138 **Genetic structuration**

139 In a first step, a Correspondence Analysis (CA) was performed to visualize the relationships
140 between individuals of the different populations, to estimate the distribution of genetic diversity
141 between populations and to visualize their degrees of admixture. Given the high sensitivity of
142 this analysis to outliers (De Meeûs, 2012), analyses were performed at different hierarchical
143 levels to detect micro-structuring. The hierarchical levels are defined by considering all the
144 samples and then progressively subtracting the populations that show significant genetic
145 differentiation with the others (F_{st} significantly greater than or equal to 0.05). These analyses
146 were performed with Genetix software version 4.0.5.2 (Belkhir et al., 2014).

147 In a second step, a genetic assignment test was performed using the method described by Paetku
148 et al. (1995). This method, based on allelic frequencies, makes it possible to estimate the
149 probability of each individual belonging a posteriori to the different populations considered.
150 This analysis was carried out using the GeneClass version 2.0 software (Piry et al., 2004),
151 considering 10 000 simulations and a significance threshold of 1%.

152 Finally, the structure of the study population was inferred using the Bayesian method
153 implemented in the Structure software version 2.3.4 (Pritchard et al., 2000). This method makes
154 it possible to infer the likelihood with which certain individuals can be grouped together and

155 considered to belong to the same group or cluster. The analyses were carried out considering:
156 a priori 1 to 8 groups or clusters (K), a preheating chain consisting of: 10^4 iterations, 10^6
157 iterations of the Marcov Monte Carlo Chain (MCMC) and 10 replications for each value of K.
158 The likelihood and Evanno methods (Evanno et al., 2005), available on the online platform
159 Structure Harvester (Earl and VonHoldt, 2012) were used to determine the most likely numbers
160 of genetic clusters. Analyses were performed on the hierarchical levels described for CA to
161 detect micro-structuring.

162 **Results and discussion**

163 **Results**

164 **Impact of technical errors and linkage disequilibrium**

165 After cleaning the data, the HEL5 marker and 5 zebus (1 Gobra from Amaly, 3 Guzera and 1
166 Moorish) were eliminated due to poor amplification. The analyses therefore covered 20
167 microsatellite markers and 175 individuals, representing 3,500 data points or genotypes.
168 Among these 3,500 genotypes, only 74 (or about 2%) were identified as null alleles (Appendix
169 1). On average, in each population and for each locus, a maximum of 2 individuals showed null
170 alleles. For all populations combined, each locus had on average 3 to 4 individuals with null
171 alleles (Appendix 1). The proportion of null alleles observed per loci is very low as it is less
172 than 5% for all loci except for HEL1 and INRA063. These two loci present a proportion of null
173 alleles equal to approximately 5.7% (which represents 10 null alleles for 175 targeted
174 genotypes).

175 If we assume that the populations studied were panmictic and that null alleles explain the Fis
176 deficits, the p-values of the binomial tests are not significant. Furthermore, no cases of stuttering
177 and/or dropout were detected (Appendix 1).

178 Out of 190 pairs of loci, only 12 show a significant p-value in the linkage disequilibrium test
179 (Appendix 2). The linkage disequilibrium signal test gives a non-significant p-value. This

180 means that the observed linkage disequilibrium for the 12 loci pairs can be explained by chance.
181 Therefore, all loci are used for further analysis as they are considered independent.

182 **Genetic differentiation and structuration**

183 All loci show a degree of differentiation (F_{st}) and a coefficient of genetic homogeneity (G_{st})
184 significantly different from 0 (Table 1). Nineteen of the twenty loci have F_{st} values indicating
185 moderate genetic differentiation (F_{st} between 0.053 and 0.157). Only BM1818 ($F_{st} = 0.045$)
186 shows weak genetic differentiation. The G_{st} values are very close to the F_{st} values. The multi-
187 loci analyses lead to the same conclusions. Indeed, F_{st} and G_{st} are also significantly different
188 from 0 and indicate moderate genetic differentiation.

189 From a racial point of view, Table 2 shows that: i) the Gobra and Moorish breeds show little
190 genetic differentiation from each other ($F_{st} < 0.05$); ii) these breeds show moderate genetic
191 differentiation from the Guzera ($0.05 < F_{st} < 0.15$); and iii) all the breeds studied are strongly
192 differentiated from the N'dama ($F_{st} > 0.15$).

193 From a population point of view, Tables 3 and 4 confirm the slight differentiation between the
194 Gobra and Moorish populations studied. These populations show low to moderate degrees of
195 differentiation (F_{st} between 0.002 and 0.077), significant gene flow and genetic distance (N_m
196 between 1.042 and 3.238 and D_{cs} between 0.258 and 0.362). In addition, the Guzera and
197 N'dama show greater genetic differentiation with the Gobra and Moorish (F_{st} ranging from
198 0.067 to 0.271; N_m ranging from 0.538 to 1.512; and D_{cs} ranging from 0.395 to 0.602).

199 It should be noted that the Gobra from the CRZ of Dahra selection nucleus are more
200 differentiated from the other Gobra and Moorish populations sampled, while the N'dama are
201 the most differentiated from all other populations.

202 Considering all populations into account, the first three axes of the CA give an overall inertia
203 of 70.19% (Figure 2). The populations contributing most to the construction of these axes
204 (Appendix 3) are: the N'dama (with a contribution of 64.7% for axis 1 and 12.6% for axis 2);
205 the Guzera (with a contribution of 45.2% for axis 2 and 31.2% for axis 1); the Gobra of Amaly
206 and the natives of the CRZ of Dahra for the construction of axis 3. Thus, a projection of the
207 individuals on the two main axes of the CA makes it possible to distinguish a genetic
208 structuration of our population into three sub-populations. These are a population of N'dama,
209 one of Guzera and another population, not differentiated at this scale, made up of Gobra and
210 Moorish.

211 Considering only the zebu populations (Figure 3), the overall variance explained by the first
212 three axes is 69.71%. The Guzera contribute almost exclusively (79%) to the construction of
213 axis 1 (Appendix 3) and the construction of the other two axes mainly involves the native Gobra
214 of the CRZ of Dahra (49% for axis 2 and 12.8 for axis 3). This CA allows us to distinguish the
215 Guzera, the native Gobra of the CRZ of Dahra, from the other zebu populations sampled.

216 At the local zebu level (Figure 4), the overall inertia is 71.87% and a micro-structuring of the
217 population is visible. Three populations contribute significantly to the construction of the first
218 two axes (Appendix 3). These are the Gobra native to the CRZ of Dahra (axis 1: 61.8%; axis 2:
219 12.6%), the Gobra of Amaly (axis 1: 32.6%; axis 2: 26%) and the Gobra of N'diané (axis 1:
220 0%; axis 2: 57.7%). These three populations are the ones that are identifiable on the CA.

221 The percentages of individuals correctly assigned to their population of origin according to the
222 Paetku method are very high (Table 5). The populations with the lowest assignment scores are
223 the new acquisitions of the CRZ of Dahra and the Guzera zebus with more than 83% and 88%
224 of individuals correctly assigned, respectively. All other populations have correct assignment
225 percentages of at least 90%.

226 The likelihood and Evano methods (Figure 5 A and B) indicate that the number of probable
227 genetic groups when considering the whole study population is 2 ($K = 2$). The resulting structure
228 shows 2 main multi-loci groups (red and green) which are present in different proportions in
229 the inferred groups (Figure 5 D). Our populations, constituted *a priori*, have varying proportions
230 of these multi-loci groups (Figure 5 C). The N'dama are mainly composed of the red multi-loci
231 group, while the zebus are mainly composed of the green multi-loci group. The N'dama group
232 shows a slight introgression of the green multi-loci genotype (zebu group) and vice versa. The
233 percentage of individuals assigned to the different groups (Appendix 4) confirms these results.
234 Indeed, 97% of the N'dama are assigned to group 1, while the zebus are assigned to group 2 in
235 proportions varying between 83 and 99%.

236 When we consider only zebu cattle, the maximum likelihood is obtained with $K = 3$ (Figure 6
237 A and B). The genetic structuring according to our *a priori* populations is less obvious (Figure
238 6 C and D). Nevertheless, it should be noted that the Gobra native to the CRZ of Dahra and the
239 Guzera have a multi-loci genotype that is in the majority. The Gobra native of the CRZ of Dahra
240 are predominantly composed of the blue multi-loci genotype, whereas the Guzeras seem to
241 possess almost exclusively the green multi-loci genotype. The other populations are mostly
242 composed of the blue and red multi-loci genotypes. These populations are distributed in various
243 proportions in the three groups inferred by the Bayesian method, while the Guzera and the
244 Gobra native to the CRZ of Dahra are mostly assigned to groups 2 and 3 respectively (Appendix
245 5).

246 Considering only Gobra and Moorish zebu, Evano's method gives a most likely K equal to 4
247 (Figure 7). The four groups inferred by the Bayesian method are each predominantly composed
248 of a Gobra population (Appendix 6) and a particular multi-loci genotype (Figure 7). Group 1 is
249 predominantly made up of the red multi-loci genotype and 53.3% of the N'diane Gobra. The
250 green multi-loci genotype is predominantly identified in group 2 which contains 67% of the

251 Gobra native of the CRZ of Dahra. The blue and yellow multi-loci genotypes are respectively
252 in the majority in groups 3 and 4. These groups respectively hold 60% of the Gobra of
253 M'beuleukhé and Amaly. The Moorish zebu and the new acquisitions of the CRZ of Dahra are
254 mainly distributed in groups 3 and 4.

255 **Discussion**

256 The indices of genetic differentiation (F_{st} , G_{st} , N_m and D_{cs}) indicate overall low differentiation
257 between the Gobra and Moorish zebu and moderate genetic differentiation between these
258 populations and the N'dama populations of the CRZ of Kolda and Guzera of the EMAAP. It
259 also appears that, among the Gobra and Moorish, the population of Gobra native of the CRZ of
260 Dahra has the greatest degree of genetic differentiation from the Guzera and N'dama
261 populations. The analysis of the population structure shows little introgression between the
262 N'dama taurines and the zebu breeds studied, but also little introgression between the Guzera
263 and the local zebu breeds. Furthermore, it appears from this analysis that genetic exchanges
264 between local populations (Gobra and Moorish zebus) are very important. All this leads to the
265 structuring of our study population into three clearly differentiated populations, namely: a
266 population mainly comprising the Gobra and the Moorish (population 1); a population
267 composed of Guzera (population 2); and a population of N'dama (population 3). The first two
268 populations (populations 1 and 2), although clearly distinguishable, are not as distinct as
269 population 3 (N'dama of the Kolda CRZ). The analyses also highlighted a micro-structuring
270 within population 1, allowing the individuals from the CRZ of Dahra to be clearly identified
271 from the other Gobra and Moorish individuals. Various studies to define the genetic
272 differentiation and structuration of cattle breeds have resulted in a genetic distinction between
273 zebu and bull populations (Bradley et al., 1994; Loftus et al., 1994; MacHugh et al., 1997;
274 Bradley et al., 1998; Hanotte et al., 2000; Freeman et al., 2004; Dayo et al., 2009). These studies
275 also show a clear genetic differentiation between African and other cattle breeds.

276 In the sylvo-pastoral area, although herders are increasingly introducing Guzera into their herds,
277 the proportion of individuals of this breed is still very low in the said area (Diack et al., 2016).
278 Due to sociological considerations such as the black colour of the Guzera's coat, although it has
279 a desirable size, the breeders does not prefer an animal with this phenotypic appearance. Thus,
280 farmers in this area only introduce males (generally only one male as a sire) to improve the
281 meat production of their animals. MacHugh et al. (1997) and Ndiaye et al. (2015) also describe
282 a strong genetic proximity between the Gobra and Moorish zebus of Senegal. Indeed, African
283 zebu populations, having overlapping areas of distribution and being most often subject to a
284 transhumant breeding system, retain a high genetic diversity and have a low degree of genetic
285 differentiation between them (Freeman et al., 2004; Dayo et al., 2009).

286 The genetic micro-structuring observed between the Gobra individuals native to the CRZ of
287 Dahra and the other Gobra and Moorish individuals is the result of the reproductive isolation
288 and long selection to which this population has been subjected since 1950. In fact, since the
289 beginning of the Gobra genetic breeding programme, every effort has been made to obtain “pure
290 bred” and high-performance animals (Sow et al., 1988). It is with this in mind that the
291 programme is based on an intra-racial selection of individuals in a system where, overall, there
292 has been very little blood supply from outside (Sambe, 2021).

293 This study reveals that the Gobra population, the result of the genetic breeding programme
294 conducted at the CRZ of Dahra since nearly 1970, is clearly different from the other bovine
295 populations studied. These include populations of other breeds (i.e. the N'dama, the Guzera and
296 the Moorish) as well as populations of the same breed that are very close historically and
297 geographically (i.e. the Gobra of Amaly, M'beuleukhé and N'diané). This differentiation would
298 be due to the long years of reproductive isolation and selection to which this population has
299 been subjected since the beginning of the genetic breeding programme. However, in the future

300 this genetic differentiation should disappear or be less important due to the introduction of new
301 individuals from neighbouring villages (i.e. the Gobra population acquired in 2017).

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407 **Appendix**

408 Appendix 1: Impact of technical errors on panmixia.

409 Appendix 2: Significance matrix for the linkage disequilibrium test (red boxes represent loci
410 pairs with a significant p-value in the linkage disequilibrium test. grey boxes represent loci pairs
411 without a significant p-value in the linkage disequilibrium test).

412 Appendix 3: Contributions of each population to the construction of the first 3 axes of the CA.

413 Appendix 4: Percentages of individuals correctly assigned to genetic clusters (N'dama and zebu
414 combined).

415 Appendix 5: Percentages of individuals correctly assigned to genetic clusters (zebu only).

416 Appendix 6: Percentages of individuals correctly assigned to genetic clusters (local zebras only).

417 **Figure**

418 Figure 1: Study areas for genotypic characterisation

419 Figure 2: Correspondence Analysis performed on the entire study population.

420 Figure 3: Correspondence Analysis performed on all zebu populations.

421 Figure 4: Correspondence Analysis performed on the Gobra and Moorish zebu populations.

422 Figure 5: Genetic structure of the studied cattle populations.

423 Figure 6: Genetic structure of the zebu populations studied.

424 Figure 7: Genetic structure of the local zebu populations studied.

425 **Table**

426 Table 1: Indices of genetic differentiation by locus, calculated on the study population.

427 Table 2: Degree of genetic differentiation (Weir and Cockerham F_{st}) per population pair
428 between the breeds studied.

429 Table 3: Degree of genetic differentiation (Weir and Cockerham F_{st}) and gene flow (N_m) per
430 population pair.

431 Table 4: Cavalli-Sforza genetic distance between populations.

432 Table 5: Assignment of individuals to their populations of origin according to the method of
433 Paetku (1995) at the 1% significance level.

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440 Data available on request from the authors.

441 **Conflict of interest**

442 The authors declare no conflict of interest.

443 **Ethics statement**

444 The authors confirm that the ethical policies of the journal, as noted on the journal's author
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447 **Authors contribution**

448 **Babacar Souleymane Sambe**: Investigation, Formal analysis, Funding acquisition,
449 Methodology, Writing original draft, Writing-review & editing; **Mame Nahé Diouf**:
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451 Supervision, Writing original draft, Writing-review & editing; **Bakary N'diaye**: Investigation,
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