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Informations

Twenty years of research in beef cattle breeding in France (1956-1976)

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(*) In cooperation with POPESCU (cytogenetics), GROSCLAUDE (biochemical polymorphisms), LAUVERGNE (visible mutants), MÉNISSIER, BIBE, COLLEAU, FOULLEY and FREBLING (polygenic traits).

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1. — Introduction

Interest for French research work in the field of beef cattle breeding is quite general. French beef cattle populations, which first appeared well fitted to the new requirements of intensive production systems and market demand are now, for most of them, widespread on all the continents. France being located at the meeting point of the main physical areas and human influences in Western Europe (oceanic, alpine, continental and mediterranean) its cattle industry is concerned with a wide variety of populations, environments and production systems. Further the early development of AI and reproduction control in France where the proportion of cows inseminated is among the highest in the world, chiefly in suckling herds, makes it easier to manage more efficient breeding programs in small holding farms. For all these reasons French research work on beef cattle breeding could lead to some original ideas and results in a field where scientists have limited the scope of studies to specific breeds (*Hereford, Brahman, Holstein*) under extensive management systems where the matings are chiefly by natural service.

The first studies on beef cattle breeding were made in France around 1956: they were devoted to measures of growth rate in farms and of carcass quality in slaughter houses. Some *Charolais* breeders of the Nièvre area (*Syndicat de contrôle des performances des éleveurs de la Nièvre*) and of the AI center of Soual (Aveyron-Tarn) in the zone where beef sires where mainly used for terminal crossing, were the first organization conducting experimental breeding programs in connection with research workers of the « *Institut National de la Recherche Agronomique* » (I.N.R.A.). After 1963, facilities became available in France for the performance testing and progeny testing of AI bulls, first on fattening traits, then in 1967 to 1970 on fertility and maternal ability of their female progeny. Such testing stations were complementing field data, giving more complete and accurate information for studies on the genetic variation of quantitative traits in beef herds. Scientists had to integrate all this information into decision procedures at the level of breeds and AI breeding units. This research work was recognized

TABLE I

Scientific (S) and technical (T) staff of the department of animal genetics involved in research works on beef cattle breeding in 1976

Équipe scientifique et technique du Département de génétique impliquée dans les travaux sur les bovins à viande en 1976

Research or technical field		Laboratory	Location	S/T	Name
Polymorphisms	Cytogenetics	Lab. de cytogénétique	Jouy-en-Josas	S**	POPESCU P.
	Abnormalities and coat color patterns	Lab. de génétique factorielle	Jouy-en-Josas	S*	LAUVERGNE J.J
	Blood groups and biochemical polymorphisms	Lab. de génétique biochimique	Jouy-en-Josas Jouy-en-Josas	S* T	GROSCLAUDE F. HOULIER G.
Breeding Improvement	Efficiency of breeding schemes	Station de génétique quantitative et appliquée	Jouy-en-Josas	S*	ELSEN J. M.
	Breeding methods — methods of analysis of genetic variability	»	»	S	FOULLEY J. L.
	Analysis of genetic variability — Fitness traits — double muscling	»	»	S	MENISSIER F.
	Growth and feed efficiency	»	»	S	BONAITI B.
	Management of breeding schemes and experimental farms	»	»	T	FREBLING J.
	Testing stations (analysis of data)	»	»	T**	GAILLARD J.
	Field crossbreeding experiments (E.E.C.)	»	»	T	SAPA J.
	Management of the double muscling herds	»	Carmaux	T	FABRE G. P.
	Management of the cross breeding experiments		Avord	T	PERREAU B.
	Breeding in harsh environments - adaptability	Station d'Amélioration génétique	Toulouse	S*	BIBE B.

(*) These scientists are working half time on beef cattle breeding.
(**) These scientists and technicians working in Laboratories of the Department of Animal Genetics belong to professional organizations: U.N.C.E.I.A. (POPESCU) and I.T.E.B. cattle breeding section (GAILLARD).

in the « Breeding Act » voted in 1967 by the French parliament: the first experimental breeding organizations were expanded at the national level. More recently (1967-1968) experimental breeding herds directly controlled by INRA were founded: Le Pin (Western Normandy), Bourges (Center North) and Carmaux (South West); they were all devoted to more detailed analyses of breeds and crossbreeding strategies predicting the orientation of the actual beef breeding programs :

— *Le Pin au Haras* for dairy cattle breeding (milking herd)

— *Bourges* for beef cattle breeding (suckling herd)

— *Carmaux* for creating new beef strains for terminal crossing (double muscling).

Since 1961, in cooperation with the *Istituto Zootecnico e Caseario per la Sardegna* in Sassari, we have broadened the field of our activities to the studies of beef cattle breeding for marginal areas. More recently we have also been involved in studies of beef cattle breeding in French overseas tropical islands (Réunion), in Ivory Coast through the « *Institut d'Élevage et de Médecine Vétérinaire Tropical* » (IEMVT) and in other parts of the world through foreign research institutions. At the same time, research work has been done in the fields of factorial genetics (1960), biochemical genetics (1957) and later on cytogenetics (1967). In each of these fields both scientific and applied research are achieved in relation with breeding organizations. The list of scientific and technical staff of the Department of animal Genetics involved in these researchs is given in table 1.

Though there is some interest to put forward this chronological trend in the French research activities on beef cattle breeding, we shall first present the results obtained and ideas developed in a more classical way : the genetic variation concerning chromosomes, single genes and quantitative effects of polygenes, then we shall deal with the breeding strategies and selection methods of cattle populations to increase beef production.

2. — Genetic variation

French cattle breeds come from local strains primarily adapted to specific environments and selected by breeding societies, for various production traits: milk, meat and draft, before the end of the last century. Among external traits considered here, the coat color has been a major selection goal, animals of a given color pattern reared on the most efficient environments being favored in the selection process. Descriptions of these populations and breeds have been given previously by DE LAPPARENT and QUITTET.

Today they can be classified in the following way:

— dual purpose breeds which constitute the majority of animals in the dairy herds widespread in a great part of the country and chiefly in the West (*Normande*), in the North (*French Friesan*) and in the East (*Montbéliarde* : the dairy type of the French *Simmental* population);
— dual purpose breeds of local extension in dairy herds (Abondance, Tarine) and whose number is declining rapidly (Brune des Alpes);
— dual purpose breeds of larger size, more and more selected for beef traits and reared in suckling herds: *Maine-Anjou* and *Pie-Rouge de l'Est* (beef type of the *French Simmental* population);
— beef breeds: *Charolaise, Limousine* and *Blonde d'Aquitaine* formerly used for draft which result in a high muscular development;
— multiple purpose breeds: milk, beef and draft (*Salers, Aubrac*) or beef and draft (*Gasconne*) from mountainous areas, the former ones being less and less milked.

We must also mention the rare breeds (only several hundred or thousand heads): those specialized for milk in the North: *Flamande* (Flandres), *Vosgienne*

(Vosges), *Villard de Lans* (Alpes) and *Bretonne Pie-Noire*, small sized (Brittany); those selected also for meat and draft: *Parthenaise, Bazadaise* (Center West), *Blonde des Pyrénées*; those reared outside all the year round in the Mediterranean area : *Corsican* breed, *Camargue* (used for bull's fighting).

2.1. — *Polymorphisms*

2.11. — *Chromosomes*

A description of somatic chromosomes was first done by POPESCU (1,7) on *Bos taurus* and *Bos grunniens* with special reference to the comparison between chromosomes and autosomes (8). Concerning meiotic chromosomes POPESCU (1,9) estimated the number of chiasma per cell (1,10) and the coefficient of terminalization: 0.61, the number of crossing over per bivalent being around 100 in agreement with FORD's formula. An abnormally high percentage of polyploid cells has been observed at several steps of the meiosis: according to FORD, they seem to result from an artefact (16). Several studies are now under way to apply the banding procedures: with the C coloration (4, 5, 7) it has been found that a polymorphism exists in the amount of heterochromatin in the first two pairs of autosomes. The exchanges between chromatids has been analyzed through the BUDR treatment (6,26): the average number of exchanges per chromosome seems to be similar for man and for cattle; it is directly proportional to the length of the chromosomes.

A survey of chromosome polymorphism in the French cattle populations was prepared by POPESCU and CRIBIU: *Laboratoire de Cytogénétique* (INRA, *Union Nationale des Coopératives d'Élevage et d'Insémination Artificielle*) located at Jouy-en-Josas (1,3), by DARRÉ and QUEINNEC (*École Nationale Vétérinaire de Toulouse*) (21). Both laboratories have observed the Robertsonian translocation (1/29, first described on cattle by GUTAVSSON). In around 1800 animals recorded by POPESCU (25) it has been found that this abnormality is chiefly expressed in the *Charolaise, Limousine* and *Blonde d'Aquitaine* breeds: between 4 to 8 p. 100 animals affected in a non random sample of 500 recorded; 2 cases have also been observed in the *Montbéliarde* breed (out of 100 animals recorded), the *French Friesian* and *Normande* breed being free of this translocation (550 animals recorded). The resulting new chromosome seems to be a monocentric one (4, 5, 7) which lead to the hypothesis of an old origin of the translocation. It is transmitted as a simple Mendelian and it significantly affects the fertility of the female progeny from translocated sires (40 p. 100 decrease in the conception rate). From an analysis of meiotic chromosomes of translocated bulls, POPESCU found around 19 p. 100 of non equilibrated metaphasis which could produce after a normal development, letal embryos and then reduce the fertility of affected bulls. Many facts indicate that, in France, this translocation seems to appear more frequently in breeds (see above), strains and lines selected for larger size and muscular development. Lastly, a new Robertsonian translocation concerning two chromosomes between the 10th and 22th pairs has been observed on an animal affected by the previous one (18). POPESCU also described a case of significantly longer Y in a *Charolais* bull (17); using different banding procedures he has analyzed a pericentric inversion affecting a *Norman* bull and transmitted to 50 p. 100 of its female progeny (14,27).

Both laboratories are also studying the chimerism on leucocytes from heterosexual twins. In about 1000 AI bulls, the frequency of animals expressing some

chimerism has been estimated to be 1.22 p. 100, that of female cells from affected animals varying between 6.25 and 100 p. 100. The fertility of two extreme bulls has been analyzed: one was over the average of the AI center, the other was significantly lower with a marked deviation of the sex-ratio favouring female calves.

2.12. — *Genes*

2.121. — *Biochemical mutants*

a) *Blood groups*

Research work on bovine blood groups started at Jouy-en-Josas in 1956; the first goal was to create and develop a typing to which breeders and breeding associations could submit cases of doubtful identification and parentage control. In this field the two main objectives were to develop the knowledge on cattle blood group systems and to establish the specific blood groups of French breeds.

A new blood group system, the 11th one, named *T'*, was discovered in 1965 (33). In addition, the 80 or more reagents produced in the laboratory have led to improved discrimination within the *B*, *C*, *F* and *S* systems (29, 31, 34, 35, 36, 37). Results on the S system are particularly spectacular since it has been shown that the system involves at least 17 alleles instead of the 5 considered initially (29, 31, 34, 35). Its characteristics are very variable from one breed to another and it effectively differentiates Northern French breeds from the Southern ones.

Data on blood groups have been gathered from most French breeds, and now work is still being done one rare breeds (*Vosgienne*, *Villard de Lans*). A phylogenic study will be carried out on all the related information. Until now, results have only been published on the genetic variability and the phylogenic situation of the *Montbéliarde* (28,30) and the *Flamande* (38) breeds. The study on the first breed (1960) showed that the genetic variability of the breed remained very large and that was becoming genetically distinct from the *Simmental*. The *Flamande*, which was formerly considered as a population of small genetic size, was found to possess in 1968 a genetic variability similar to the most widespread *French Friesian* breed (F.F.P.N.).

b) *Antigens of white cells and fluids*

Immuno-genetic studies have been devoted to antigens in serum and saliva (39) and on platelets (41, 42). In addition, hetero and iso-antiglobulinic reactions were performed in cattle; the first type of reaction gave evidence of antigenic factors non detectable by hemolysis the second type was used to determine inhibitory serum-groups (40, 43, 41, 45, 46). The genetic of 3 inhibitory factors was studied (47, 48); two are present on immunoglobulins and are similar to human G_m factors; the third one is related to the soluble J substance. It is possible, using several refined methods, to subdivide this J substance.

In man and several laboratory species, the major histocompatibility system, which concerns lymphocyte antigens, is closely linked to genes involved in control of the immune response. A study of cattle lymphocyte groups was started in cooperation with R.L. SPOONER (*Animal Breeding Research Organization*) (A.B.R.O. Edinburgh) and M. VAIMAN (*Commissariat à l'Énergie Atomique*). At the present time, more than 30 specific reagents have been obtained in a pure state.

c) *Antigens of spermatozoa*

Some antigenic characteristics of bull spermatozoa were investigated in order to establish if populations of spermatozoa could be fractionated on the basis of these properties (49). A technique for the purification of spermatozoa was first described (51). Further work led to the conclusion that several blood group antigens of the S system were present on spermatozoa (50). However, the immunization of heifers with spermatozoa was unsuccessful (52).

d) *Milk proteins*

Combined biochemical and genetic research has been undertaken since 1964 in order to elucidate the genetic determinism of the main protein components of milk.

A survey of the electrophoretic polymorphism of α-lactalbumin, β-lactoglobulin, α_{s_1} $\bar{\beta}$ and $\overline{K}$ caseins has been made in 15 French bovine breeds, in some African and Asiatic bovine breeds and in African and Malagasy zebus (56, 53, 65). A new variant of α_{s_1} casein was discovered in the *Flamande* breed and later in several other breeds (55). In addition, a new variant of β-lactoglobulin has been found to occur in the *Montbéliarde* (55). The data on electrophoretic polymorphisms have the same value for phylogenic studies as those on blood groups. The alterations specific to all the genetic variants of α_{s_1} $\bar{\beta}$ and $\overline{K}$ caseins were determined (57, 58, 59, 60, 61, 64, 65). It was shown that the common variants were the same in zebu and in bovine; this indicates a close genetic similarity between the two species (63).

The genetic determinism of α_{s_1}, β and K caseins was found to be original since these proteins are synthesized by a group of three closely linked loci; this situation is comparable with the structure known in modern biology as an « operon » and it may be supposed that it plays a role in the overall synthesis mechanisms of these proteins (53, 54, 56, 62, 65). Recently it was shown that the fourth casein species (α_{s_2}) is also synthesized by a locus closely linked to the α_{s_1}, β, K cluster; the 4 caseins are thus controlled by a group of 4 loci behaving in fact like a single hereditary unit. The genetic analysis of this unit in cattle populations shows the existence of a strong linkage desequilibrium between these loci (65). Bovine caseins thus represent the only concrete situation where the evolution of relationships between closely linked loci under the effect of recombination, genetic drift and selection may be evaluated empirically (65).

Further, the study of several genetic variants of caseins have provided clues for understanding the mechanisms of phosphorylation of these proteins (60, 62, 64, 65).

2.122. — *Visible mutants*

a) *Coat color*

A genetic study of the variation in the coat color patterns of French, Italian and Swiss cattle breeds is now underway by LAUVERGNE (68, 69, 75, 76); biochemical analyses of the maelanin were done in connection with MISUCARA *et al.*: Naples (77).

b) *Hereditary defects*

Systematic studies were completed on abnormal defects which appear in the progeny of AI bulls when a genetic determinism is suspected (LAUVERGNE).

Out of several studies involving cases of polydactyly (84) and hypotrichosis (90) in the *Norman* breed, amputation (84) and bulldog (87) in the *Friesian*, hydrocephaly (89) in the *Limousin*, two types of genetic defects have been analysed more in detail. The probatocephaly (also named " sheep head "), observed only in the progeny of *a Limousin* bull, is a subletal abnormality, death occurring during the embryonic life (around 15 p. 100 of ova), the fetal stage and after birth. From field data and several types of experimental planned matings, it appears that this trait is determined by a dominant gene with incomplete penetrance : 20 p. 100 of the ova (91, 94). The syndrom of arthrogryposis and palatoschisis (SAP) in the *Charolaise* population is generally expressed at the same time by a cleft palate and arthrogryposis of legs. It is due to a recessive gene, the frequency of which, under several hypotheses, is around 0,20 with a very low penetrance (0.12) in both sexes (92, 98). The persistance of this gene, however unfavoured by natural selection, may be explained by a superiority of heterozygotes for productive traits, but at present, nothing has been found in France to support this hypothesis. An international project coordinated by LAUVERGNE is now in progress on this defect. Further, LAUVERGNE and LEFORT (79) have derived a general model to express the frequency and the penetrance of the gene at the equilibrium state from the analysis of progeny testing of AI bulls.

c) *Horns*

A polled mutant which seems to be dominant with incomplete penetrance and variable expressivity has been observed 6 years ago in a Charolais pedigree herd; from different kinds of matings observed in this herd it is now questionable whether this mutant can have a negative effect on fitness and productive traits in general or not. This mutant which seems to be phenotypically different from that observed in *Aberdeen Angus* or *Hereford* could have some interest for selection in large sized beef cattle.

d) *Double muscling* (DM)

Detailed studies have been done since 1960 on double muscling which affects all French beef breeds, its expression being less evident in the *Limousin* (97, 100, 101, 102, 103, 104, 105). The incidence of this trait on growth (107, 111), reproduction (112), adaptability (110) and maternal ability (111) has been analyzed chiefly in *Charolais*. Double muscling is influencing the following traits :

1. — the shape of growth curve: higher birth weight and growth rate before 3.4 months; lower growth rate after weaning and probably delayed age at body maturity;

2. — body and carcass composition (between tissues and within tissues): gradients of muscular hypertrophy and skeleton hypotrophy have been described;

3. — the adaptation to nutritional (low adaptability to roughages), climatic (low heat tolerance) and physical stresses;

4. — the fertility and chiefly the puberty which is delayed in both sexes;

5. — the maternal ability: the calving problems are mainly the consequences of the feto-maternal disequilibrium in size (item 1) and morphology (item 2); these is also a lack of maternal behaviour in dams at calving, after calving and during the suckling period, milk production being sharply lowered;

6. — the vitality and viability of calves: heart defects and respiratory diseases are the most frequent causes of death.

Studies on the genetic determinism are difficult, the variation of expressivity in DM being large and partly related to the sensitivity to various environmental stresses. Attempts have been made to establish scoring systems and indexes using live and carcass measurements in order to find a more objective and reliable recording system. Most of results from French studies on the *Charolaise* breed are in agreement with the hypothesis of a major gene effect with incomplete penetrance: 90 p. 100 of progeny calves from matings DM × DM are affected; 10 p. 100 in the case of DM × Normal or Normal × DM matings, this percentage being positively related to the muscularity of the sample of normal animals (109, 114). It seems further that the muscularity of normal animals from DM × Normal matings is intermediate between that of normal and DM animals.

The path from the gene to the traits has been explored at different levels : muscular hypertrophy is chiefly due to a hyperplasia of muscular fibers which seems to be more or less intense for each muscle according to its relative degree of hypertrophy (106). This fact together with the higher percentage of polyploid somatic cells (leucocytes) indicates the existence of disorders in the cell division. The differences occurring in the organization and chemical composition of the connective tissue have been analyzed: its lower amount is related to a smaller quantity of collagen presenting some metabolic specificity.

a) A higher urinary excretion of hydroxyprolin might indicate a larger collagen degradation or a lack of prolin for its synthesis leading to a more soluble type.

b) A lower rate of collagen sysnthesis might also be due to a reduction of the respiratory capacity in DM animals (102). Further, difference in the structure of the nephron could explain a specific filtration ability of DM for particular blood components (108).

Due to the numerous organic effects of double muscling it seems that the gene is acting very early in the embryonic life.

Research work in this field is increasingly devoted to the description and transmission of the trait in relation to its practical use for the beef industry: improving the amount and quality of meat in crossing schemes and chiefly through terminal crossing: see further (116, 117, 118, 119, 120).

2.2. — *Polygenic variation*

2.21. — *Preliminary research on growth traits* (127 to 140)

The world trend of the demand for lean meat brings into focus the interest of French beef breeds whose muscular development had been favored by selection for draft and beef production. These breeds are now used in crossbreeding all over the world to increase the beef potential of small sized hardy, dairy or beef cow populations. A similar trend was already noticed around 1950 in S. W. and Central France with dual purpose and multiple purpose cow populations no longer used for draft or milking: beef crossing gave to farmers a short term opportunity to convert milk into meat through veal and young bull production systems.

This situation explains the former interest (1960) for comparing the genetic differences of growth potential between beef breeds in pure breeding and crosses. The superiority of the *Charolaise* breed in this respect appeared more marked when the nutritional environment was better (maternal ability of dams in terminal

crossing with beef sires of other breeds). For a given growth potential, the *Limousin* breed (or *Limousin* cross) expresses a larger muscling and a better feed efficiency which is related to a lower body fat content. *Blonde d'Aquitaine* and *Piemontese* animals generally lie in an intermediate position between *Charolaise* and *Limousine* for all these traits. The within-breed variation of the growth potential of *Charolais* and *Limousin* calves before weaning has been analyzed on field data in purebred (pedigree herds) and crossbred (commercial herds using beef sires for terminal crossing through AI) (130, 134, 166). All traits involved in the direct effect of genes on growth rate and conformation score appear more variable in *Charolais*, the variation of growth rate independently of birth weight is larger in *Limousin*. Furthermore, significant genetic differences in Charolais are occurring between zones (they are related to a geographical variation in the muscular development and frequency of double muscling in the breeding area of the *Charolais*) and between pedigree herds for growth rate in the *Limousin* (131).

These studies on growth are now developed in relation with the selection of paternal breeds and strains for terminal crossing. They involve the overall genetic analysis of the growth curve up to slaughtering, feed efficiency and morphology in their effects on calving ability and carcass value.

2.22. — *Analysis of direct and maternal effects* (141 to 162)

Overall comparisons between French cattle breeds used in beef herds (*Charolaise, Limousine, Salers, Aubrac*) and between breeding types (double muscle and Normal *Charolaise*) indicated, around 1965, several genetic antagonisms between muscular development and some components of fitness. This also appeared when genetic comparisons were done between *Charolaises* strains now existing in different countries and selected under different goals and management systems, all of them being imported (153) after 1910 from the same French population. The more intensive the system and the higher the muscular growth, the lower are the fitness traits and adaptability.

Such results lead to analyzing the between and within-breed variation of direct and maternal effects of genes for each component of the overall efficiency. Several crossbreeding experiments have been done with the aim of:

1. — comparing the paternal and maternal values of hardy, dairy and beef breeds on hardy cow populations in Sardinia: *Sarda* and *Modicana* and Southern France: *Gasconne* and *Aubrac* (173-209-211);

2. — analyzing the overall genetic variation in a factorial experiment involving the *Charolaise, Maine-Anjou* and *Limousine* breeds, a sample or pure *Hereford* being used as a control (178);

3. — performing more detailed analyses on the within-breed variation using data from the progeny test stations of AI beef sires on the value of their heifer progeny in an intensive reproduction system: first calving at 2 years (*Charolaise, Limousine, Blonde d'Aquitaine*) (162).

First results obtained between hardy and beef breeds as well as within the *Charolaise* confirm the genetic antagonism between the direct effect of genes on the muscular development and all the maternal effects influencing the fitness traits.

The attention of research workers has notably been drawn upon these last traits that are particularly depressed in French beef breeds due to the extreme

selection in favor of muscular growth and to the confined environment in which this selection has been accomplished. This problem is now important for the adaptation of French beef animals to more extensive management systems. The most comprehensive studies have been devoted to calving ability (146 to 161). This trait is determined by incompatibilities between the relative dimensions of the fetus and the pelvic opening of the dam at birth: they are expressed under threshold effects. The genetic variation of the sire and dam components of calving ability have been estimated in purebreds and crossbreds. Some studies have also been devoted to the fertility of heifer and cow and to the endocrinological effects: Particular attention has been paid to twinning ability, the level of which seems to be the highest in *Charolais* and *Maine-Anjou* breeds (145): the natural variation of this trait has been analyzed within the latter breed showing large age, season and herd effects. Such an analysis on field data is now completed by studies on the LH content and ovulation rate of animals from an experimental herd of cows selected on their twinning ability. The natural between-breed variation of this trait seems to be directly related to their ovarian sensitivity to PMS. These results have been observed on contemporary double muscle animals from different beef breeds (Carmaux experimental herd-144).

In such a research field we are concerned with studies in other disciplins (physiology, nutrition, pathology) to analyze the mechanisms underlying the relations and chiefly the antagonisms between genotypic contributions of calf and dam. These antagonisms which explain the genetic homeostasis of breeds should be particularly well explored when developing crossbreeding schemes between extreme biological types and, furthermore, when considering a practical use of ova transfer technics.

2.23. — *Adaptability*

It is more and more clear that beef enterprises will often make profit through the use of marginal lands and by products of crops using their own female calves and those in excess from the dairy herd for replacement. Contrary to the dairy situation, this leads to the use of a wide variety of breeding types in a large scale of environments. This is to stress the importance of studies on the adaptability of animals to fixed and random effects of environmental components: nutritional, pathological, climatic and behavioural.

Several experiments run in Sardinia and in the Central part of France showed that under an extensive management, local hardy breeds expressed a more efficient overall maternal value than beef or dual purpose breeds. If the use of first crosses: beef × hardy, generally results in a higher weaning weight than that of pure hardy calves, this advantages is reduced when the feed allowance of dams is lowered (higher stocking rate for example). It completely disappears when hardy beef cows are managed under the traditional raising system involving a partial milking (165): only the residual milk being available for calves which are reared apart of cows. In another experiment where dairy, dual purpose and beef cows were raised in a dairy system we have stressed the very low ability of beef animals (*Charolais*) for milking (cows) and artificial feeding (calves).

During the postweaning phase, differences in the relative growth rate and food conversion of dairy (*Friesian*), hardy (*Salers*) and beef (*Charolaise, Limousine*) bulls and steers fed at different energy levels have been analyzed; the efficiency of fattening young bulls appeared more favourable under intensive systems (BERAN-

GER, personal communication). Variations have also been observed in the relative ability of *Charolaise, Blonde d'Aquitaine* and dairy bulls to grow on grass and pelleted feeds.

Research work is in progress to find simple tests expressing directly the adaptability of animals to a specific stress or to a combination of stresses which characterizes a harsh environment. The monthly variation of weight and that of rectal temperature are explored in relation to the adaptation of beef cows to a low feed allowance and high temperatures in the Mediterranean area (Sardinia). More recently the between-breed variation of heat tolerance has been recorded (test of 10 hours in a climatic chamber) on 500 animals of the same age (14 months). Hardy breeds and breeds located in Southern France are generally more tolerant than Northern beef and dairy types. Some differences also occur in the way of transferring heat during the stress period: sweating panting (etc.). The value of such tests has to be checked in field trials conducted in tropical or subtropical environment.

3. — Breeding improvement

3.1. — *Practical breeding schemes*

The situation of beef cattle breeding was the following when research work began in this field in France:

— existence of powerful breeding societies promoting their breeding stock
— spreading of AI in dairy and commercial beef herds chiefly for commercial crossing.

The first goal of research workers was to establish breeding schemes which could operate efficiently through breeding societies and AI centers:

1) for terminal crossing in dairy or beef herds (breeding for growth traits and direct effects of genes)
2) for purebreeding in our large population of beef cows (1.5 million).

3.11. — *Terminal crossing* (181 to 196)

It was clear at the beginning and from previous studies on the genetic variability that these two types of goals were largely conflicting (see above). After some field trials devoted to finding simple recording systems of live weight on farms (direct and indirect estimations through live measurements) (121, 122, 125, 126) and of carcass value (estimation of fleshiness through live and carcass assessments, 123, 124), it appeared that the most efficient way of increasing beef production from breeding methods was to select sires for terminal crossing and to expand their semen through AI in the Southern and Central part of France where this type of crossing was developing. Further, AI centers in this area proved to be more receptive than breeding societies to the use of objective breeding methods.

The selection scheme of AI beef bulls for terminal crossing developed progressively from 1957 to 1970 in successive steps which were not logical but imposed by the official regulation.

1957-1965: *Progeny testing of AI bulls* for veal production (the most important

production); a progeny test index was first developed to classify samples of bulls whose progeny was recorded in the same area at the same period (185). It was designed for the growth rate and conformation score. This index has been progressively modified to fit new situations:

— the necessary limitation of calving difficulties closely related to the direct effect of sires on the birth weight of their progeny calves (188),
— the correction of genetic differences between years and breeding units through the use of a national control group of sires (192, 194),
— the evolution of a progeny test on veal production in farms to a progeny test on young bull production in stations,
— the possible use of BLUP procedures (207).

1963-1970: *Performance testing of young bulls.* This was done on a pelleted diet (alfalfa and barley) animals being fed ad libitum for some breeds, restricted for others (*Charolaise*) to avoid defects of legs. If performance testing was done after normal weaning time (6-7 months), this restriction limited the influence of variation in the milk production of dams on the following growth rate of their calves. This was particularly important with double muscle animals (Carmaux).

The performance test index gives the same statistical weight to conformation score, growth rate and feed efficiency (expressed independently of growth rate and weight).

1966 *and there after: Organization of contract matings* between top progeny tested sires and a nucleus of beef cows to completely integrate the scheme from one generation to the next. At this stage several ways of producing young sires are compared:

— normal purebred beef animals,
— normal crossbred beef animals,
— D.M. crossbred animals (INRA experimental farm of Carmaux). The production of crossbred sires aims at exploiting the benefit of heterosis on traits like sexual precocity which is delayed with increased muscling and at associating the growth potential of breeds like *Charolaise* and *Maine-Anjou* with the long-bodied shape and lower birth weight of others (*Blonde d'Aquitaine, Limousine*).

Procedures have been developed to estimate the breeding value of sires at each step of the scheme taking into account the accumulated information obtained during the operation. The realized genetic progress resulting from the application of this scheme has been analyzed according to the incidence of decisions taken at each step described above (190, 193). Cooperative organizations in charge of managing such schemes need general advice as to the most efficient way to spend their money for livestock improvement (203). Following the procedures used in a former study on the optimization of progeny testing schemes of AI sires for terminal crossing (201), we have compared different strategies involving performance testing, progeny testing and a combination of both selection methods. It appears that performance testing is sufficient to select bulls for a commercial use, progeny testing being limited to the choice of top sires to produce young sires for the next generation (202). The development of such integrated schemes is now limited on the sire paths (sire-son and sire-daughter) but the possible use of ova transfer technics could be a good opportunity to develop breeding methods taking into consideration the dam paths (205). For a given increase in the inbreeding coefficient and with the actual feasibility of the technics, such a strategy

can result in a large increase of genetic progress. One is faced here with many risks, those related to the technology and those biologically involved in selecting a specialized sire line whose females selected on traits expressed before puberty will then never calve and express those traits for which their genetic potential is low (reproduction, adaptability).

An important point in developing terminal crossing operations is the choice of cows to be crossed with beef sires according to their age. It appears that the same sire line should not be used on cows and heifers. Theoretical studies for optimizing the sample of cows to be crossed with beef sires in a dairy herd have been done considering the discounted relative profits from milk and meat (206). The advantage of avoiding beef crossing on any heifer is variable according to several parameters among which is the difference in the overall breeding value for meat production between terminal sire lines to be used on cows and those to be used on heifers. Following this result, experimental work was done (*Union Auvergne-Limousin*) to select a small sire line suitable for crossing on heifers (chiefly the dairy heifers).

3.12. — *Schemes for reproductive traits* (197 to 200)

In the purebreeding area, chiefly with *Charolais*, after previous studies on the variation of growth rate before weaning it appeared necessary to give more consideration to fitness traits (fertility, calving and maternal ability). Such traits were not selected in small French beef herds as they were selected under natural selection in large herds of British breeds (America, Australia, South Africa). The breeding improvement of such maternal traits involved progeny testing of bulls. Developing this method to obtain a random sample of female progeny calves and to spread the genetic progress was facilitated in France because of the large development of AI, mainly in the Limousin and Blonde d'Aquitaine areas. The breeding schemes now operating for 5-10 years involve the following steps:

1) Sampling of top dams at 6 years on their numerical efficiency and on their index concerning the weaning weight and weaning conformation score of their progeny calves (mothering ability). They are promoted for AI and bred with semen from the top progeny tested sires.

2) Selection of male calves thus obtained on their preweaning growth rate and conformation, animals with the heaviest birth weight being discarded.

3) Performance testing of these male calves including traits in addition to those considered in the terminal crossing scheme such as pelvic measurements which proved to be useful for the culling of extreme young bulls which will transmit poor calving ability to their progeny calves.

4) Progeny recording: around 150 progeny calves are produced at random from each young bull; this number is required to estimate in field conditions the frequency of calving risks and hereditary defects with low penetrance (arthrogryposis for example).

5) Progeny testing: 20 heifer progeny calves are sampled at weaning for each sire. They are fed at a high level at one location and they are all inseminated with the semen of a control bull for a first calving at 2 years. This standard and intensive system, not common in the French beef industry, is supposed to increase the efficiency of the scheme by shortening the generation interval and allowing a larger expression of the genetic variability of traits like calving and mothering ability.

Standard indexing procedures of beef sires are now in progress. On the other hand, studies on the optimum way of integrating these different selection steps are difficult, due to the uncertainty in the possibilities of partitioning costs and benefits between users of natural service and AI, between pedigree breeders and commercial producers. We are now considering a scheme in which the genetic progress would be spread not only through AI with the top sires bul also through the production of young bulls for natural service by inseminating the elite cows of pedigree breeders with semen from these top sires.

Like for the terminal crossing scheme, INRA is selecting sires on specific goals and using more sophisticated procedures. It is done in two directions:

1) Breeding scheme for twinning ability in an open herd of Charolais and Maine Anjou cows: we plan to use early indirect measurements of twinning ability and ova transfer technics in order to increase the efficiency of the scheme (145).

2) Breeding for a synthetic beef breed, crossing top sires and dams from the purebred beef schemes. These projects are underway in the experimental farms of Le Pin-au-Haras and La Minière.

3.2. — *Crossbreeding systems* (208 to 212)

Many facts and figures (see above) support a larger and more efficient use of crossbreeding in the beef industry (Crossing is now practical limited in France to terminal crossing):

— the incompatibilities and genetic antagonisms between the direct and maternal effects of genes acting on the overall efficiency.

— the hybrid vigor resulting from both direct and maternal effects of genes.

— the genotype × environment interaction which can be exploited best when locating each breeding type of a crossbreeding scheme (calf and dam being or not separated) in its optimal environment;

— the age effects on some maternal influences (calving and maternal ability) which could lead to choose the sire breed for each dam according to her age (complementarity). On the other hand, the large variation of cattle breeds in size and muscling and the large expansion of AI in beef herds are creating favourable conditions for the use of crossbreeding systems. Conversely, the small size of herds and the lack of organization of the beef industry are real limiting factors in this process.

Several studies have been completed on this subject or are now in progress, using the experimental facilities available after 1967 (Le Pin, Bourges, Carmaux), all of them being devoted to the comparison of crossbreeding systems starting from our dairy, dual purpose, hardy or beef cow populations. They are summarrised in Table 2 and figure 1 gives the locations on the French area.

Concerning the dairy herds, several strategies are compared (Le Pin au Haras) starting from the most widespread French dual-purpose breed: the *Normande*:

— grading up to *Holstein* (U.S. or Canadian);

— criss crossing with *Holstein*;

— selection for or against milk (using the best and the worst indexed sires from the French national AI dairy scheme).

TABLE 2

Gross-breeding experiments operated by the department of animal genetics.
Expériences de croisement menées par le Département de génétique animale

Breeding goal	Population	Location	Scientific leader	G_0' Dam (2) (Breeds in the experiment)	G_1' Heifer progeny for breeding : (1) (2)	
					Breeding type	Breeding system
Cross-breeding	Hardy breeds	La Minière (3)	MÉNISSIER BIBÉ	*Aubrac* (AU)	*1967* AU × AU = (H.H) CH × AU = } (B.H) BA × AU = } (B.H)	*1969-1971* Terminal crossing with selected CH and BA sires
		Carmaux and La Minière (4)	MÉNISSIER BIBÉ	*Gascon* (GA) *Blond d'Aquitaine* (BA) *Charolais* (CH)	*1968* GA × GA = (H.H) CH × GA } (B.H) BA × GA } (B.H) BA × BA } (B.B) CH × CH } (B.B)	*1970-1972* Terminal crossing with selected CH and BA sires
		Sardinia (5)	CASU BIBÉ	*1964-1970* *Sarda* (SA) *Modicana* (MO) *Brown Swiss* (BR)	*1972-1976* SA × SA } (H.H) MO × MO } (H.H) CH × SA } CH × MO } (B.H) PI × SA } BH × BR = (B.D) BR × BR = (D.D) (PI = Piémontais)	*1975* Terminal crossing with CH and PI sires
	Beef breeds	Bourges (Avord) and Le Pin (6)	MÉNISSIER BONAITI	*1970* *Charolais* (CH) *Limousin* (LI) *Maine-Anjou* (MA) *Hereford* (HE)	*1972-1976* Purebreeding (B. B.) Reciprocal, 2 way crossing Purebreeding	*1974-1983* Two way crossing Three breed crossing Purebreeding
	Dairy-purpose breeds	Le Pin-au-Haras (7)	COLLEAU	*1965-1973* *Holstein* (HO) *Normande* (NO) *Charolais* (CH)	*1968-1976* HO.HO = (D.D.) HO.NO } = (D.D) NO.NO } = (D.D) CH.NO = (B.D) CH.CH = (B.B)	*1971* Purebreeding (US and Canadian) Crisscrossing Breeding for and against milk } out of experiment
		Farms and A.I. breeding units (S.W) and Center France)	MÉNISSIER BONAITI	*French Friesian* (FR)	*1977-1978* SD (South Devon) CI (Chianina) HE CH } Sire lines for synthetic goals LI } BA } PR (Pie-Rouge) × FR	*1978-1979* Slaughtering

	Dairy and du				LI, BA, (CH.LI.BA), (CH.BA), (MA.LI), PI, B B B (white blue Belgium) — sire lines / DM sire lines × FR	Slaughtering
Crossbreeding and selection for terminal crossing	Breeds	Carmaux (8)	MÉNISSIER	*1967-1968* *Charolais* (CH) *Blond d'Aquitaine* (BA) (D M cows)	*1970-1977* CH.CH, CH.BA, BA.CH, BA.BA (B. B)	*1978* Gene pool
				1971 *Maine-Anjou* (MA) *Blonde du Sud-Ouest* (BA and LI) (DM cows)	*1974-1980* MA × BA,LI; BA,LI × MA (B. B)	Gene pool
Selection for twinning ability	Beef	La Minière (9)	MÉNISSIER	*1971-1980* *Maine-Anjou* (MA)	*1974-1983* MA.MA, CH.CH (B. B)	*1979-1987* Not yet planned

(1) H = Hardy breed; B = Beef breed; D = Dairy or dual purpose breed.

(2) Generation number, G_0 corresponding to foundation cows; for each experiment and generation number the target birth dates of animals are indicated.

(3) Regular feeding and intensive management: 1st calving at two years; synchronization of estrus (and short breeding period); use of DM sires (G_1 and G_2).

(4) Same conditions but less regular feeding and limitation of size and muscling of beef sires.

(5) Extensive feeding (grazing all the year without supplementary feed in winter) and management (1st calving at 3 years; natural service with DM sires in *Piemontage* and normal sires in *Charolais*).

(6) Confined environment: zero grazing with regular feeding all the year round; the foundation cows are transferred in Le Pin when 6 years old to be reared under a traditional system (grazing in summer; hay and silage in winter); AI on natural estrus during a short (70 days) breeding season; specific bulls are used for 1st calvings occurring at 2 years:

for G_0 heifers: progeny tested bulls giving calves with low birth weight; 20 p. 100 heifers with small pelvic opening according to their weight are crossed with Hereford for French beef cows, with Jersey for Hereford.

for G_1 heifers: *Jersey, Aberdeen Angus* and *Limousin* bulls (for this last breed we have chosen progeny tested *Limousin* bulls giving calves with very low birth weight).

(7) Experimental dairy herd with autumn and winter calvings; foundation NO cows are splitted in two groups in G_2: one selected for milk, the other selected against (use of best and worst progeny tested AI bulls for this trait).

(8) Normal feeding system for cows: grazing in summer, hay and silage in winter; artificial control of reproduction: two calving seasons with synchronization of estrus and short breeding season (60 days); this experimental herd is part of the nucleus of beef cows used to produce sires for the terminal crossing schemes (in cooperation with *Mida-test* and *Union Auvergne-Limousin*).

(9) Foundation cows selected from the national beef recording scheme on their twinning ability (2 or more twin calvings during their life); sires selected on the twinning ability of their heifers.

The use of *Charolais* crossing is also considered in these comparisons.

Using financial supports from EEC, a large field experiment involving crosses between *Friesian* cows and sires from 17 paternal breeds, breeding types or strains from France or other Western countries is now in progress. Considering the variation between paternal breeds and strains in their sexuality and rate of maturity

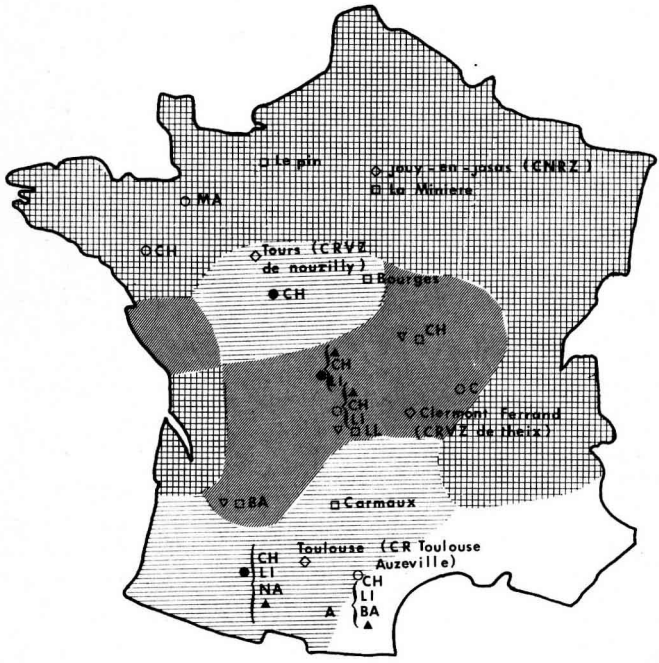

FIG. 1. — *Location of research laboratories, experimental facilities and testing stations (Beef cattle breeding)*

Localisation des laboratoires de recherche, des possibilités expérimentales et des stations de testage pour les bovins à viande

Dominant production systems

Dairy herds (purebreeding)
Dairy herds (beef crossing)
Beef herds
No cattle

☒ Research centers (3)
□ Cattle experimental herds (1)
○ Performance test stations (2)
● Progeny test stations (fattening traits of male calves) (2)
★ Progeny test stations (fertility and maternal traits of female calves) (2)
TOURS (CRVZ de Nouzilly) and CLERMONT-FERRAND (CRZV de Theix) represent research centers interested by research on beef in other scientific disciplins.

(1) All experimental male calves and culled cows of experimental breeding herds are fattened in La Minière and slaughtered in the experimental abattoirs of Theix and Jouy-en-Josas.

(2) Only testing stations involved in the beef breeding schemes are given; breeds are indicated for each of them in an abbreviated form: *Maine-Anjou* (MA), *Charolaise* (CY), *Limousine* (LI), *Blonde d'Aquitaine* (BA), specialized synthetic line (X).

(3) The national computing center (CTI) where data are processed form the national beef recording scheme is also located in the research center of Jouy-en-Josas.

progeny calves will be compared at two slaughter ages for male calves, under two management systems for female calves: those from the largest muscular breeding types (the so-called terminal crossing types), chiefly the double muscle strains, will be used as once bred heifers (1st calving at two years), the other ones will be used as beef cows.

The beef crossbreeding experiment of Bourges has put foward several interesting and practical results:

— the superiority of *Limousine* as a maternal or paternal breed in the confined environment which was used (zero grazing and partial estrus control);

— the good reciprocal complementarity between the *Maine-Anjou* and *Limousine* breeds not crossed anywhere before this experiment. Starting from the results of this experiment and from field data, calculations have been done to fit the right paternal breed on each breed and age of dam for a fixed risk of calving difficulties. This type of approach seems to be essential, the main limitation of beef potential using large sized beef breeds in intensive systems (including the dairy one) being more and more the calving ability of cows (155-156).

From studies on local breeds (173-209-211) used in extensive range lands of Southern France or Sardinia it clearly appears that terminal crossing (in the harsch environments) and two-step crossing (in the improved ones) with several beef breeds are the most efficient crossbreeding schemes at the commercial level. In the same range conditions (Sardinia), the local dams perform better than the dual purpose (*European Brown Swiss*) coming from the dairy farms located in the lowlands. Increasing the muscling from the local breeds by crossing with beef bulls is limited by the low sexuality of extreme double muscle beef sires in natural service (usual mating system in range conditions). Further, the adaptability and fertility of F_1 beef cows from double muscle sires (after AI in the lowlands) are strongly depressed in the extensive areas.

3.3. — *Optimum use of vegetable land resources*

In fact, all crossbreeding experiments show a trend forward the adaptation of breeds in beef herds according to the nutritional level: from the dairy types adapted to the highest level (regular feeding on a yearly cycle), to the beef types for the intermediate level (no supplement in summertime under continental climatic conditions) and to the extreme hardy types (no concentrate, no wintering under Mediterranean climate).

The beef industry being more and more efficient only by converting into meat, vegetable resources from marginal lands and agricultural or industrial by products, on is faced with the general situation of finding optimum low-cost conversion systems. They involve a transfer of nutrients taking into account:

— the seasonal and geographical variation of plant resources

— the fluctuation of nutritional requirements with the physiological status of cattle.

Beside the classical ways of realizing this transfer:

— storing and (or) transferring food from different places to feed the cattle;

— moving the cattle between areas under different geographical and climatic conditions: Highlands and Lowlands, Alpine and Mediterranean for the coordination of supply and feeding locations;

Animal breeding can play a major and efficient role in this context. Two ways of transferring food to cattle can be considered using benefit from the genetic variation;

— the natural adaptation which occurs in some breeding types (breeds from Corsica) where animals develop habits (moving-feeding) to find by themselves available resources: some stable equilibrium of natural ecosystems can be obtained in this process which is close to that of wildlife.

— the transfer of « cattle genes » by locating the breeding type according to the level of shortage. This principle can be integrated in crossbreeding schemes starting from dairy typed cows (in intensive environments) or hardy typed ones (in harsh environments) both being crossed with beef sires to produce F_1 cows for intermediate environments.

In this field, research workers have to cooperate with those from other biological disciplins to evaluate beef production systems using local breeds and populations already adapted to harsh environments. This genetic material is now disappearing with the intensification of cattle production which has promoted the most productive animals in the richest areas and has led to the desertion of the other zones. This is probably the most acceptable and efficient way for the society to preserve most of the rare breeds (1979).

French research workers in beef cattle breeding are therefore cooperating with others in biology and human sciences in different marginal areas where local breeds could help to find low cost beef production systems using disappearing local breeds. A pilot interdisciplinary study has been conducted in this way 15 years ago in Aubrac: South Massif Central (168). We are more recently considering the following situations:

1) the grazing Highlands of the " Pyrénées " (*Gasconne* breed),

2) the intensive pine florest of the " Landes " under oceanic climatic conditions (*Bazadaise* breed),

3) the Mediterranean dry areas (South Eastern France and Corsica).

In the last two cases, beef production has to be considered as part of a joint industry involving wood production (item 2) and touristic activities (item 3). The prevention against fire spreading which is more and more important for these productions and activities, can be obtained more efficiently than with machines if cattle are allowed to clean the forest. A similar kind of approach is considered in a research project conducted in the Northern part of the Ivory Coast: the overall relationships between plant, cattle and local populations are described before going further in studying breeding improvement procedures of animals.

4. — Conclusion

Beside its scientific originality, the variability of the genetic material and environments involved which may interest many European countries, the French research work on beef cattle breeding may have several other accomplishments

Beef cattle breeding was first developed through strong connections with breeding organizations, field operations preceding more artificial testing procedures then experimental work. Although this perhaps limits the actual statement of scientific results it has however a favourable influence on the practical efficiency of research work for the beef industry.

Due to the large extension of AI, breeding methods have been established using similar procedures to those developed by dairy cattle breeding units. They can help to foreward the breeding improvement of beef cattle in most countries where AI is developing.

The most interesting result of field and experimental works has been to stress the genetic antagonisms which exist between the direct and maternal effects of genes, the first ones being chiefly expressed in the size and muscling, the other ones in the fitness traits. These antagonisms occur between breeds as well as within breeds. Their analysis for each trait like calving ability, mothering ability and fertility seems to be an efficient way of finding optimal combinations between paternal and maternal breeds: such studies have to take into account the fact that most of these traits are determined by threshold effects resulting from an equilibrium between the calf and dam genotypes.

The understanding of such characteristics of the genetic variation in beef herds can be made easier by a full description of chromosomal or other polymorphisms which occur locally in beef breeds, most of them being probably related at the same time to the muscling and to the components of fitness.

The dairy industry being more and more devoted to intensive and artificial environments, beef cattle breeding is particularly faced with the general problem of maintaining the genetic variability of cattle; this problem is a part of the more and more urgent need for developping low-cost feeding and management systems: marginal lands now abandoned but formerly used by local breeds often represent the main plant resources for cattle in such systems. French research work in animal breeding is engaged here in interdisciplinary works concerning continental and mediterranean marginal lands where beef production is connected with wood production, land preservation and touristic activities.

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1st part: Polymorphisms

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2nd part: Polygenic variation

A. — RESEARCH ON GROWTH CHARACTERS

1. — *Recording procedures :*

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2. — *Genetic variation* (Direct effect of genes) *:*

a) *Veal production* (Field data)

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(133) BONHOMME D., FOULLEY J. L., 1974. Facteurs de variation de l'hématocrite des bovins. III. Analyse de la variabilité génétique et phénotypique en croisement industriel. *Ann. Génét. Sél. anim.*, **6**, 49-67.
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b) *Young bull production* (testing stations) *:*

(135) FREBLING J., POUJARDIEU B., VISSAC B., BERANGER C., TEISSIER J. H., 1967. Stations de sélection bovine. Compte rendu technique n° 1. Note générale. *Bull. tech. Inf.*, **225**, 887-894.

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(138) FREBLING J., JOUYS P., POUJARDIEU B., VISSAC B., 1969. Stations de sélection bovine. Compte rendu technique n° 4. Étude du contrôle de descendance des taureaux *Limousins* sur les performances d'engraissement et d'abattage. *Bull. tech. Inf.*, **236**, 31-41.

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