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TRANSFER TO THE PROGENY OF ALTERATIONS INDUCED IN THE WHITE LEGHORN BY REPEATED INJECTIONS OF HETEROLOGOUS BLOOD

by

J. STROUN, L. STROUN-GUTTIÈRES, J. ROSSI and M. STROUN

In recent years, various authors have studied the effect of repeated injections of heterologous blood or DNA (deoxyribonucleic acid) to higher vertebrates, birds or small laboratory mammals. Thus, some have tried to reproduce the transformation phenomenon already observed at the level of micro-organisms (1, 2-4, 18, 20, 21); the others were looking for the way to influence the genotype by causing alterations in the intermediate processes (5-13, 19, 22-24, 29).

The results published up to this day are contradictory: some investigators relate that they have provoked alterations capable of being transmitted to the non-treated offspring of the injected animals (2-5, 5, 7-8, 10-19, 22-29), while others report failures (1, 6, 9, 20, 21).

We have explored since 1957 the influence of repeated intra-peritoneal injections of whole blood of the grey guinea-fowl (*numida meleagris*) into cocks and hens of the white Leghorn breed (25-28).

MATERIAL AND METHOD

Our Leghorn strain comes from a stock-breeder specialized in white Leghorn since more than 25 years; this strain has stable characteristics. The feathers are of a uniform white, while the chick's down is more or less yellow. The legs and the beaks are yellow.

The feathers of the grey guinea-fowl are bluish-grey, the neck has some brown, more widely spread on the younger birds. The chick's down is brown, with dark-brown stripes. The young feathers which are at first barred white become more and more spotted by white pearls when the fowl gets older (Plate I A).

Figure 1 presents the general plan of the experiment. We have first made three groups out of the Leghorn strain: the non-injected *Control Group*, the *Leghorn Check Group* injected with white Leghorn blood and the *Leghorn Test Group* injected with grey guinea-fowl blood.

From F_4 of the Control Group, we have then formed three new groups representing F_0 of this new series: *Group A* injected with Australorp blood (Australorp is a heavy, black chicken), *Group RIR* injected with Rhode Island Red blood (a red chicken with some black spotted feathers, of a size between Australorp and Leghorn), and *Check Group II* injected with white Leghorn blood. The symbols Fm_0 and Ft_0 designate the parents of two modified lineages coming from the Test Group; these lineages have no longer been injected.

Citrated venous blood, taken aseptically from males and females, is injected by intra-peritoneal route into the chicks, as soon as they are from 10 to 30 days old. The amount is gradually increased from 0,5 ml to 5 or 7 ml according to the birds' age. At the rate of one injection every 3 to 5 days during 6 to 7 months, our animals receive at each generation between 180 and 220 ml of blood. For further injections in each new generation, we select from the groups of treated birds those which have retained the standard white Leghorn phenotypes (Fig. 2). The modified birds are usually not injected.

We have used artificial insemination. Males and females are maintained in separate cages.

Among the biological studies we have undertaken, we will talk in this paper about the agglutination of the guinea-fowl's erythrocytes by the serum of the Leghorn coming from the different groups. We have done these agglutinations in salted and albuminated medium at the temperature of the animal (40°C) and of the laboratory (about 20°C).

RESULTS

A. — Non treated Control Group and Check Groups I and II injected with white Leghorn blood.

From F_0 to F_6 , we have not observed any alteration of the Leghorn standards in more than 1600 birds examined (Table I).

B. — Test Group injected with grey guinea-fowl blood.

a) Alterations of the plumage :

Starting with generation F_1 and at each succeeding generation, the down of a certain number of chicks was of an ashy white shade, instead of yellow. But the feathers which appeared later remained white in most cases.

Starting with generation F_2 descended from injected F_1 , and at each succeeding generation, new alterations have appeared on the feathers of a few birds. There is an ashy shade appearing on the head and the neck like a cap and spreading on the whole body of the animal; this shade is often accompanied, especially among adults, by golden glints which are found predominantly on the caps of the females,

on the backs and shoulders of the males. The second alteration, which usually coexists with the first, is the occurrence, without any particular localisation, of more or less grey or black spotted feathers irregularly designed (Plate I B). The third and less usual alteration consists in the appearing of feathers with more or less golden tinge, or buff, brown, red colored with often grey or black spots. These feathers, generally found in males, are situated predominantly on their backs and shoulders; but when found in females, they are on their caps. The down of the feathers remains usually white. We have not been able to establish a correlation between the presence of an ashy white down on the chicks and the ultimate coming out of modified feathers.

TABLE I

Number of Leghorn fowls studied in the Control and Check Groups

Generations	Groups		
	Control	Check I	Check II
F_0	34	20	—
F_1	107	60	—
F_2	106	101	—
F_3	99	113	—
F_4	139	64	20
F_5	129	85	64
F_6	110	205	160
Total	724	648	244

Figure 2 shows the number of animals studied and those of which the feathers have been modified in this lineage, up to F_6 .

The offspring of non-modified F_1 and F_2 fowls which have received no more blood, has remained similar to the white Leghorn standards.

b) *Alteration of the pigmentation of the legs and the beaks :*

We have noticed since F_1 rather important fluctuations of the yellow pigmentation of the legs and beaks, peculiar to the Leghorn, even outside of the laying period of the hens: the pigmentation disappeared more or less and in some cases the legs were white with a pearly lustre or pink. These alterations remained stable in a few birds: in F_2 , one male and one female, the latter with ashy white feathers and grey spots; in F_3 , again a male and a female, the hen with some black spotted feathers; in F_4 two females, one had an ashy white cap and grey or black spotted feathers; in F_5 , 2 cocks and 2 hens, one of the males with a greyish-buff coloured plumage; in F_6 , 4 males and 1 female, one cock with ashy white plumage (Table II).

Except for a few fluctuations, particularly of the colour of the feathers during the growth of the males, all these alterations of the plumage and the leg and beak pigmentation remained stable, although the fowls were not injected. When injected (in F_4), the modified birds were not changed.

TABLE II

Modification of the beak and leg pigmentation in the Test Group : F offspring

Generations	Number of birds		
	observed	modified	
		♂	♀
F_0	55	0	0
F_1	125	0	0
F_2	115	1	1
F_3	225	1	1
F_4	65	0	2
F_5	166	2	2
F_6	82	4	1

C. — Fm offspring.

From F_1 injected with guinea-fowl blood, we have obtained in F_2 three Leghorns in which the plumage was not standard (Figure 2): one male with buff or brown coloured feathers with grey spots, and two females: one died prematurely, the other one had an ashy white plumage with grey spots and white legs. These fowls have never received blood.

We consider that the male and the surviving female modified in F_2 represent Fm_0 of a lineage modified by somatic way; starting with Fm_1 , most birds did not receive any injection. We shall use the symbol Fm to designate this lineage.

In order to obtain Fm_1 , we have crossed by artificial insemination the two Fm_0 with control Leghorns or non modified, non treated Test Leghorns. To obtain Fm_2 , the Fm_1 birds of which the plumage and sometimes the legs' pigmentation were modified, were either crossed between themselves or with control Leghorns. Except for a small group of Fm_1 birds, Fm_1 fowls did not receive blood. In order to obtain Fm_3 , we have crossed between themselves fowls showing similar alterations of the plumage. Figures 3 and 4 show these various cross-breeds and indicate the distribution of the various phenotypes among the male and female offspring from the crosses. Tables III and IV give the number of modified and non-modified birds.

In Fm_1 , we have noticed the same alterations as after the guinea-fowl blood injections to the Leghorns of lineage F in the Test Group, but these alterations were

more frequent and more marked (Plate II A and B). Some chicks already had black spots on their down; once they were grown up, they kept their modified plumage. Among the 7 females issued from the Fm_0 hen, two had white legs.

TABLE III

Alterations of the plumage colour in the offspring Fm descending from a modified male Fm_0

Generations	Crosses	Type of plumage															
		White standard				ashy white, buff feathers, grey, black spots				very spotted				cuckoo, homogenous grey			
		♂	%	♀	%	♂	%	♀	%	♂	%	♀	%	♂	%	♀	%
Fm_1	<i>a</i>	56	78	43	43	16	22	57	57	0	—	0	—	0	—	0	—
Fm_2	<i>b</i>	12	—	8	—	11	—	11	—	0	—	0	—	0	—	0	—
	<i>c</i>	4	—	6	—	3	—	4	—	0	—	0	—	0	—	0	—
	<i>d</i>	62	66	37	35	24	25	55	53	8	9	2	2	0	—	10	10
	<i>e</i>	30	56	8	19	11	20	20	48	13	24	0	—	0	—	14	33
	<i>f</i>	8	—	5	—	5	—	11	—	0	—	0	—	0	—	0	—
	<i>g</i>	6	—	7	—	3	—	7	—	0	—	0	—	0	—	0	—
	<i>h</i>	69	76	36	41	19	21	43	49	3	3	0	—	0	—	9	10
Fm_3	<i>i</i>	10	—	12	—	10	—	4	—	0	—	0	—	0	—	0	—
	<i>j</i>	24	47	18	28	23	45	41	64	3	6	0	—	1	2	5	8
	<i>k</i>	0	—	0	—	1	2,5	0	—	37	95	0	—	1	2,5	37	100
	<i>l</i>	20	71	13	42	6	22	16	51,5	2	7	0	—	0	—	2	6,5
	<i>m</i>	1	3	0	—	3	8	0	—	30	83	1	2	2	6	53	98
	<i>n</i>	28	52	9	19	11	20	30	64	12	22	4	8,5	3	6	4	8,5
	<i>o</i>	24	69	17	43,5	7	20	17	43,5	4	11	0	—	0	—	5	13

a: modified male Fm_0 X non treated, non modified Leghorn female;

b: modified female Fm_1 X control Leghorn male;

c: modified male Fm_1 X control Leghorn female;

d: modified male Fm_1 X modified female Fm_1 ;

e: modified male Fm_1 X modified female Fm_1 , both injected with guinea-fowl blood;

f: modified male Fm_1 , injected with guinea-fowl blood X control Leghorn female;

g: modified female Fm_1 , injected with guinea-fowl blood X control Leghorn male;

h: modified b-male Fm_2 X modified b-female Fm_2 , both ashy white, grey spotted type;

i: modified c-male Fm_2 , X modified c-female Fm_2 , both ashy white, grey spotted type;

j: modified d-male Fm_2 X modified d-male Fm_2 , both ashy white, grey spotted type;

k: modified d-male Fm_2 , very spotted type X modified d-female Fm_2 , cuckoo type;

l: modified e-male Fm_2 X modified e-female Fm_2 , both ashy white, grey spotted type;

m: modified e-female Fm_2 , very spotted type X modified e-female Fm_2 , cuckoo type;

n: modified f-male Fm_2 X modified f-female Fm_2 , bosh ashy white, grey spotted type;

o: modified g-male Fm_2 X modified g-female Fm_2 , both ashy white, grey spotted type

TABLE IV

Alterations of the plumage colour in the offspring Fm descending from a modified female Fm₀

Generations	Crosses	Type of plumage															
		White standard				ashy white, buff feathers, grey, black spots				very spotted				cuckoo, homogenous grey			
		♂	%	♀	%	♂	%	♀	%	♂	%	♀	%	♂	%	♀	%
<i>Fm₁</i>	<i>a</i>	0	—	5	—	0	—	2	—	0	—	0	—	0	—	0	—
<i>Fm₂</i>	<i>b</i>	6	—	7	—	6	—	5	—	0	—	0	—	0	—	0	—
	<i>c</i>	9	—	6	—	7	—	13	—	3	—	0	—	0	—	4	—
<i>Fm₃</i>	<i>d</i>	31	94	26	63	2	6	15	37	0	—	0	—	0	—	0	—
	<i>e</i>	24	52	11	31	14	31	23	64	8	17	0	—	0	—	2	5
	<i>f</i>	0	—	0	—	0	—	0	—	13	—	0	—	6	—	14	—

a: modified female Fm₀ X non treated, non modified Leghorn male;*b*: modified female Fm₁ X control Leghorn male;*c*: modified female Fm₁ X modified male Fm₁ descending from male Fm₀;*d*: modified b-female Fm₂ X modified b-male Fm₂;*e*: modified c-female Fm₂ X modified c-male Fm₂, both ashy white, grey spotted type;*f*: modified c-female Fm₂, cuckoo type X modified c-male Fm₂, very spotted type.

In Fm₂, the alterations already described in Fm₁ reappeared on the one hand. On the other hand, we noticed new characteristics. The down of some chicks was predominately grey or black. These adult fowls have shown more or less greyish feathers printed with cuckoo or stippel black designs, sometimes with a dark grey edge and seldom with bars (Plate III A). The plumage could also be homogenous grey, the cap being darker than the other parts of the body (Plate III B). We often noticed golden glints on the cap; brown or red feathers were less usual. The down of the modified feathers was grey. The whole plumage of the female was thus altered. Then again the plumage of the male was less regular: light ashy white, it was sprinkled by many grey, black and sometimes reddish-brown spots; cuckoo feathers were less common (Plate IV A). The quality of this cuckoo type of modified plumage was different from the Leghorn plumage: it was distinctly softer to the touch.

In our Fm₁ crosses between modified birds and control Leghorns, we have noticed in Fm₂ alterations similar to those found in Fm₁.

In Fm₃, we have observed the same alterations as in Fm₂ (Plate IV B, Plate V A and B). However, by crossing very spotted Fm₁ cocks which were black or grey

as chicks with Fm_1 cuckoo-stippled type hens, we have obtained in Fm_1 nearly only cuckoo-stippled hens; most of the males were very spotted and a few were cuckoo.

TABLE V

Modification of the beak and leg pigmentation in the offspring Fm descending from a modified female Fm_0

Generations	Crosses	Number of birds		
		observed	modified	
			♂	♀
Fm_1	<i>a</i>	7	0	2
Fm_2	<i>b</i>	24	4	4
	<i>c</i>	42	3	7
Fm_3	<i>d</i>	74	17	20
	<i>e</i>	82	19	16
	<i>f</i>	33	9	6

a: modified female Fm_0 X non treated, non modified Leghorn male;

b: modified female Fm_1 X control Leghorn male;

c: modified female Fm_1 X modified male Fm_1 descending from male Fm_0 ;

d: modified b-female Fm_2 X modified b-male Fm_2 ;

e: modified c-female Fm_2 X modified c-male Fm_2 , both ashy white, grey spotted type;

f: modified c-female Fm_2 , cuckoo type X modified c-male Fm_2 , very spotted type.

It should be noted that the cuckoo-stippled or homogenous grey types have appeared only in the offspring of the modified Fm_0 male. The offspring of the modified Fm_0 female have shown only the type of alterations noticed in Fm_1 , although rarely a few cuckoo feathers have appeared on some of the females. However the rate of pearly-white or pink legs and non-pigmented beaks was high in this lineage (Table V).

D. — Ft offspring.

Among the birds modified in F_5 , we have selected two ashy white females with black spotted feathers (Plate I B) and two males, one ashy white, the other buff-grey coloured. We consider that these males and females modified in F_5 and issued from injected F_4 represent Ft_0 of a lineage lately modified by somatic way; starting with Ft_0 , the birds did not receive any injection. We shall use the symbol Ft to designate this lineage. We have crossed the modified Ft_0 birds with Control males and females in order to obtain Ft_1 .

In F_{t_1} , we notice, like in F_{m_1} , chicks with grey or black spots on their down. They become more or less ashy white coloured adults with grey or black spotted feathers (Table VI). We have seen a few more or less cuckoo feathers on three F_{t_1} females descended from two F_{t_0} females, and on one female issued from one of the F_{t_0} males. In this lineage again, the males are less frequently modified than the females.

TABLE VI

Alterations of the plumage colour in the offspring F_{t_1}

Crosses	Type of plumage			
	White standard		Ashy white, buff feathers, grey, black spots	
	♂	♀	♂	♀
<i>a</i>	3	6	7	10
<i>b</i>	10	1	2	8
<i>c</i>	10	4	4	10
<i>d</i>	8	2	3	8

a: modified female F_{t_0} 18363 X control Leghorn male;

b: modified female F_{t_0} 18405 X control Leghorn male;

c: modified male F_{t_0} 14624 X control Leghorn female;

d: modified male F_{t_0} 14622 X control Leghorn female.

E. Groups of Leghorns injected with Australorp and Rhode Island Red blood.

In F_2 , we have only observed a slight melanisation of the feathers of a few birds in both groups A and RIR.

Agglutination of the guinea-fowl erythrocytes by the Leghorn serum:

When comparing the results obtained in the various groups of injected or non-injected Leghorns, we do not notice any significant difference except a common hyperagglutination in the fowls under treatment.

DISCUSSION

All our observations seem to indicate that it is possible to provoke alterations of certain plumage characteristics and of the beak and the leg pigmentation in both

sexes of the white Leghorn when they are subjected to repeated intraperitoneal injections of grey guinea-fowl whole blood. These alterations may be transferred to the progeny of both males and females without any treatment. White Leghorn blood given the same way remains without any effect.

The birds susceptibility to the treatment appears quite variable, some fowls having been modified at the second generation, others only at the sixth. The feathers of males seem harder to alter than those of females, perhaps because of the presence of the sex-linked "barring" gene. Yet the most marked alterations of the plumage colour were found in the offspring of the modified male Fm_0 , while the offspring of the modified female Fm_0 disclosed more pronounced modifications of leg and beak pigmentation.

Alterations do not appear in birds which are under treatment, but in the next generation, in non injected birds. Injections do not seem to influence an already modified bird. We think therefore that our treatment acts at the level of the reproductive organs.

While crossing between themselves descendants of a male modified in F_2 , issued from injected F_1 fowls, we have noticed in Fm_2 a new type of plumage, cuckoo or homogenous grey masked in Fm_1 . This type is more pronounced in females than in males. It is only in Fm_3 , after having crossed between themselves cuckoo type fowls, that we have obtained a few pure cuckoo males. We may look forward to selecting a cuckoo type breed, descended from our white Leghorn strain.

While it is possible to establish analogies between some of the alterations obtained and some guinea-fowl characteristics, we do not have at present any modification which would permit us to think we have transferred guinea-fowl characteristics to our white Leghorns. In the contrary, our results suggest that the treatment has disclosed masked Leghorn characteristics.

In view of the indications that the observed modifications may involve the "unmasking" of Leghorn characteristics, it is necessary to consider the possibility that the results obtained are a consequence of the breeding program and not of the treatment. We might for instance imagine that when we established our three groups from the white Leghorn strain, cryptic genes in this strain could have all passed in the Test Group solely, and alterations would only be inbred qualities. This hypothesis is statistically unlikely, but for the moment it cannot be completely ignored. We believe that our experimental system will give us a definite answer, for the alterations obtained in the groups injected with Australorp and Rhode Island Red blood can be attributed only to the treatment and not to chance.

Spontaneous mutations seem not to be involved, all the alterations appearing only in the groups injected with heterologous blood and the rate of the modifications being unusually high.

Whatever the interpretations one might consider, at the present stage of our investigations it must be admitted that the treatment has disturbed the activity of

the genetic factor I, which inhibits the expression of colour genes in the white Leghorn, as an epistatic dominant gene. Our hypothesis at present is that the treatment has deeply affected a regulatory mechanism so as to favour the expression of cryptic genes. Intervention of a virus or some other parasite, induced mutagenic effects, transformation or regulation phenomenon are now being considered as possible mechanisms for the changes produced and transferred to the progeny.

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RÉSUMÉ

Transmission à la descendance de modifications provoquées chez la Leghorn blanche par injections répétées de sang hétérologue

Dans le cadre d'études sur l'influence d'injections répétées de sang ou d'acide désoxyribonucléique hétérologues à des vertébrés supérieurs, les auteurs ont injecté du sang complet de pintade grise à des poules et coqs de race Leghorn blanche.

Ils ont utilisé une souche Leghorn blanche dont les caractères sont stables et contrôlés par l'éleveur depuis plus de 25 ans.

A partir de la souche Leghorn, ils ont constitué d'abord trois groupes (Figure 1): Groupe de Contrôle non traité, Groupe Leghorn Témoin traité au sang de Leghorn blanche et Groupe d'Essai traité au sang de pintade grise. A partir de F₄ du Groupe de Contrôle, ils ont ensuite formé trois nouveaux groupes: Groupe A traité au sang d'Australorp, Groupe RIR traité au sang de Rhode Island Red et Groupe Témoin II traité au sang de Leghorn blanche. Ils ont suivi la descendance F_m et F_t non traitée, issue de mâles et femelles Leghorn modifiés, dont les ascendants avaient reçu du sang de pintade.

Les injections de sang, faites par voie intra-péritonéale, commencent chez les jeunes poussins et se poursuivent pendant six à sept mois, apportant par génération à chaque animal de 180 à 220 ml de sang. A chaque nouvelle génération on choisit dans les groupes traités, pour les soumettre aux injections, une partie des volatiles dont les phénotypes sont restés conformes au standard Leghorn blanche (Figure 2), alors que les oiseaux modifiés ne sont généralement plus traités. Les volatiles étant élevés en batterie, sexes séparés, les femelles sont inséminées artificiellement.

Les auteurs n'ont observé aucune modification du standard Leghorn blanche de F_0 à F_6 , dans les Groupes de Contrôle et Témoin I et II, soit plus de 1600 animaux (Tableau I).

En revanche, dans le Groupe d'Essai traité au sang de pintade grise, à chaque génération dès F_2 ils ont vu apparaître chez quelques volatiles mâles et femelles des modifications de la couleur du plumage et de la pigmentation des pattes et du bec qui restaient stables (Figure 2 et Tableau II). Ces modifications ont été retrouvées plus fréquentes et plus intenses dans les descendance F_m et F_t non traitées, issues de volatiles modifiés. En outre, des types de plumage nouveaux, coucou ou gris homogène, se sont révélés à la suite de divers croisements (Figures 3 et 4, Tableaux III à VI, Planches II à V).

Jusqu'ici, soit en F_2 , les auteurs ont observé une légère mélanisation de quelques animaux dans les Groupes injectés au sang d'Australorp et de Rhode Island Red.

L'agglutination des érythrocytes de pintade par le sérum des Leghorn des divers groupes traités ou non, n'a rien révélé de notable, hormis une banale hyperagglutination chez les volatiles en cours d'injections.

Sur la base de leurs observations, les auteurs estiment qu'il est possible de provoquer des modifications des caractères du plumage et de la pigmentation du bec et des pattes chez la Leghorn blanche des deux sexes, soumise à des injections répétées de sang complet de pintade grise. Ces modifications peuvent être transmises à la descendance non traitée, aussi bien par les mâles que par les femelles. En revanche, le sang de Leghorn blanche reste sans effet. Les modifications n'apparaissent pas chez les volatiles injectés, mais à la génération suivante, indépendamment de toute injection. De même les transfusions n'exercent pas d'influence notable sur l'animal déjà modifié. Il apparaît donc que le traitement agit au niveau des organes reproducteurs. S'il est possible d'établir des analogies entre certaines des modifications obtenues et quelques caractères de la pintade, il n'existe actuellement aucun élément en faveur d'un transfert de ces derniers aux Leghorn.

Les auteurs discutent la part éventuelle du hasard dans leurs résultats, soit par sélection, soit par mutations spontanées. Ils pensent que les modifications ont été provoquées par le traitement. Celui-ci, selon l'hypothèse qu'ils formulent pour l'instant, aurait inhibé certains mécanismes répresseurs et favorisé l'expression de gènes cryptiques par des voies qui restent encore à découvrir.

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GENERAL DIAGRAM OF THE EXPERIMENT

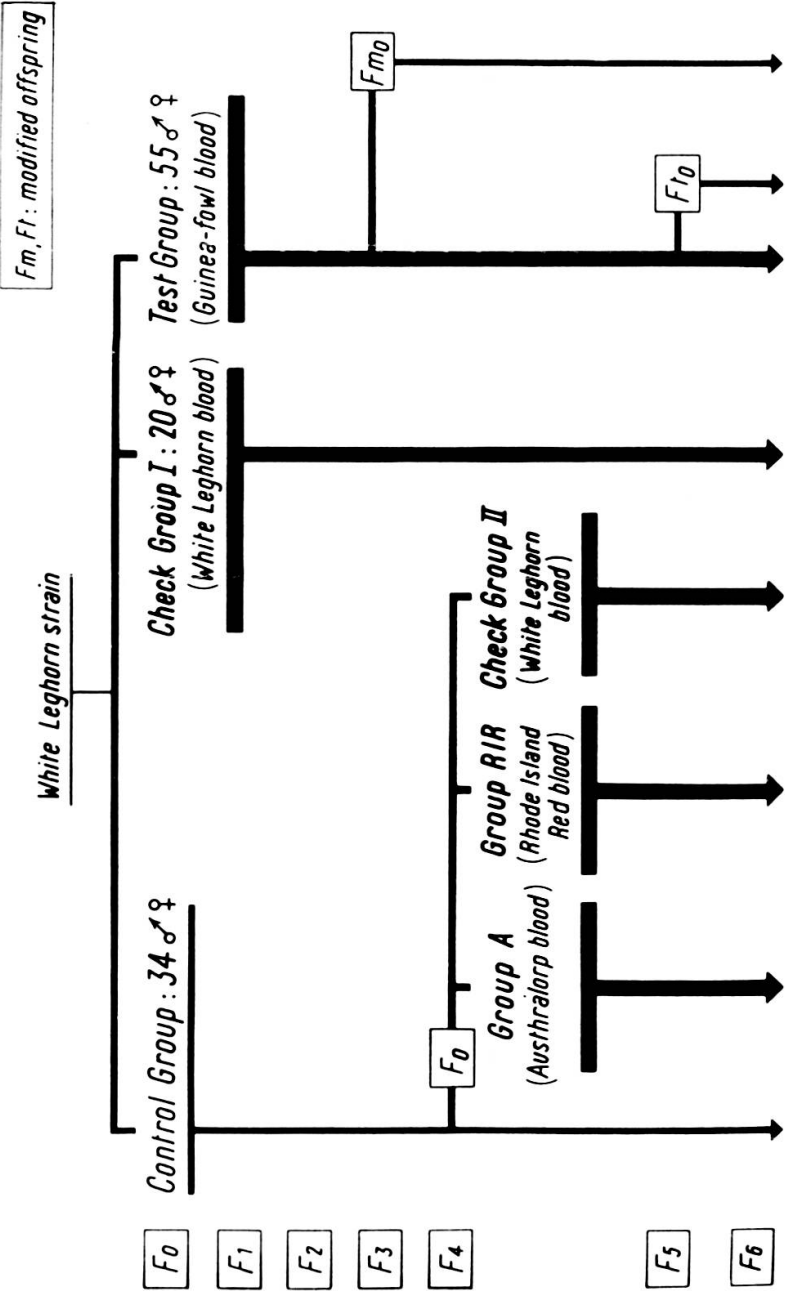


Fig. 1

ALTERATIONS OF THE PLUMAGE COLOUR

IN THE TEST GROUP: F offspring

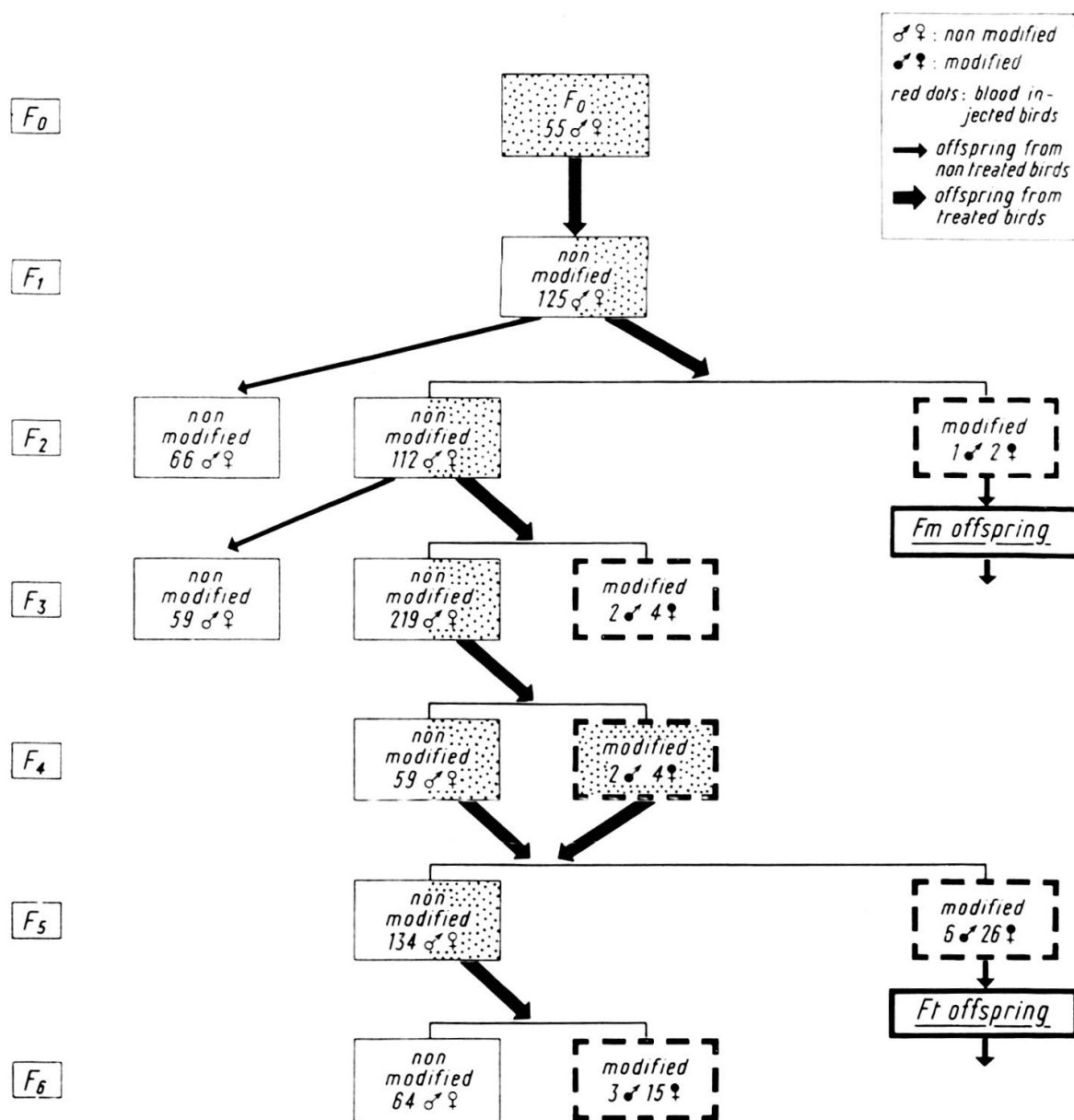


Fig. 2

ALTERATIONS OF THE PLUMAGE COLOUR IN THE OFFSPRING Fm DESCENDING FROM A MODIFIED MALE Fm_0

PER CENT DISTRIBUTION

Male Fm_0 mated with non treated, non modified Q Leghorn

white standard type
 ash - white, buff coat; grey, black, red spotted type
 very spotted type
 cuckoo or homogenous grey type
 injected with guinea-fowl blood

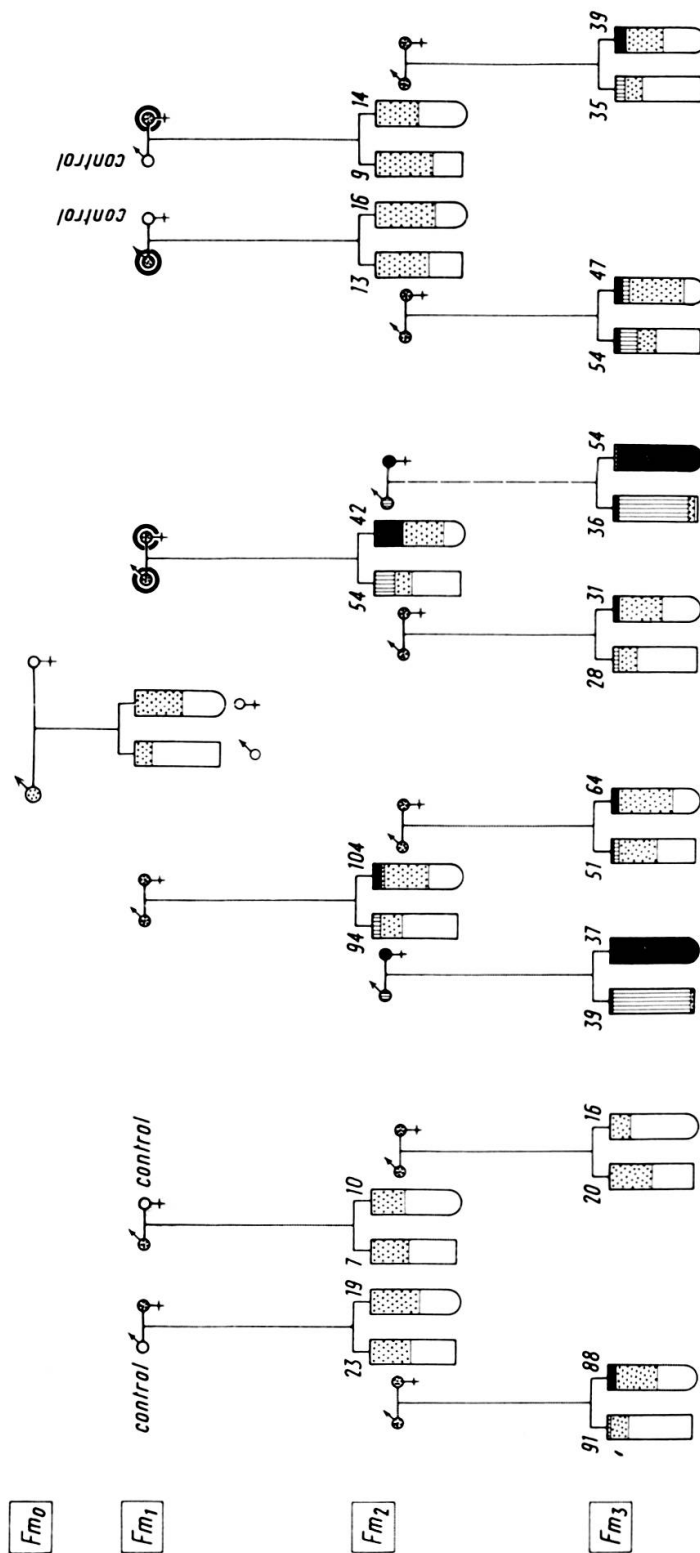






Fig. 3

ALTERATIONS OF THE PLUMAGE COLOUR
IN THE OFFSPRING F_m DESCENDING FROM
A MODIFIED FEMALE Fm_0

PER CENT DISTRIBUTION

Female Fm_0 mated with non treated, non modified ♂ Leghorn

- | | |
|---|---|
|  white standard type |  ash - white, buff coat; grey, black, red spotted type |
|  very spotted type |  cuckoo or homogenous grey type |

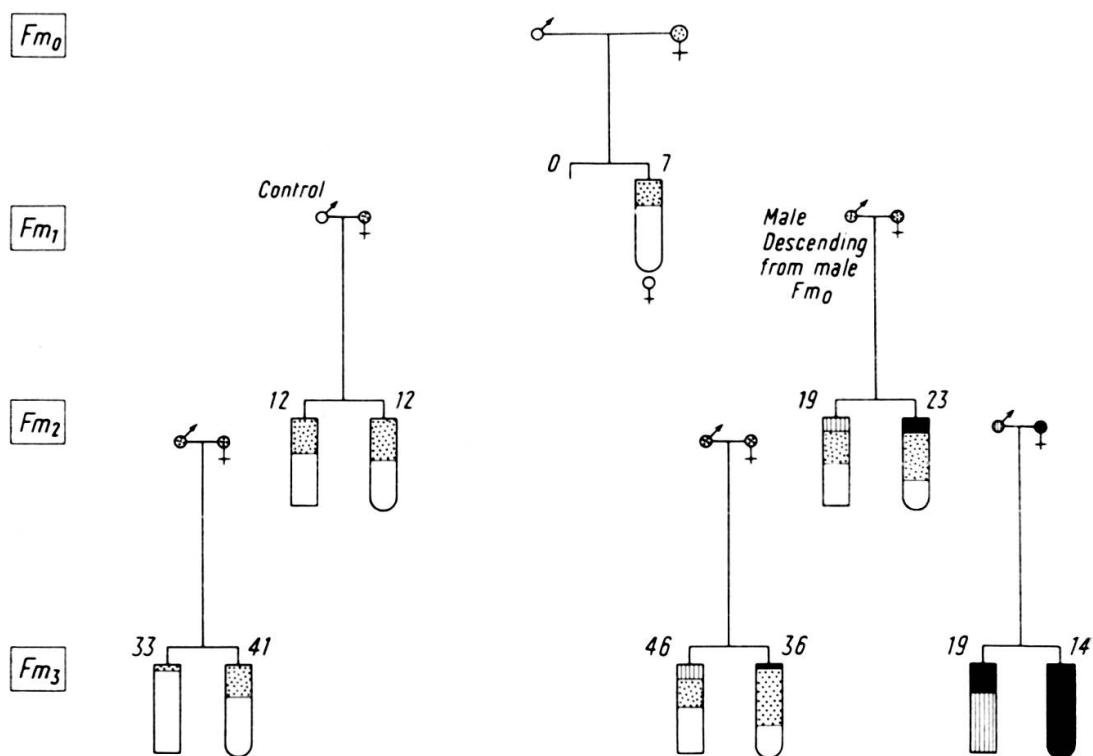
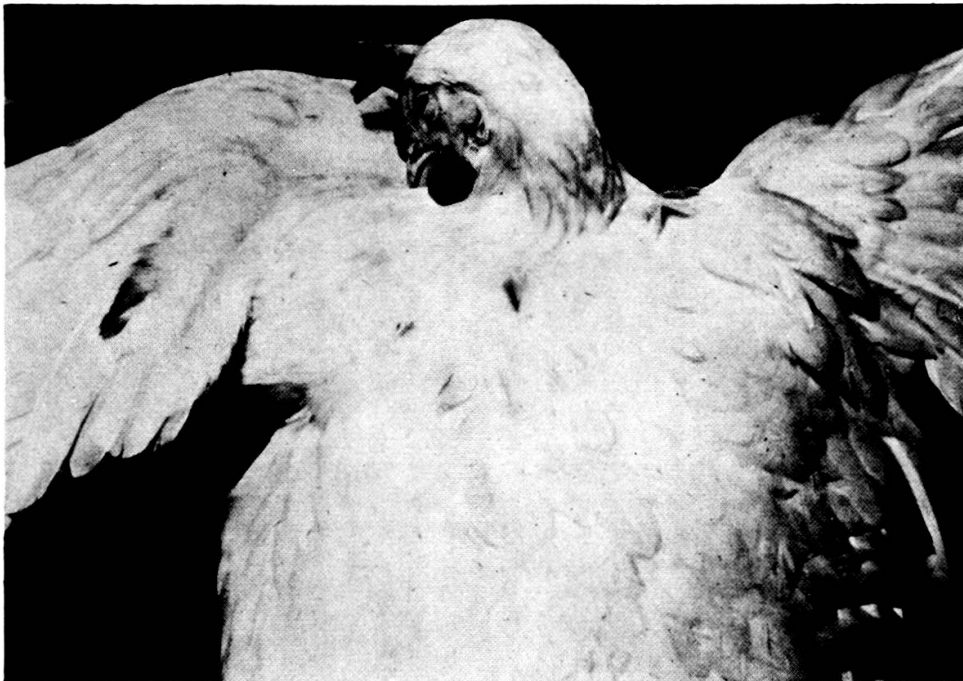


Fig. 4



A. Adult guinea-fowl.

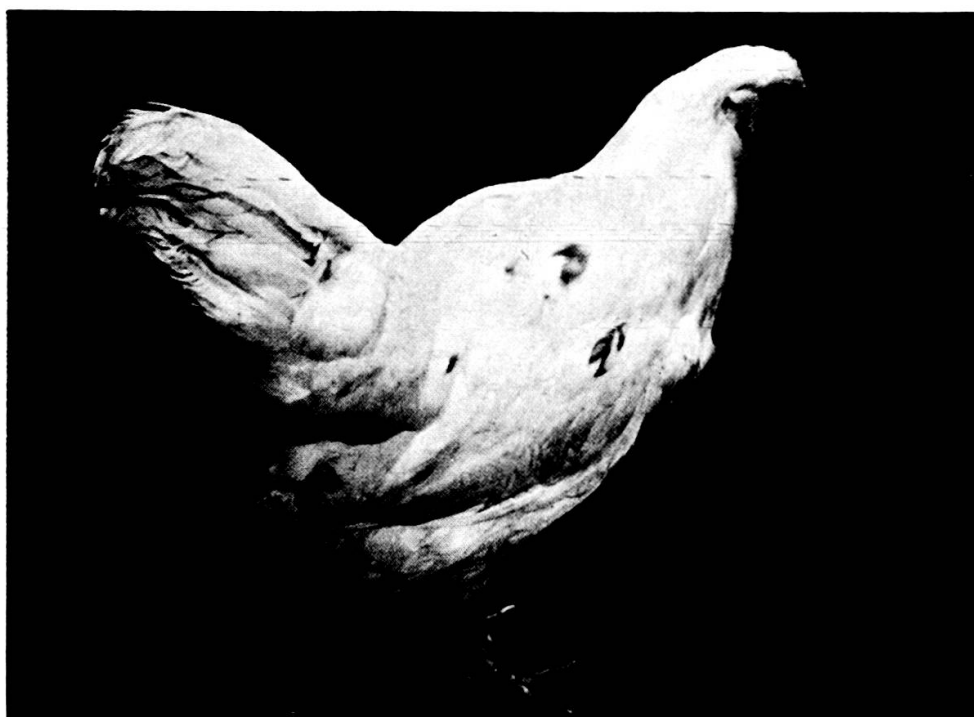


B. Female F₅ and Ft₀ with some black spotted feathers.

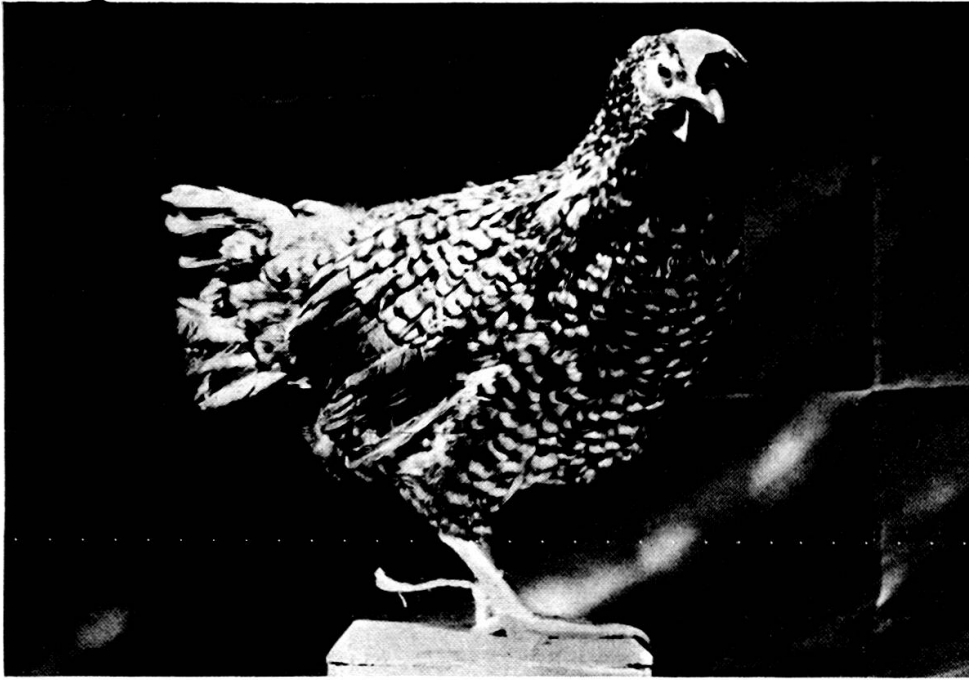
(Ghez)



A. Check Group I female with Fm_1 ashy white female. (Rossier)

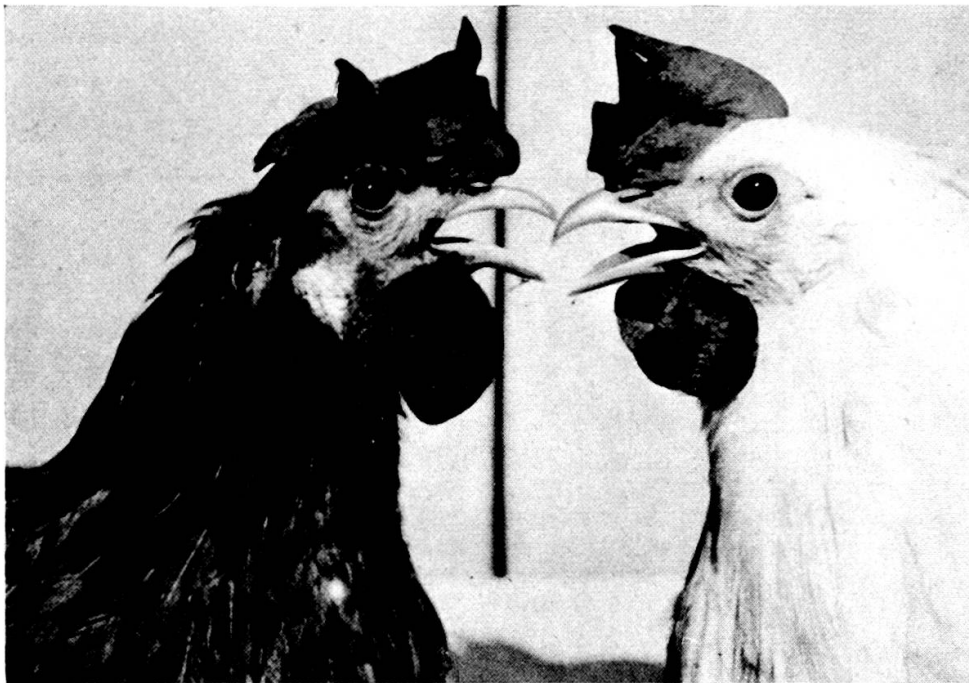


B. Fm_1 female with black spotted feathers. (Ghez)



A. Fm_2 female with cuckoo type plumage.

(Rossier)



B. Fm_2 female with homogenous grey type plumage and control female.

(Schauenberg)



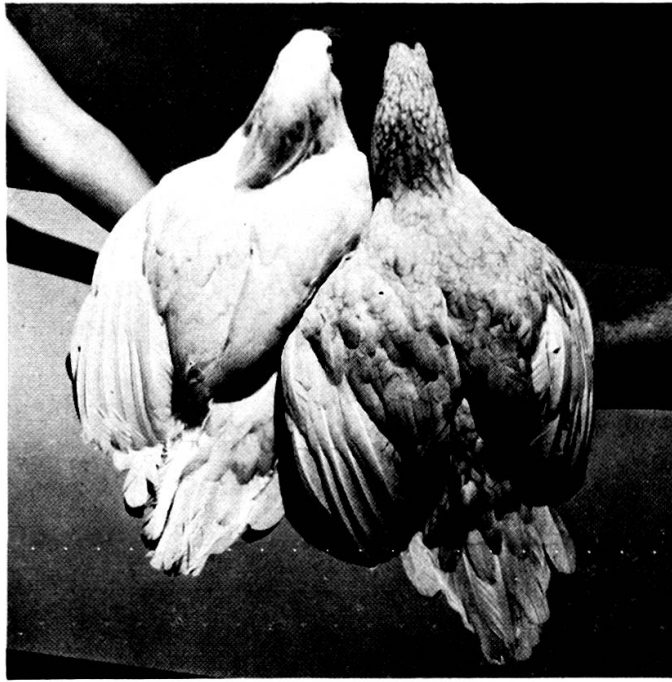
A. Fm₂ male with very spotted type plumage.

(Rossier)



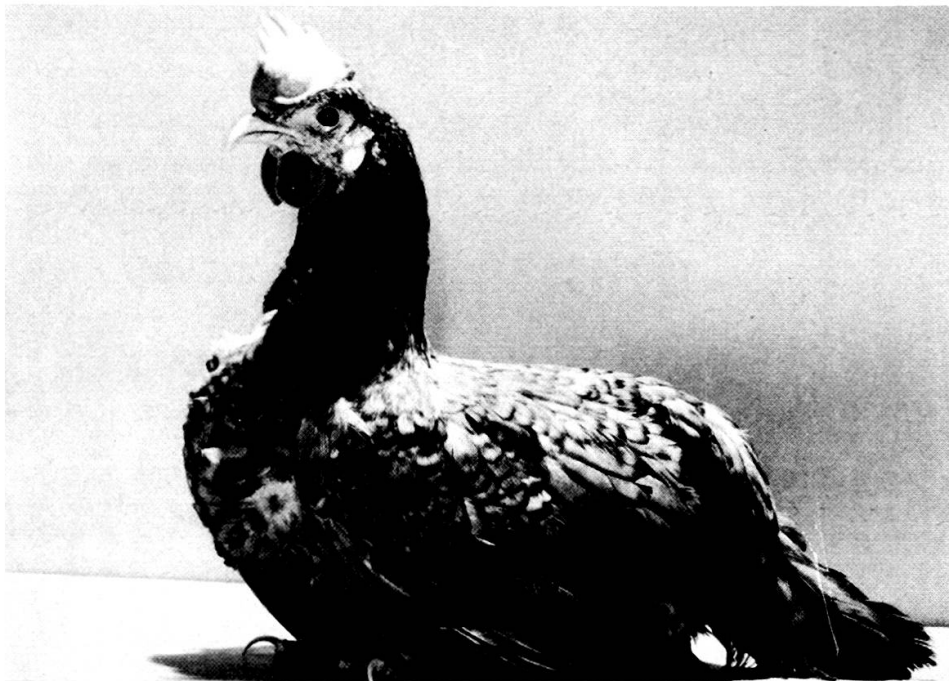
B. Fm₃ female with very spotted type plumage and cuckoo feathers.

(Ghez)



(Ghez)

A. Fm_3 female with homogenous light grey type plumage and darker feathers' edges on the neck, and control female.



(Ghez)

B. Fm_3 female with cuckoo type plumage.

