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On the genetic determinism of muscular hypertrophy in the *Belgian White and Blue* cattle breed

II. Population data (*)

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Summary

In this paper, the transmission of the double-muscled condition is studied in the *Belgian White and Blue* cattle breed in a large body of testing station and field data. The distribution within the population of several phenotypic criteria related to the muscle development is shown to be systematically bimodal. In other words, 2 biological entities [conventional (conv) and double-muscling (dm)] segregate within the commercial herds using A.I. The 4 mating types (dm × dm ; dm × conv ; conv × dm ; conv × conv) produce the following percentages of dm offspring : 86.1 p. 100, 42.4 p. 100, 49.2 p. 100, 24.1 p. 100. If environmental factors known to have an effect on the expression of the double-muscled condition are taken into account, the percentage of double-muscled calves born from dm × dm matings comes close to 100 p. 100. The finding of a break in the regression line of the percentage of double-muscled calves on the score of fleshiness of the parents is incompatible with a polygenic model with threshold. In agreement with an earlier paper analyzing experimental data (HANSET & MICHAUX, 1985) it is also concluded from this study that a major gene (symbol *mh*) is involved. It is also shown that there is further genetic variation, although smaller in magnitude, playing a role in the expression of the double-muscled condition and that this would be amenable to selection.

Key words : Belgian White and Blue *breed, muscle hypertrophy, inheritance, major gene, cattle.*

Résumé

Le déterminisme génétique de l'hypertrophie musculaire dans la race bovine Blanc-Bleu Belge. *II. - Données de population*

Le déterminisme génétique du caractère « culard » est étudié dans la race bovine *Blanc-Bleu Belge* sur des données de station et de fermes. La distribution, au sein de la population, de différents critères liés au développement de la musculature est systématiquement bimodale. En d'autres termes, 2 entités biologiques, le normal et le culard, apparaissent dans les troupeaux se reproduisant par insémination artificielle. Les 4 types d'accouplements (culard × culard ; culard × normal ; normal × culard, normal × normal) donnent les pourcentages suivants de descendants culards : 86,1 p. 100, 42,4 p. 100, 49,2 p. 100, 24,1 p. 100.

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Si on tient compte de certaines conditions de milieu influençant l'expression du caractère, la proportion de descendants culards nés de parents culards s'approche des 100 p. 100. La présence d'une discontinuité dans la régression du pourcentage de veaux culards sur le degré de musculature des parents est incompatible avec un modèle polygénique à seuil. Comme dans la première étude consacrée au sujet, on arrive à la conclusion qu'un gène majeur (symbole *mh*) est en jeu mais on montre qu'une variation génétique additionnelle, bien que de plus faible amplitude, joue un rôle dans l'expression du caractère et qu'elle peut être l'objet d'une sélection.

Mots clés : Race Blanc-bleu Belge, *hypertrophie musculaire, hérédité, gène majeur, bovin.*

I. Introduction

In a first paper, the results of the analysis of backcross data were presented (Hanset & Michaux, 1985). They confirm that a major gene, partially recessive, — symbol *mh* — is involved in the determination of double-muscling. In that experiment, the muscle development was characterized by the total weight of dissected muscles from calves slaughtered at the constant weight of 84 kg.

In the present paper, we report on the analysis of field data regarding the transmission of the so-called « double-muscled » conformation within the *Belgian White and Blue* cattle breed. Segregation studies are possible in the commercial cow population bred by A.I. where most (70 p. 100) of the cows are of the conventional type. Conversely, most of the A.I. bulls of the double-muscled type and very few are of the conventional type.

II. Material and methods

A. *Distribution of the phenotypes*

The distribution of the phenotypes within the population is studied on two kinds of data (station and farm).

1. *Station data*

The use of double-muscled A.I. bulls in commercial herds leaves offspring covering a wide range of conformation. During the first three years (1976 to 1978) of the progeny-test in station, each progeny group was drawn at random from the population of offspring.

As the largest number of muscling criteria was available for the 1978 test, only the data of this series were used to illustrate their distribution. This material consists of 145 male calves slaughtered at 12 months of age. These animals, sired by 11 fathers, entered the station in march and april, at the age of 1 month and were fed a high energy diet during the entire period.

The muscling criteria recorded are : the dressing-out percentage, the lean and fat percentages in the 7th rib cut, the price per kg liveweight, the plasma creatinine level and the content in creatine of the red blood cells. The dressing-out percentage was computed as the ratio of the weight of the cold carcass (24 hours after slaughter) on the final liveweight at the station (24 hours before slaughter), without previous fasting. The creatine and creatinine concentrations were determined respectively by the methods of EGGLETON *et al.* (1943) and OWEN *et al.* (1954).

2. *Field data*

For new bulls entering A.I., a progeny test is carried out on the farm. Their offspring are born in february and march, and the following features, among others, are recorded by technicians : at a first visit, during april, may and june, the conformation of the dam and of the calf [2 classes : double-muscled and conventional] ; at a second visit, at 12 months of age, a score of fleshiness is ascribed to each offspring, if still present on the farm at that time. In fact, this score corresponds to the price per kg liveweight that would be paid if this animal were ready for slaughter. The scale runs from 45 to 125 with steps of 5 units.

The data for 3 successive years, 1978, 1979, 1980 concerning 64 A.I. sires (59 double-muscled and 5 conventionals) and their 16.261 offspring of both sexes were analysed. The overall population could thus be divided according to the conformation of the parents. Four parental combinations or mating types are possible : double-muscled × double-muscled, double-muscled × conventional, conventional × double-muscled, and conventional × conventional.

The normality of the frequency distributions was tested by the KOLMOGOROV-SMIRNOV procedure D (Durbin's version). The Statistical Analysis System (SAS) package was used to perform this test. Furthermore, the non-normality was also illustrated by the probit transformation of the cumulative frequencies (FISHER & YATES, 1963).

On the other hand, bimodal and skewed distributions were resolved in 2 normal distributions, with means μ_1 and μ_2 common variance σ^2 and proportions p and q. These parameters are estimated by a Maximum Likelihood Procedure, as explained in the first paper (HANSET & MICHAUX, 1985). Nevertheless, in the case of grouped data, the expression of the log-likelihood of the sample becomes :

$$\log L = -\frac{N}{2} \ell n\, 2\pi - \frac{N}{2} \ell n\, \sigma^2 + \Sigma f_i\, \ell n\, \{p.\exp[-(X_i - \mu_1)^2/2\sigma^2] + q.\exp[-(X_i - \mu_2)^2/2\sigma^2]\}.$$

Where f_i is the frequency of the i class and $\Sigma f_i = N$.

As before, the Maximum Likelihood Estimation Program of KAPLAN & ELSTON (1978) was used.

B. *Parent-offspring regression*

A total of 3 529 cows were scored for fleshiness when 12 months old. The regression of the proportion of their double-muscled calves on their own score could be calculated.

Similarly, 38 sires born from contract matings and leaving the performance testing station for the A.I. center were also scored for fleshiness, a few among them were of the conventional type. The regression of the percentage of double-muscled calves produced by these sires, either with conventional cows (n = 5 803) or with double-muscled cows (n = 1 084), on their muscling score was also calculated.

Linear trend in the proportions were tested according to the procedure proposed by Armitage (1955) and recommended by Snedecor & Cochran (1980, p. 207). The total variation among R proportions (p_i) is measured by a χ^2 with (R — 1) degrees of freedom. As there is a score (X_i) for each of these proportions, a weighted regression coefficient of p_i on X_i is calculated. A χ^2 for linear regression with 1 degree of freedom, is obtained. The difference $\chi^2_{R-1} - \chi^2_1$ is a χ^2 with (R — 2) degrees of freedom for testing the deviations of the p_i from their linear regression on the X_i.

C. « *Between sires* » *variation*

For double-muscled sires only (n = 59), the « sire effect » on the score of fleshiness was estimated for each sex — conformation class of the offspring. The linear model used contains the following main effects (the number of levels are given in brackets) : year (3), region (11), parity (5) and conformation of the dam (2), level of feeding (2).

III. Results

A. *Distribution of the phenotypes*

1. *Station data*

The distributions of the muscling criteria are illustrated in figure 1 : price per kg liveweight in Belgian Francs, in figure 2 : the dressing-out percentage, in figure 3 : the lean percentage in the 7th rib cut, in figure 4 : the fat percentage, in figure 5 : the plasma level in creatinine (γ/100 ml), in figure 6 : the content in creatine of the red blood cells (γ/100 ml). These distributions have been submitted to a normality test (D test) and where bimodality was indicated they were resolved in 2 component distributions in the proportions p and q with means μ_1 and μ_2 and common variance σ^2 (tabl. 1).

Each of these variables exhibits a bimodal distribution corresponding to the segregation within the population of 2 distinct biological types : the conventional type and the double-muscled type. The price, the dressing-out percentage, the lean percentage, the creatinine level are higher in double-muscled animals while the fat percentage and the creatine content are lower. The same characteristics of double-muscled animals regarding the creatine and creatinine levels in plasma and red blood cells have been shown previously (Hanset & Michaux, 1982).

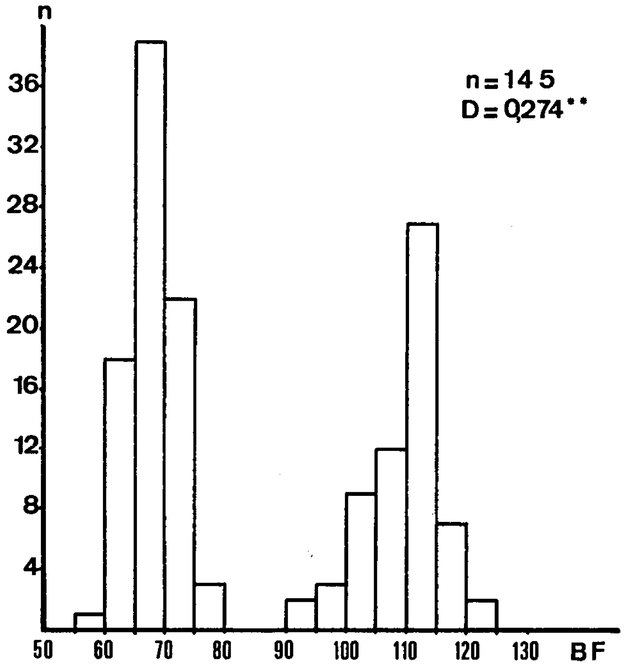

FIG. 1

Frequency distribution of the price per kg liveweight (in Belgian Francs), testing station data.
Distribution du prix au kg de poids vif (francs belges), données de station.

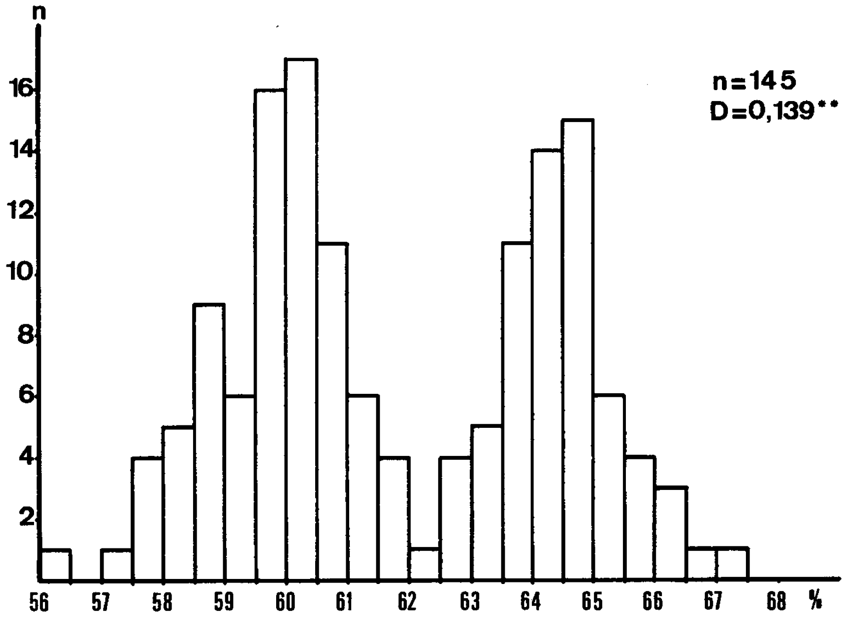

FIG. 2

Frequency distribution of the dressing-out percentage, testing station data.
Distribution du rendement à l'abattage, données de station.

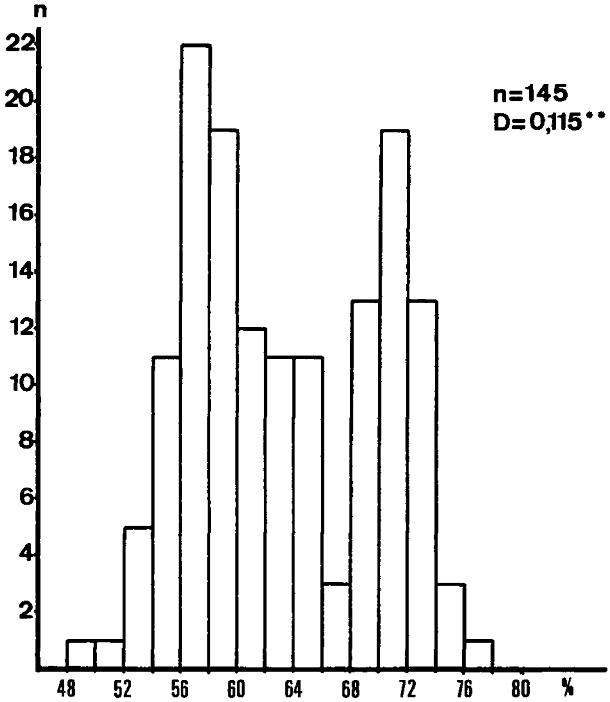

FIG. 3

Frequency distribution of the lean content of the 7th rib cut, testing station data.
Distribution du pourcentage de muscles dans le monocostal 7, données de station.

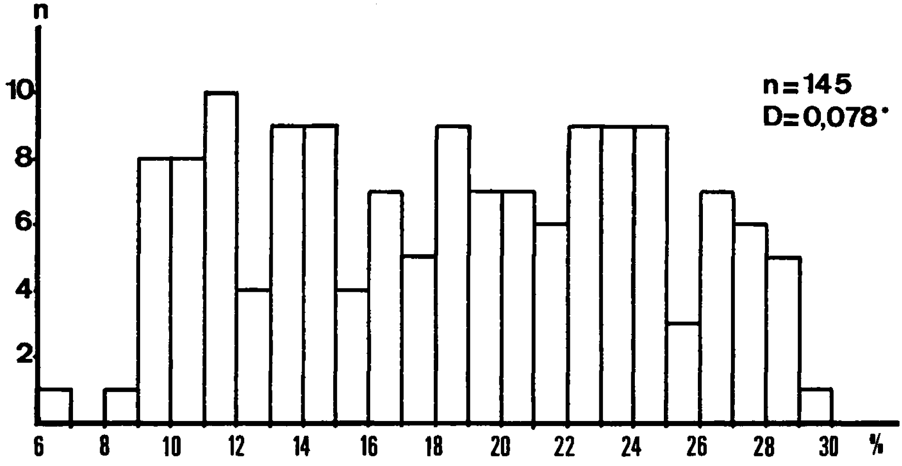

FIG. 4

Frequency distribution of the fat content of the 7th rib cut, testing station data.
Distribution du pourcentage de graisse dans le monocostal 7, données de station.

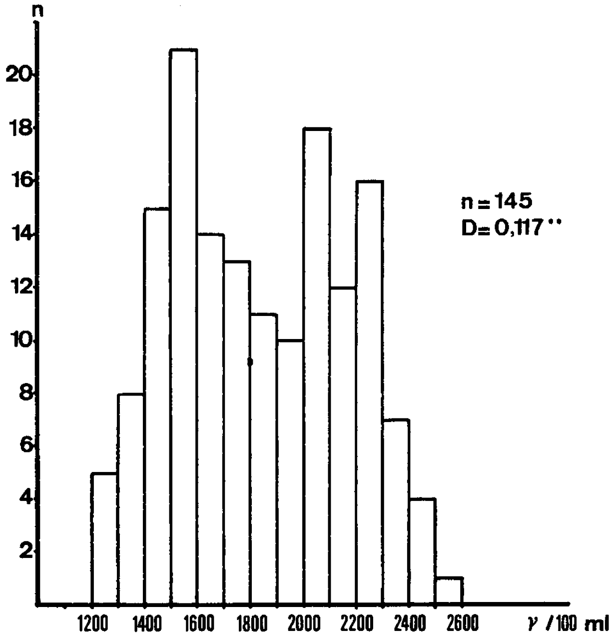

FIG. 5

Frequency distribution of the plasma content in creatinine (γ/100 ml), testing station data.
Distribution de la concentration de la créatinine plasmatique (γ/100 ml), données de station.

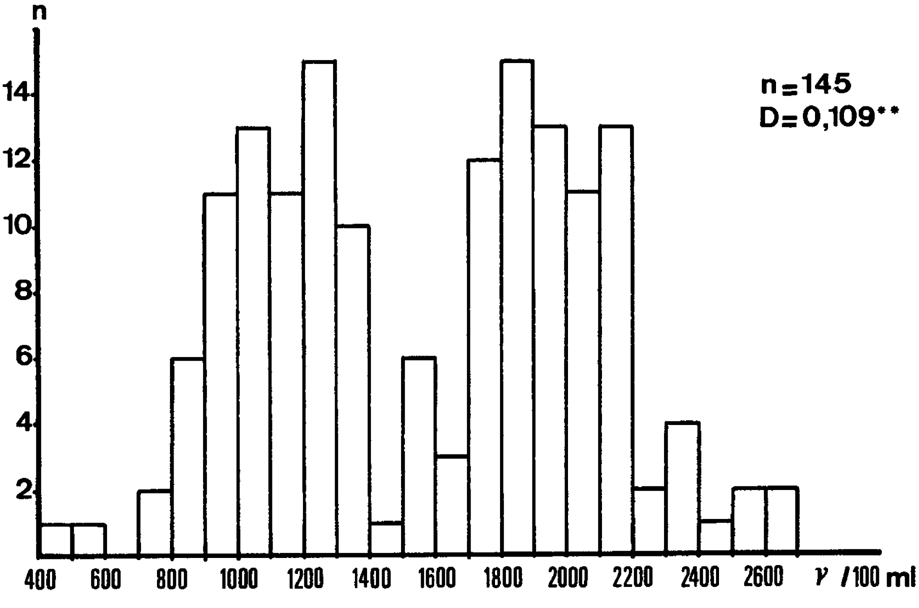

FIG. 6

Frequency distribution of the creatine content of the red blood cells (γ/100 ml), testing station data.

Distribution de la concentration de la créatine dans les érythrocytes (γ/100 ml), données de station.

TABLE 1

Test of Normality (D) and the parameters of the component distributions (means μ_1 and μ_2, common variance σ^2, proportion q of double-muscled bulls, and their standard error SE) of the distribution of 6 variables measured in station on one year old bulls ($n = 145$).

Test de normalité (D) et paramètres des distributions composantes (moyennes μ_1 et μ_2, variance commune σ^2, proportion q de taureaux culards et leur erreur standard SE) de la distribution de 6 variables mesurées en station chez des taureaux d'un an ($n = 145$).

	D (prob)	μ_1 (SE)	μ_2 (SE)	σ^2 (SE)	q (SE)
Price (B.F.)	< 0.01	65.48 (0.57)	107.10 (0.66)	26.97 (3.17)	0.43 (0.04)
Dressing (%)	< 0.01	59.55 (0.13)	64.18 (0.14)	1.20 (0.15)	0.45 (0.04)
Lean (%)	< 0.01	57.48 (0.41)	69.23 (0.52)	10.50 (1.38)	0.41 (0.05)
Fat (%)	< 0.025	12.99 (0.53)	22.89 (0.50)	10.55 (1.55)	0.52 (0.05)
Creatinine (γ/100 ml)	< 0.01	1 521.82 (23.70)	2 084.91 (25.54)	29 998 (4 174)	0.47 (0.05)
Creatine (γ/100 ml) .	< 0.01	1 075.15 (30.97)	1 934.70 (29.20)	55 746 (7 336)	0.52 (0.04)

2. *Field data*

The distribution of the score of fleshiness in the overall population is pictured in figure 7. Once again, this graph shows a bimodal distribution. The non-normality is illustrated by the probit transformation of the cumulative frequencies (fig. 7). The test of normality is significant ($D = 0.124$, $P < 0.01$) ; the characteristics of the 2 component distributions are given in table 2. The distance between the means of the 2 distributions is about 3.5 standard deviations. The factor 4.5 was found for the two component distributions of the backcross (HANSET & MICHAUX, 1985).

The distributions of the score of fleshiness in the offspring of the 4 mating types are shown in figure 8. In each case, the test of non-normality is highly significant. The characteristics of the component distributions and their proportions are given in table 2.

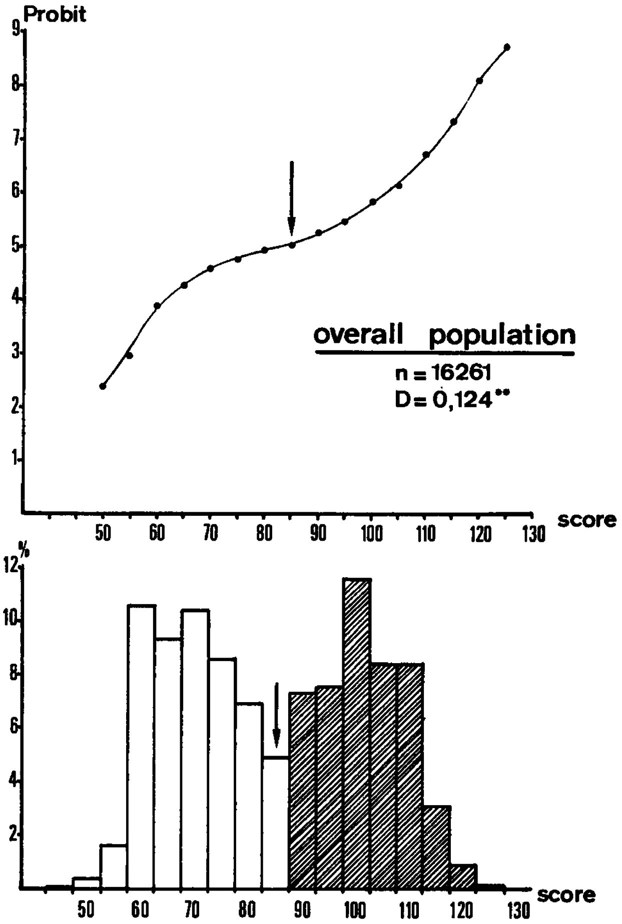

FIG. 7

Frequency distribution in field data of the score fleshiness in the overall population born from A.I. bulls.

Distribution du score de développement musculaire dans la population générale née de taureaux I.A. (données de fermes).

The striped area corresponds to the double-muscled phenotype. Above : the probit curve as a test of normality.

La zone hachurée correspond au phénotype culard. En haut : la courbe des « probits » en tant que test de normalité.

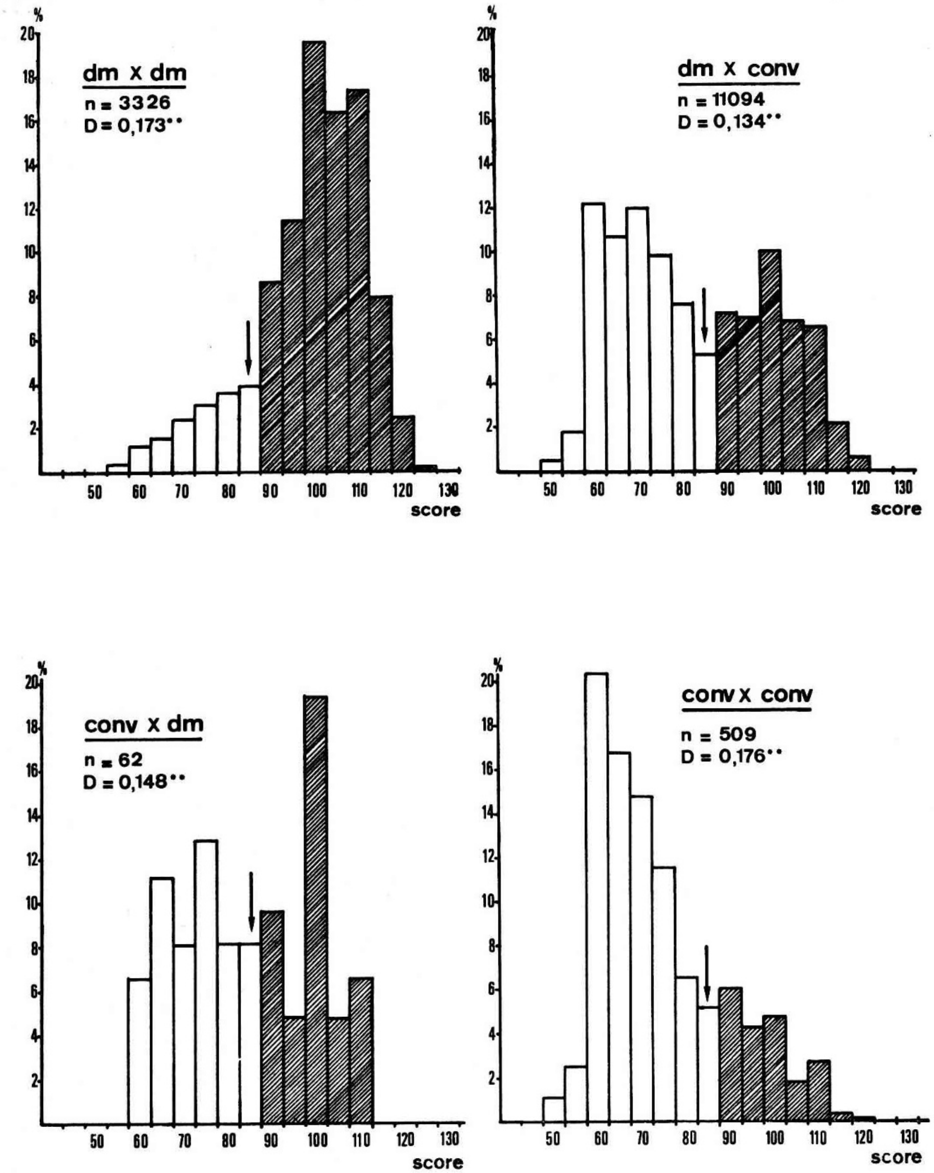

FIG. 8

The frequency distribution of the score of fleshiness for each of the 4 mating types in field data :
double-muscled × double-muscled ; double-muscled × conventional ;
conventional × double-muscled ; conventional × conventional
(dm = double-muscled, conv = conventional).

Distribution du score de développement musculaire
pour chaque type d'accouplement (données de fermes) :
culard × culard ; culard × normal ;
normal × culard ; normal × normal (dm = culard, conv = normal).

The striped area corresponds to the double-muscled phenotype.
La zone hachurée correspond au phénotype culard.

TABLE 2

Test of normality (D) and the parameters of the component distributions (means μ_1 and μ_2, common variance σ^2, proportion q of double-muscled animals and their standard error SE) of the distribution of the score of fleshiness at 12 months of age in the overall population, for each mating type and for the cow population.

Test de normalité (D) et paramètres des distributions composantes (moyennes μ_1 et μ_2, variance commune σ^2, proportion q d'animaux culards et leur erreur standard SE) de la distribution du score de développement musculaire à 12 mois dans la population générale, pour chacun des types d'accouplement et pour la population de vaches.

	D (Prob.)	μ_1 (SE)	μ_2 (SE)	σ^2 (SE)	q	Antimode
Overall population						
n = 16 261	< 0.01	69.64 (0.11)	100.84 (0.11)	75.60 (0.97)	49.31 (0.44)	85.24
Mating types (dm = double-muscled, conv = conventional) Sire × dam						
dm × dm n = 3 326	< 0.01	74.76 (0.58)	102.83 (0.19)	73.55 (2.20)	86.11 (0.78)	88.79
dm × conv n = 11 094	< 0.01	69.51 (0.13)	99.83 (0.15)	74.56 (1.18)	42.37 (0.53)	84.67
conv × dm n = 62	< 0.01	71.92 (1.75)	97.86 (1.78)	60.66 (13.00)	49.16 (7.51)	84.89
conv × conv n = 509	< 0.01	67.47 (0.49)	95.78 (0.95)	65.57 (4.94)	24.12 (2.23)	81.62
Cow population						
n = 3 529	< 0.01	68.31 (0.19)	102.35 (0.27)	68.17 (1.79)	33.35 (0.84)	85.33

C. *Parent-offspring regression*

The distribution of the score of fleshiness of the cow population (n = 3 529) is depicted in figure 9. The characteristics of the 2 component distributions are given in table 2.

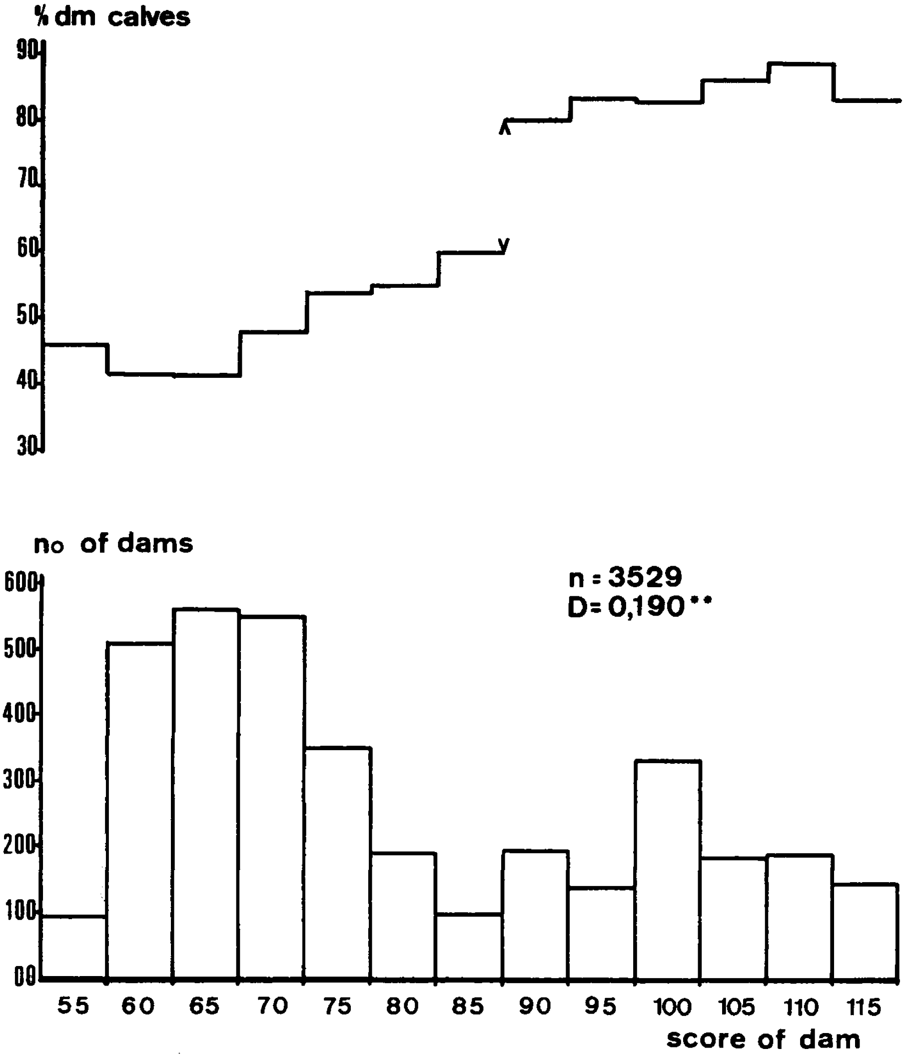

FIG. 9

Regression of the proportion of double-muscled (dm) calves on the score of fleshiness of the dams in field data.

Régression de la proportion de veaux culards (dm) sur le score de développement musculaire des mères (données de fermes).

Below : the frequency distribution of the muscle score of the dams. Above : the proportion of double-muscled calves for each dams' score.

En bas : la distribution du score des mères. En haut : la proportion de veaux culards pour chaque score des mères.

The proportions of double-muscled calves (scored soon after birth) for each score class of the mothers are also shown in figure 9. A trend is obvious but with a break at score 85 (the antimode) although all cows, whatever their conformation, were bred to the same A.I. bulls. The deviations of these percentages from their linear regression on the fleshiness score could be tested. The total variation of the proportions is partitioned in a part due to the linear trend and in a part due to deviations from the regression line (table 3). The hypothesis of linearity is not accepted.

TABLE 3

Regression of the proportions of dm calves on the score of fleshiness of the dams and of the sires.

Regression des proportions de veaux culards sur le score de développement musculaire des mères et des pères.

	Dams	Performance-tested sires mated to	
	Cow population (n = 3 529) (fig. 9)	conventional cows (n = 5 803) (fig. 10)	double-muscled cows (n = 1 084) (fig. 10)
Total variation	$\chi^2_{11} = 39.847$	$\chi^2_6 = 81.49$	$\chi^2_5 = 43,85$
Linear trend	$\chi^2_{12} = 478.86$	$\chi^2_1 = 71,32$	$\chi^2_1 = 31.98$
Deviations from regression line	$\chi^2_1 = 438.99$	$\chi^2_5 = 10.17$	$\chi^2_4 = 11.87$
Test of linearity	$P < 1\%$	$P < 10\%$	$P < 2\%$
		Joint probability : $\chi^2_4 + \chi^2_5 = 22.04$, $P < 1\%$	

Subscript numbers are degrees of freedom.

The percentages of double-muscled calves produced by the 38 performance tested sires either with conventional cows of with double-muscled cows were plotted on the muscling score of the sires, figure 10. A break at score 100 is shown for both conventional and double-muscled cows. This break point is higher than above (100 vs 85), the likely reason is that these animals are selected bulls reared on a high energy diet in contrast to heifers distributed in a wide range of environments. The test of linearity within cow type are also given in table 3. The combination of these 2 tests leads to a joint probability smaller than 1 p. 100, again rejecting linearity of percentage of double-muscled calves on bull muscle score.

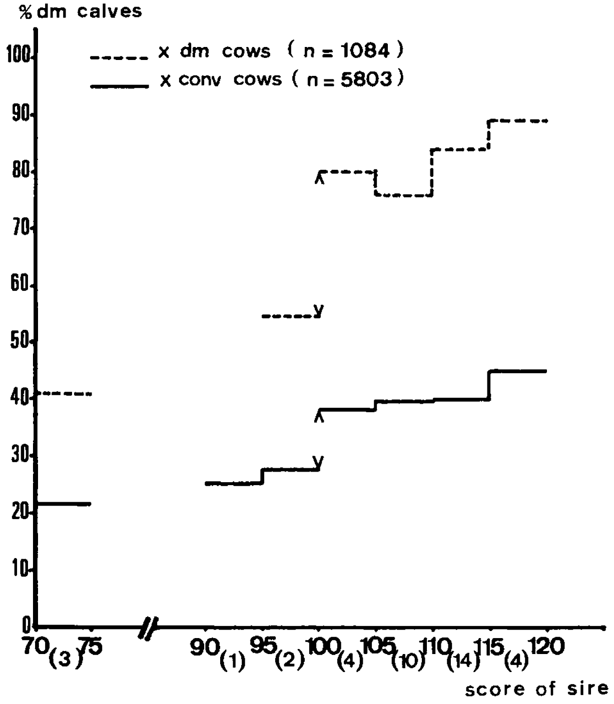

FIG. 10

Regression of the proportion of double-muscled (dm) calves on the score of fleshiness of the sires (performance-tested A.I. bulls) mated either to double-muscled cows (broken line) or to conventional cows (conv, solid line) in field data.
On the x-axis, in brackets, the number of A.I. sires corresponding to each score.

Régression de la proportion de veaux culards (dm) sur le score de développement musculaire des pères (taureaux I.A. testés sur leurs performances) accouplés soit à des vaches culardes (en pointillés) ou à des vaches normales (conv, trait plein) (données de fermes).
En abscisse, et entre parenthèses, le nombre de taureaux correspondant à chaque score.

C. « *Between sires* » *variation*

The influence of the sire on the score of fleshiness of its offspring was studied in an analysis of variance where the « between sires » component was estimated. The analysis, which concerns double-muscled sires only, has been repeated for each conformation and each sex. The results of these analyses are given in table 4.

TABLE 4

Mean (μ), phenotypic (σ) and genotypic (σ_g) standard deviation, heritability (h^2) and its standard error (SE) of the score of fleshiness for each sex - conformation class.

Moyenne (μ), déviation standard phénotypique (σ) et génotypique (σ_g), héritabilité (h^2) et son erreur standard (SE) du score de développement musculaire pour chaque classe sexe - conformation.

Sex - conformation classes	Sample size	N° of sires	μ	σ	σ_g	h^2	(SE)
Male dm	1 330	40	103.6	7.46	3.21	.186	(.066)
Female dm	5 668	59	101.5	7.40	3.17	.183	(.039)
Male conv	947	40	69.8	8.19	2.24	.075	(.056)
Female conv	5 653	59	70.6	7.85	2.00	.065	(.019)

(dm = double-muscled, conv = conventional).

IV. Discussion

The segregation of two biological types within the commercial population of *White and Blue* cattle bred by A.I. is clearly demonstrated on station data and also on field data, in spite of the lack in precision regarding classification and scoring performed on the farm.

Considered alone, the segregation of 2 entities within a population does not prove but supports the hypothesis that a single major gene is involved. The shape of the distributions of the score of fleshiness for the different mating types, the similarity of the means of the component distributions across the matings, the proportions of double-muscled offspring, all these features strongly suggest that a major gene, mainly recessive, is involved as was already concluded in the first paper.

100 p. 100 double-muscled calves are theoretically expected from double-muscled × double-muscled matings *(mh/mh × mh/mh)* while only 86 p. 100 were found. Nevertheless, the conventional calves born from this mating type have a better average score (tabl. 2) (74.8 vs 69.6) than conventional type calves from other mating types. Also the observed percentage could be biased downwards. In fact, cows could be recorded as double-muscled while they are really conventional and calves be considered as conventional while they are really double-muscled. Any error of recording will thus result in a decrease of the expected percentage.

Theoretically, the mating double-muscled × conventional will produce a maximum of 50 p. 100 of double-muscled calves (from *mh/mh* × *mh/+* matings) depending on the gene frequency among the conventional cows. The observed percentages were 42.37 p. 100 and 49.16 p. 100 for the 2 reciprocal crosses. Similarly, the mating : conventional × conventional could give at most 25 p. 100 of double-muscled calves if both parents were heterozygous ; 24.12 p. 100 were found, showing the high frequency of *mh*/+ among conventional type in this breed. In cases where *mh*/*mh* cows are classified as conventional cows, the percentages of double-muscled calves in matings involving conventional cows will be biased upwards.

Summarizing all previous studies, MENISSIER (1982) finds that the mating double-muscled × double-muscled gives from 86 to 87.3 p. 100 of double-muscled calves, the mating double-muscled × conventional from 20.6 to 33 p. 100 and the mating conventional × conventional from 4.5 to 6.4 p. 100. The percentages reported for the mating double-muscled × double-muscled are identical with those found in this study while the results regarding the other mating types are different which is quite understandable since the *mh* gene is expected to be less frequent among normal animals of any breed other than the *Belgian White and Blue* where the sires have been mostly of the double-muscled type for several years. Therefore, the frequency of the *mh* gene among normal cows must be close to 0.5.

On the other hand, MENISSIER (1982) writes that : « the possibility of a polygenic determination of the double-muscled character, considered as an « all-or nothing » trait, cannot be totally excluded ». However, our observation of a break in the regression line of the proportions of double-muscled calves on the score of fleshiness either of the dam or of the sire on a level with the antimode of the distribution of the score is incompatible with such a genetic model since it implies an unbroken linear regression. But the fact remains that the double-muscled × double-muscled mating does not give 100 p. 100 double-muscled calves, as expected for a completely penetrant recessive gene, while such observation might be expected if more than one gene were involved. It is know that environmental factors can affect the expression of the character. The age at scoring could influence the frequency of double-muscled animals. A rise of 2 to 3 p. 100 in the proportion of double-muscled calves, whatever the mating type, takes place between the first visit at 3 months and the second visit at 12 months. On the other hand, as the feeding level, the health status and the rearing system are recorded by the technicians for each calf, it was possible to extract a subsample of animals having a good feeding level, being in good health and being in a suckler herd. In this case, the proportion, at 3 months, of double-muscled calves born from double-muscled × double-muscled matings is 97.7 p. 100 (computed on 433 calves out of 3 326).

Therefore, the segregation of the 2 biological types within the population can be fairly well explained by the segregation of a major gene if account is taken of recording errors and of an environmentally induced variation in the expression of the condition. Thus we arrive at the same conclusion as in the first paper.

But other genetic factors may also play a role in the expression of the double-muscled character. As shown in table 4, significant differences exist between double-muscled sires for the score of fleshiness of their offspring. Sex of calf has no influence on the heritability estimate, but the heritability was distinctly higher for double-muscled than for conventional offspring. In other words, within the double-muscled class, there is significant genetic variation in the degree of fleshiness which could be exploited by selection, there could be independent loci and be specific modifiers of the *mh*/*mh* genotype.

Compared with the effect of the major gene, this additional genetic variation (3.2 units)^2 is much smaller since the variance between the two genotypes, *mh*/*mh* and *mh*/+, is given by :

$$(\mu_1 - \mu_2)^2/4 = (16 \text{ units})^2 \quad \text{if} \quad \mu_1 = 102 \text{ and } \mu_2 = 70.$$

The question of whether the accumulation of modifiers by selection could alter the recessivity of the *mh* gene remains unanswered. A reliable method of identification of the 3 genotypes at the *mh* locus is needed for a more precise understanding of the gene expression in the heterozygote and in the homozygote. Therefore, it seems that the formal genetics of the double-muscling condition in cattle is now understood and new approaches (linkage studies) and new genetic tools (molecular biology) are now needed for the dissection of the genome.

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