AN HEREDITARY COMPLEX IN THE DOMESTIC FOWL

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Brachydactyly, syndactyly, and leg-feathering or ptilopody¹ are among the many characteristics of the domestic fowl that have been studied from the standpoint of genetics. The last in particular, owing to its widespread occurrence, has aroused especial interest. Its heredity has been investigated by HURST (1905), DAVENPORT (1909), and more recently by PUNNETT and BAILEY (1918). The genetic behavior of syndactyly has been studied by DAVENPORT (1909) and that of brachydactyly by DANFORTH (1919 a).

The purpose of this paper is to present evidence that these three characteristics, at first sight apparently distinct and unrelated, are in reality the product of a single gene or a single combination of genes. The possibility that this is the case was suggested in the earlier paper on brachydactyly, but at the time that paper was written, sufficiently critical breeding tests had not been made, the suggestion being based largely on morphological evidence. The additional data now available, while not abundant, seem to be significant, and are therefore put on record.

Except where otherwise indicated the descriptions and data are all from individuals derived, on one side at least, from a single family, the relationships of the principal members of which are shown in the accompanying pedigree chart. None of those indicated in the chart was syndactyl.

¹Two terms, "leg-feathering" and "booting" have been employed to indicate the presence of feathers on the tarsus and toes. Both of these terms are inappropriate; the former because it is not the leg, but the tarsus and toes that is meant, the latter because the term is already in use to indicate a fusion of tarsal scutella. Since no other convenient term seems to be available the word ptilopody (πτίλον, feather; πούς, foot) is used in this paper to designate the condition in which down or feathers tend to appear on the tarsus and toes.

PEDIGREE CHART

The individuals of mixed ancestry may be characterized as follows:

No. 5. Male. A mongrel of unknown ancestry, but with a general appearance suggestive of Brahma extraction. Moderately ptilopod. No record as to brachydactyl.

No. 6. Female with three legs (*Pygopus parasiticus*). Small, showing no indication of Asiatic origin. Neither brachydactyl nor ptilopod.

No. 8. Male. Brachydactyl, ptilopod.

Nos. 21-25. Females. Brachydactyl, ptilopod.

No. 27. Male. Brachydactyl, ptilopod.

No. 28. Male. Brachydactyl, ptilopod.

No. 29. Male. Not brachydactyl, ptilopod.

No. 30. Female. Not brachydactyl, not ptilopod.

No. 31. Female. Brachydactyl, not ptilopod.

No. 32. Female. Brachydactyl, not ptilopod.

No. 33. Female. Brachydactyl, not ptilopod.

No. 35. Female. Not brachydactyl, ptilopod.

No. 36. Male. Brachydactyl, not ptilopod.

No. 37. Male. Brachydactyl, not ptilopod.

Chicks were raised from these birds, bred together and with barred Plymouth Rocks, White Leghorns or Black Minorcas. The distribution of brachydactyly, ptilopody and syndactyly among the offspring is indicated in table 1 where chicks and embryos of 13 days and over are considered. (Besides those shown in the table, 305 additional chicks were produced by some of these parents after having been treated with alcohol. Of these 49 percent were brachydactyl, 37 percent ptilopod and 0 percent syndactyl. 50 percent of them showed either brachydactyly or ptilopody. These data are not included here. The effect of alcohol on the distribution of traits is discussed in another paper (DANFORTH 1919 b).

The table shows first of all a high degree of correlation between brachydactyly and ptilopody. The correlation, however, is not complete

TABLE I
Parental matings and offspring.

Parental traits and matings	Distribution of traits in the offspring (Data from 508 chicks of thirteen days and over)			
	Brachydactyl ptilopod	Brachydactyl non-ptilopod	Ptilopod non- brachydactyl	Non-ptilopod non- brachydactyl
I. Brachydactyl ptilopod $\times$ normal				
1. Leghorn ♀♀ $\times$ 8 ♂	49	2	5	78
2. Barred Plymouth Rock ♀♀ $\times$ 8 ♂	2	0	0	1
3. Minorca ♀♀ $\times$ 27 ♂	15	7	0	45
4. Minorca ♀♀ $\times$ 28 ♂	49	10	3	66
5. 21-25 ♀♀ $\times$ Minorca ♂	23	21	0	65
Total	138	40	8	255
II. Non-brachydactyl ptilopod $\times$ normal				
6. Minorca ♀♀ $\times$ 29 ♂	7	5	1	11 (19)
7. 35 ♀ $\times$ Minorca ♂	3	5 ¹	0	2
Total	10	10	1	13 (21)
III. Non-ptilopod brachydactyl $\times$ normal				
8. Minorca ♀♀ $\times$ 37 ♂	4	5	1	7
IV. Non-ptilopod brachydactyl $\times$ non- ptilopod brachydactyl				
9. 32 ♀ $\times$ 37 ♂	2	2	0	1
V. Brachydactyl ptilopod $\times$ brachydactyl ptilopod				
10. 21 ♀ $\times$ 28 ♂	6 ²	0	0	4
VI. Miscellaneous				
11. 21-25 ♀♀ $\times$ 27-28 ♂♂	9	1	1	8
12. 21, 30, 33. ♀♀ $\times$ 36 ♂	6 ¹	3	0	3
Total	15	4	1	11
Number in each class, irrespective of ancestry	175	61	11	291 (299)

¹ One of these was syndactyl.

² Two of these were syndactyl.

since some individuals are brachydactyl but not ptilopod while others are ptilopod without being brachydactyl. This immediately suggests linkage of genes and "crossing over." At the time the first paper was written this possibility could not be excluded, although it was pointed out that the fact that the two traits tend to parallel each other in their fluctuation does not favor such an interpretation.

The results of matings 6-9 seem to settle the question of two possible linked genes. In mating 6 the male was not brachydactyl but did have a very few small feathers on the tarsus and fourth toe. Mated to normal Minorca hens which did not carry determiners for either brachydactyly or ptilopody he produced both brachydactyl and ptilopod offspring. Mating No. 7 represents the reciprocal cross and yielded similar results except that, probably owing to the small numbers, no long-toed ptilopod chicks appeared. Mating 8 between a brachydactyl male with no feathers on the tarsi or toes and normal Black Minorca hens likewise yielded chicks that showed brachydactyly only, ptilopody only, brachydactyly and ptilopody combined, and the absence of both traits. Finally mating 9 in which neither parent showed ptilopody gave two chicks that were both brachydactyl and ptilopod, two that were brachydactyl only, and one that was neither.

These results seem to exclude the possibility of the different somatic combinations being due to separation of linked genes. If there are indeed two genes there is no evidence that they are ever separated since individuals showing one trait and lacking the other reproduce the missing trait as readily as those that actually have it. So far as breeding tests show, brachydactyly and ptilopody may be regarded as two manifestations of the same hereditary factor.

This interchangeability of brachydactyly and ptilopody may possibly explain some supposedly aberrant cases discussed by PUNNETT and BAILY (1918). In one case (*loc. cit.*, p. 208) a female derived from a Langshan-Hamburg cross had no feathers on the tarsi or toes but nevertheless behaved in breeding tests like a true ptilopod individual. It will be apparent that if this particular bird were brachydactyl, its behavior was entirely in accord with expectations and could not be regarded as in any way aberrant.

Similarly on p. 212, in discussing some work of BONHOTE (1914), PUNNETT and BAILEY quote a case in which two clean-legged F_1 birds from a Silky-Yokohama cross when bred together gave 8 ptilopod and 16 clean-legged offspring. If, as is highly probable, the F_1 parents were brachydactyl, the mating would be entirely comparable to mating 9 in

the table and the results are essentially the same since in both cases ptilopod and non-ptilopod young were produced. The total number of chicks in this case is so small that the relative size of the two classes has little significance especially when it is recalled that some of the 16 chicks recorded as clean-legged may nevertheless have been brachydactyl.

Likewise the data on which DAVENPORT (1909) based his statement that "two extracted clean-footed birds sometimes throw boot and sometimes not" may have come from matings in which at least one of the individuals involved was brachydactyl. In other words, if the interpretation suggested here be accepted, one of the difficulties encountered by students of ptilopody will have been removed.

The failure to recognize brachydactyly as another form of ptilopody tends in some measure to vitiate the observations thus far reported. For example, in the results from matings recorded in this paper it would make a difference of over 10 percent whether the brachydactyl non-ptilopod group were counted on one side or the other. This is a matter of considerable importance in an investigation of the genetic behavior of a trait.

The evidence for associating syndactyly with the other two traits is less conclusive but is such as to create a very strong presumption in favor of the view that such an association exists. DAVENPORT (1909) has described the trait in detail and indicated its range of variability. His data come from about one hundred and fifty individuals all descended from a single Brahma hen which was herself somewhat syndactyl. It is clear from the descriptions and figure that the progenitor of this family was also ptilopod. It is apparent too that many, possibly all, of her syndactyl descendants were likewise ptilopod. DAVENPORT's data show clearly that the trait is dominant.

Only four syndactyl chicks were obtained from the experiments reported in this paper. Two came from mating 10 and one each from matings 7 and 12. None of the parents of these four chicks was in the least syndactyl nor did syndactyly occur elsewhere in the immediate ancestry. The chicks themselves were all brachydactyl; those from matings 10 and 12 were also ptilopod. The appearance of a normally dominant trait in this manner adds some support to the suggestion that the condition found in the parent is really the same trait in a different form. Unfortunately none of these syndactyl chicks became available for breeding tests.

Another thing that strongly suggests the common origin of the three traits is the fact referred to in the paper on brachydactyly, that the same

combination of traits tends to occur in the pigeon. It is much simpler to suppose that a single mutation has occurred in one homologous gene of the pigeon and fowl than that three different genes have undergone mutation at the same time and in the same manner in these two very different species.

On the basis of the data that have now been presented the simplest and most adequate working hypothesis would seem to be that the three morphologically distinct traits, brachydactyly, syndactyly and ptilopody, owe their existence to the action of a single gene. The tendency of the trait to manifest itself in some crosses more frequently in one form, and in other crosses in another, is perhaps to be explained by the action of modifying genes unequally distributed among individuals and is in harmony with DAVENPORT'S observation that within a single manifestation (ptilopody) the grade represented by the parent shows some tendency to be reproduced in the offspring.

The characteristics and to some extent the ontogeny of these traits have been discussed by the authors to whose work reference has already been made.¹ One point, however, seems to have been entirely overlooked in previous studies of the subject, namely, the range within which the ptilopod trait varies. Ptilopody involves not only the usual presence of feathers on the tarsus but also rather fundamental changes in the scales of the foot. A normal non-ptilopod individual shows scutella arranged with great regularity over the lateral side of the tarsus and along the dorsum of the fourth toe. In the Minorca, for example, (figure 1) there are about 31 such scales in linear sequence, 17 on the toe and 14 on the tarsus. These numbers are subject to some variation but are reasonably constant. The scales themselves are smooth and regular with the distal free margins approximately straight and parallel. Only rarely is a scale divided. In ptilopod specimens (figures 2 and 3) not only are some of the scales reduced in size and thrown out of alignment but they are modified structurally, frequently showing a tendency to become raised and cylindrical. In some instances forms occur which are intermediate in character between scales and feathers. Where the reduction is carried still farther the tarsus and toe may be essentially smooth but with some of the individual scales showing longitudinal lines and grooves (figures 4 and 5). This sculptured appearance is almost always

¹ "Le vieux coq," a well known etching by the artist Felix Bracquemond, which is doubtless to be found in most museums of fine arts, portrays with remarkable fidelity all the peculiarities mentioned here except syndactyly.

FIGURE 1.—Lateral aspect of the left foot of a Black Minorca chick showing normal proportions and the usual arrangement of scales on the antero-lateral aspect of the tarsus and on the dorsum of the fourth toe.

associated with some irregular imbrication of the scales. A series of individuals could easily be arranged to show a complete gradual transition from a condition with only a few irregular and sculptured scales to one with the heaviest degree of feathering. Indeed it might perhaps be more accurate to regard the ptilopod factor as one primarily affecting the scale-forming tissues of certain parts of the foot. In its mildest manifestation only the scales are involved. In slightly more pronounced instances there appears in addition a modified quill or rudimentary feather, generally on the basal phalanx of the fourth toe. Further intensities of manifestation may be traced through the ten stages recognized by DAVENPORT. Morphologically each feather may represent a part of the rudiment which, in the absence of the ptilopod factor, would have gone into the formation of a scale.

Despite the fact that the three traits are morphologically very different—webbing of the toes, modification of scales or feathers, and reduction in the size and number of bones are quite unlike—the possibility of their being traceable to the action of a common gene is by no means excluded. It is now commonly admitted that each gene in the germ plasm tends to affect all parts of the body more or less but that the reactions in different

FIGURE 2

FIGURE 3

FIGURE 2.—Anterior view of a (left) brachydactyl, ptilopod foot. Few of the birds referred to in the body of the paper showed a greater degree of ptilopody than this one. In addition to those on the tarsus and fourth toe a few small feathers may be seen also on the third toe. The brachydactyly which is of the more pronounced type is, as usual, most manifest in the fourth toe. This digit has only two phalanges in place of the normal five. The specimen is not syndactyl.

FIGURE 3.—Anterior view of the left foot of an individual in which the trait is present in all three forms. One or two feathers are present (ptilopody), the fourth toe is greatly reduced (brachydactyly) and the third and fourth toes are fully webbed (syndactyly).

parts may be quite diverse. With the cases in question it is easy to imagine that a disturbing factor coming into action on the 7th-8th days of incubation might be effective in producing permanent webbing of the toes. This is the time when the webbing, already present in the normal embryo, shows its most rapid involution and might be expected to be most susceptible to modifying influences. The same factor becoming effective on the 8th-10th days might be too late to have any effect on the webbing of the toes but would find the cartilages in their formative, and

FIGURE 4

FIGURE 5

FIGURE 4.—Lateral view of a left foot showing no feathering whatever but clearly revealing the presence of the ptilopod factor by the irregularities in the scutella, some of which are "sculptured" (A). The specimen is moderately brachydactyl, the dorsal scutella being reduced from the normal 17 to about 10. The third and fourth toes are fully webbed. The falciform free margin of the web is indicated at B.

FIGURE 5.—Right foot. Similar to figure 4, but showing the sculpturing of the scales more clearly. There is a slight indication of syndactyly. Figures 4 and 5 should be compared with figure 1 in reference to the number, form and arrangement of scutella and the relative lengths of the toes.

therefore, perhaps, most susceptible stage. Finally, if not effective before the 11th-12th days, the normal webbing and skeleton of the toes would have already been determined but the possibility of feather-germ development would still remain. (For a discussion of the embryological relations of these traits the reader is referred to the paper on brachydactyly (DANFORTH 1919 a).

If one may be permitted to speculate on the mode of production of such traits several possibilities at once suggest themselves. (a) The simplest and crudest explanation suggests that the observed manifestations are the product of the action of some internal secretion upon the

normal tissues of the foot. In this case we are in reality studying the hereditary character and fluctuations in an endocrine gland through the effects produced by its secretion. (b) Conversely it might be assumed that the effect of the factor is to "sensitize" certain parts to some normal product of the endocrine system. (c) Still again, it is possible that the factor acts intrinsically and when a certain stage of development is reached the presence of a given gene in each cell of a rudiment determines the behavior of the whole mass, more or less irrespective of developments in other parts of the embryo. The problem of deciding among these and other possible alternatives belongs in the field of experimental embryology, but is necessarily of interest also to genetics.

Two interesting points raised by PUNNETT and BAILEY (1918) call for brief consideration in this connection. One of these concerns their suggestion that in the Cochin and Dark Brahma races "two factors *A* and *B* may be present, either of which determines leg-feathering," while in the Langshan and Silky only one such factor is present. The data here recorded throw no direct light on the question since no evidence appears to indicate the presence of more than one factor. But since the progenitor of these birds was a hybrid, and since the degree of ptilopody in none of his descendants was very pronounced, it is quite possible that even though the race may have been of Brahma extraction one factor had already been lost from the line of descent when the present breeding tests were begun. PUNNETT and BAILEY seem to imply that factor *A* is the more constant one, and since they offer no means of differentiating between them we may assume that their factor *A* and the gene postulated to explain the brachydactyl-syndactyl-ptilopod complex are the same. If the factor *B* is ultimately isolated in a strain of fowl it will be of considerable importance to determine whether or not it too carries the potentiality of brachydactyly and syndactyly.

The other point brought out in PUNNETT and BAILEY's report is the possible presence of an inhibitor *I*, assumed to be present in certain normal strains and tending to prevent the development of feathers, even in the presence of factor *A*. While, as previously suggested, the particular case for which the *I* factor was postulated is perhaps open to a different explanation, the possibility of such a factor being present in some cases is of interest. Such a factor introduced by the homozygous parent and coming into effect on the tenth to twelfth days might explain the very high percentage of brachydactyl non-ptilopod chicks from matings 5-9. If the existence of the *I* factor can be substantiated, a

more detailed study of its interaction with the peculiar *A* factor may yield interesting results.

To summarize briefly: The data presented in this paper show that ptilopody (the tendency to produce feathers on the tarsi and toes) is subject to a much wider range of variation than has hitherto been supposed, and that the three traits, ptilopody, syndactyly and brachydactyly, are associated in heredity. All the available evidence points strongly to the conclusion that the three traits just mentioned are primarily caused by a single gene. If the conclusions arrived at in this paper are accepted it will be necessary to revise in some measure much of the work that has been done on the heredity of ptilopody ("booting" or "leg-feathering").

The stock used for these experiments was kept in the animal quarters of the Department of Anatomy, the eggs were hatched in the laboratory incubators and the chicks raised for the most part on the roof. The writer wishes to take this opportunity of acknowledging his indebtedness to Dr. R. J. TERRY, Director of the Laboratories, for making these facilities available and for his assistance in many other ways.

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