GENETICS OF THE FOWL

V. THE MODIFIED FRIZZLE

BY F. B. HUTT

Department of Poultry Husbandry, Cornell University, ¹
Ithaca, N.Y., U.S.A.

(With Plate XV)

INTRODUCTION

In the first paper of this series it was shown (Hutt, 1930) that frizzling is caused by a single dominant autosomal gene, F, which produces in fowls homozygous for it a narrow, much-curled plumage, markedly different from that of the heterozygote. A similar conclusion was also reached by Landauer and Dunn (1930).

In all progeny raised by the writer from the original stock obtained from Major G. S. Williams, Tredrea, Perranwell, Cornwall, there were observed only these two types of frizzling, but, after outcrossing to entirely unrelated stock, there appeared a new type of plumage which was earlier briefly reported and designated as modified frizzling (Hutt, 1932). Investigations of that condition are reported in this paper.

DESCRIPTIONS

Unmodified heterozygous Frizzles (Plate XV, figs. 1 and 2) have body feathers the shafts of which are recurved so that the feathers curl toward the head or have their apices pointed outward in planes roughly perpendicular to the surface of the body. The vane of the feather is usually intact, except in the outer remiges, where the barbs, in groups of three to ten or more, are twisted and partially curled around the rachis (Plate XV, fig. 2). This effect is least in evidence at the distal end of the rachis, which is also slightly recurved. It is most pronounced in the outer remiges, less so in the inner primaries, and much less so in the secondaries.

Unmodified homozygous Frizzles are characterised by a woolly appearance resulting from the fact that in all feathers both rachis and barbs are so curled that the normal flat vane is completely destroyed

¹ The greater part of this investigation was conducted at the University of Minnesota, but the work was completed at Cornell University.

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(Plate XV, figs. 5 and 7). Shafts of the remiges and rectrices are markedly recurved. Barbs of these feathers are originally closely twisted around the shaft, but in most cases these barbs quickly wear off, leaving only a single spike which in turn frequently breaks off or is moulted. Wings of the homozygotes frequently have the outer remiges in several different stages of growth even at times other than that of the regular moult (Plate XV, fig. 7).

Modified heterozygous Frizzles sometimes exhibit so little frizzling as to be almost indistinguishable from normal fowls (Plate XV, fig. 4). There is only very slight recurving of the shafts of body feathers, and the normally somewhat convex outer surface of the remiges is often fully retained. The rectrices sometimes seem entirely unaffected, but, in any case of doubtful identity, the presence or absence of the frizzling gene is readily detected by examination of the outer remiges. In the sub-apical region of these feathers the vane on the inner side of the rachis is broken by varying degrees of curling in small clusters of barbs (Plate XV, fig. 3). This effect is usually localised, being less evident at the proximal end of the vane, and entirely lacking at the tip. It is most marked in the outermost remex and becomes progressively less extensive in each succeeding inner remex, being sometimes entirely absent in the inner two of the ten primary remiges. Secondaries of modified heterozygous Frizzles are usually almost normal, but in any case, the inner ones are least affected. Feathers of the neck usually stand out just enough to appear somewhat ruffled.

Most modified heterozygotes show somewhat more frizzling than the one illustrated, particularly in the feathers of the wing.

Modified homozygous Frizzles differ from those not modified in that, while the latter have a woolly appearance, the former seem to have a softer velvety covering almost as if the feathers constituted a deep pile on an enveloping rug. This general effect results from the fact that each feather is less extremely curled than in unmodified homozygotes and is somewhat wider, but, nevertheless, has all of its barbs curled, so that no feather has a normal flat vane (Plate XV, fig. 6). In most feathers the curling of the barbs begins farther from the rachis than in feathers of unmodified heterozygotes, and a narrow strip on each side of the rachis has thus a normal vane. The shafts of the rectrices and remiges are less extremely curled, and the outspread wings of the modified and unmodified homozygotes (Plate XV, figs. 6 and 7) present decidedly contrasting appearances.

Frizzled chicks homozygous for the modifier show less of its effects
than do adults. At from 1 to 5 weeks of age it is difficult to determine the exact type of frizzling present, but there is no difficulty in distinguishing frizzled chicks from normal ones. As the birds become older and feathered out, the effects of the modifier are much more evident.

**Genetic Analysis**

The results secured in several different types of crosses involving the frizzling gene, *F*, its normal allele, and the modifier, justify the conclusion that the modified types of frizzling just described arise from the action of a recessive autosomal gene. For it the symbol *mf* is proposed. In fowls heterozygous for the modifier there are no readily perceptible effects, but, when homozygous, it induces the modified plumage in all birds heterozygous for *F* and in some, but not all, of those homozygous for that gene.

The first modified frizzles appeared in 1929 in the progeny of a White Leghorn *♀ × *Ff* and *FF ♀♀*. Among 76 *Ff* birds raised to maturity there were only four with modified frizzling, and all of these, together with seven unmodified ones, were produced by a single *FF* hen, No. A 5. It was obvious, therefore, that the White Leghorn was either *Mmf* or *MfF*, and that the modifier exerted no effect in birds only heterozygous for it. Apparently only one of the females carried the modifier.

This mating also demonstrated that the gene *mf* is not sex-linked. If it were so and were effective in the hemizygous state, then modified frizzling should have been evident in either all or half of the White Leghorn's frizzled daughters, depending upon whether he were *mfmf* or *MfF*. This was not the case. If *mf* were sex-linked, but unexpressed except where homozygous, then modified frizzling when it appeared (in the progeny of any frizzled female also carrying *mf*, as did A 5) should have been manifested only in the sons, whereas actually two of the four modified birds were females. Obviously *mf* is autosomal.

Data from seven different types of matings involving *F* and *mf* are presented in Table I.

Mating 5 indicates clearly that heterozygous frizzles showing the modified type of frizzling must be homozygous for the modifier, since the 11 *Ff* offspring were all modified.

Matings 4 and 5 bring out the interesting point that in fowls homozygous for both *F* and *mf*, there is frequently no manifestation whatever of the modifier. In mating 4 the segregation of *F*—20 *FF* : 41 *Ff* : 26 *ff*—shows a close fit to the expected 1 : 2 : 1 ratio, but, whereas the expectation for the homozygotes is that half should also be homozygous
for the modifier, only 3 out of 20 had the modified phenotype. Considering matings 4 and 5 together, the modified plumage was manifested in only six (or 40 per cent.) of the 15 \textit{FF} birds which should have shown it.

These same two matings also demonstrate that homozygosity for \textit{mf} is manifested in 100 per cent. of the birds heterozygous for the frizzling gene. The expectations that half of the \textit{FI} progeny would be modified in mating 4, and all modified in mating 5, were both realised.

\textbf{TABLE I}

\textit{Matings involving \textit{F}, \textit{mf} and their normal alleles}

\begin{tabular}{|c|c|c|c|c|}
\hline
\multicolumn{5}{|c|}{Frizzled offspring} \\
\hline
\multicolumn{2}{|c|}{Homozygous} & \multicolumn{2}{|c|}{Heterozygous} & \\
\hline
\multicolumn{1}{|c|}{Nature of mating} & \multicolumn{1}{|c|}{Modified} & \multicolumn{1}{|c|}{Not modified} & \multicolumn{1}{|c|}{Modified} & \multicolumn{1}{|c|}{Not modified} \\
\hline
1. \textit{FF} unmod. \(\varphi \times \varphi \) \textit{mf}, carrying \textit{mf} & - & - & - & 33 \\
2. \textit{FF} unmod. \(\varphi \times \varphi \) \textit{mf} carrying \textit{mf} & - & - & 4 & 7 \\
3. \textit{ff} unmod. \(\varphi \times \varphi \) \textit{mf}, \textit{mf} & 3 & 17 & 23 & 18 \\
4. \textit{ff} \textit{mf}, \textit{mf} \(\times \text{FI} \) mod. & 3 & 2 & 11 & 7 \\
5. \textit{FI} \textit{mod.} \(\times \text{FI} \) mod. & & & & \\
6. \textit{FI} \textit{mod.} \(\times \varphi \) to be tested for \textit{mf} & & & & \\
\(\textit{\(a\)} \times \text{Unknown} \) & - & - & 18 & - \\
\(\textit{\(b\)} \times \text{Barred Rock} \) & - & - & 22 & - \\
\(\textit{\(c\)} \times \text{18 Rhode Island Red and} \) & - & - & 68 & - \\
\text{Barred Rock} & & & & \\
\(\textit{\(d\)} \times \text{0 Polish} \) & - & - & 22 & - \\
\(\textit{\(e\)} \times \text{1 Silkie} \) & - & - & 1 & - \\
7. \textit{FF} \textit{mod.} & - & - & 18 & - \\
\textit{\(\varphi \times \text{2 Brown Leghorn} \) & - & - & 4 & - \\
\(\textit{\(b\)} \times \text{2 White Wyandotte} \) & - & - & & \\
\hline
\end{tabular}

In mating 7, a male with the type of plumage attributed to the genotype \textit{FFmf}, with manifestation of the modifier (Plate XV, fig. 6), was tested by outcrossing to entirely unrelated Brown Leghorns and White Wyandottes. Since all the 22 progeny from this mating showed the characteristic modified plumage of \textit{Fmf} birds, it was evident that the phenotype of this male was dependent upon homozygosity for both \textit{F} and \textit{mf}.

\textbf{DISCUSSION}

In its behaviour the modifier of frizzling resembles somewhat the recessive semiforked gene of \textit{Drosophila} which Lancefield (1918) found to be a modifier of the sex-linked character, forked, but only in flies heterozygous for the forked gene. Homozygotes for forked were unaffected, whereas in Frizzles about 40 per cent. of the homozygotes are
affected by the modifier. In both cases the modifying gene exerts no perceptible effect except when the modified character is present.

Landauer (1933) has reported a recessive modifier of frizzling which is probably identical with mf, but, contrary to the finding of the present writer, states that in his material all fowls homozygous for the frizzling gene and for the modifier showed the modified phenotype.

**Independence of F and mf.** Different degrees in modification of a structure in one direction are frequently the results of multiple alleles. This is definitely not the case here, since some birds were proven to be of the genotype FfMfMf, which would be impossible if multiple alleles were responsible. From mating 4, with only two pairs of genes affecting frizzling, there emerged five different phenotypes, which could not have occurred even if four different members of a series of alleles were involved, but could arise from different combinations of two pairs of independent but interacting genes.

**Other modification of frizzling.** While the processes of development responsible for frizzled feathers have not yet been determined, it seems probable that in these, as in curly hair, there may be different rates of growth on opposite sides of the follicle. Such a difference would be accentuated in rapidly growing feathers and minimised in those growing slowly. On this basis it is not surprising that the modifier exerts its least effect on the plumage of the chick during the period of its most rapid growth, and its greatest effects upon the feathers acquired at or near maturity.

It is evident from the descriptions and illustrations of the wings of modified and unmodified frizzles that in the primary remiges there is a postero-anterior gradient of increasing manifestation of the gene for frizzling. This gradient is most conspicuous in Ff birds homozygous for the modifier (Plate XV, fig. 3). Its course is the same as the order of moulting of these feathers both when juvenile birds are assuming adult plumage and when adults are moulting. The first primary to be replaced is the inner, or most posterior one, after which the other primaries are replaced in order, the last to grow being the outer or most anterior of the ten primaries. If in modified birds, frizzling is least manifest in feathers with slow growth rates, the inner primaries must grow in at a slower rate than the outer ones, even though the former are acquired first, before the general rate of body growth has slowed down as much as when the outer primaries are grown. This is not as paradoxical as it may seem. The inner primaries are acquired before moults is general, the outer ones are replaced when many feathers are being acquired all
over the body and frequently two or more remiges are shed at once. Larionov et al. (1932) found in the pigeon that when many feathers were being acquired at once the rate of growth of individual remiges was more rapid than when few feathers were being replaced.

Within individual remiges, especially in the outer primaries, the manifestation of frizzling varies both in modified and unmodified heterozygotes. In general, the distal and proximal ends of the feather are least affected, while the intervening area shows most frizzling. This may possibly be associated with retarded growth in early development prior to expulsion of the antecedent feather, and again when the new feather is nearing completion.

The role of different growth rates in modifying the structure and pattern of feathers in different parts of the body has been demonstrated by Juhn, Faulkner and Gustavson (1931) and by Lillie and Juhn (1932). In frizzled fowls the action of the gene, \( F \), is apparently conditioned by such regional differences as well as by the modifier, which exerts its effects on all parts of the plumage.

Significance of \( mf \) in evolution. There can be little doubt that in nature fowls carrying the frizzling gene, \( F \), would be somewhat at a disadvantage in comparison with those having normal plumage. Heterozygotes are frequently almost bare after the mating season. Benedict, Landauer and Fox (1932) found that homozygous Frizzles have a much higher rate of metabolism and greater food requirement than normal fowls, especially at low temperatures, and Landauer and Dunn (1930) state that in their experience "a high percentage of homozygous Frizzles of both sexes never reach maturity".

However, as Fisher (1930) points out, the persistence or elimination of an undesirable mutation depends almost entirely upon the degree of disadvantage which it brings to the heterozygote and very little upon the disadvantage to the homozygote, even if it were there fully lethal. There is little definite evidence that \( F^1 \) birds are at a disadvantage under modern conditions of domestication. The writer's earlier data (Hutt, 1930) do not support the conclusions of Landauer and Dunn (1930) and of Landauer (1932) that eggs of unmodified heterozygous frizzled females are subject to greater embryonic mortality than are those of non-frizzled fowls. There can be no doubt, however, that in nature the heterozygote's chances of survival in competition with fowls of normal plumage would be considerably reduced. Their plumage provides less protection against extremely low temperature and against rain. The remiges and rectrices are so abnormal that flight is quite impossible, and,
since many of these birds are unable to reach roosts only three feet from
the ground, they would be caught by predaceous enemies more easily
than normal fowls.

The modifier, which not only improves the covering but also restores
somewhat the ability to fly, is evidently a very desirable gene, having
definite "survival value". The fact that it has no effect on more than
half of the birds homozygous for F makes little or no difference in its
value to the species, so long as it conveys a definite advantage to the
heterozygotes which are much more numerous in the wild population
than are the homozygotes.

Distribution of the modifier. Where man got his first Frizzles is
unknown, but there can be little doubt that the mutation has occurred
many times in the history of the species. In fact, since frizzling is also
found in canaries and pigeons, the mutation has probably occurred even
farther back in the ancestry of the domestic fowl. If it were an old
mutation, one would expect to find the modifier well distributed in
divers breeds of present-day poultry. With this in mind, a number of
breeds and varieties have been tested for the presence or absence of
the modifier.

In Table I, the various breeds used in matings 6 and 7 are listed
to show that the modifier was present in at least seven different breeds.
Moreover, while some of them were not adequately tested for homo-
zygosity, the fact that all frizzled progeny were shown by their phenotypes
to be homozygous for the modifier indicates that practically all of the
29 non-frizzled fowls tested must likewise have been homozygous for it.
In addition to those listed the modifying gene was also found in Mottled
Houdauns, Silver Laced Wyandottes, White Leghorns and White
Orpingtons, making a total of eleven breeds or varieties found to carry it.
Since these breeds represent both Mediterranean and Asiatic ancestry
such a distribution may be some indication that its "survival value"
has resulted in its early inclusion in the germ plasm of the ancestors of
the domestic fowl.

It would be of considerable interest to determine the distribution of
the modifier in native stocks of poultry in various parts of the world.
Evidence that frizzled fowls have a wide distribution in southern Asia,
the East Indies, Surinam, Mauritius and Mozambique was summarised
in the writer's earlier paper (1930). Prof. J. B. S. Haldane informs me
that they also occur in Dahomey and Jamaica, and Rattray (1927) found
them in Ashanti. Such a distribution suggests that in warm climates
frizzling may be less of a handicap than in colder ones, but whether its
survival in these regions has been facilitated by the modifier or not is
an interesting but unanswered problem. Some of the descriptions, and
the fact that frizzled fowls are especially prized in some countries,
suggest that unmodified frizzles are available through much of the range
given above.

Modification of dominance. The interactions of F, mf and their
normal alleles provide an excellent example of the modification of
dominance in accordance with the theory of Fisher (1930). Without
modification, F is an incompletely dominant gene, but the selective
disadvantage which it conveys to the heterozygote results, with natural
selection, in the accumulation of modifying genes which suppress its
effects. The result is that the heterozygote becomes modified toward
the phenotype of whichever homozygote has the greater chance against
natural selection, in this case the wild (non-frizzled) type. In this way
a character originally having marked, though incomplete, dominance
becomes eventually almost or entirely recessive.

Preservation of the full effects of the frizzling gene is therefore
dependent upon man's efforts to eliminate the modifier. The modern
fancier does so because his show-room standards prefer the unmodified
heterozygotes. Presumably his forerunners preserved them from
curiosity, for sacrificial rites as in Ashanti (Rattray, 1927), or because
of special properties believed associated with frizzled fowls such as their
supposed ability in Malaya to ward off "the evil eye", to which Fisher
(1935) refers.

Summary

Partial suppression of the frizzled plumage of heterozygous Frizzles
is induced by a recessive autosomal gene, mf, which is independent of
the gene for frizzling.

This modifying gene is manifested when homozygous in all birds
heterozygous for frizzling and in about 40 per cent. of those homozygous
for frizzling.

Modified heterozygotes may show only a slight ruffling of the body
feathers, but always have abnormal feathers in the primary remiges.
Modified homozygotes have less curling of the feathers in all parts of
the body.

The manifestation of frizzling is also apparently conditioned by
growth rates of feathers, which vary with age, in different regions of the
body and within certain feathers.
The modifying gene is widely distributed among domestic fowls, presumably because of its selective advantage in their ancestors.

REFERENCES


EXPLANATION OF PLATE XV

Fig. 1. Unmodified heterozygous Frizzle, Ffmmmf.
Fig. 2. Outspread wing of the same.
Fig. 3. Outspread wing of a modified heterozygote.
Fig. 4. Modified heterozygous Frizzle, Ffmmmf.
Fig. 5. Unmodified homozygous Frizzle, Ffmmmf.
Fig. 6. Modified homozygous Frizzle, Ffmmmf.
Fig. 7. Outspread wing of the unmodified homozygote shown in Fig. 5.