INHERITANCE OF STRUCTURAL TYPES IN THE DORSOSACRUM OF DOMESTIC POULTRY.

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(With Four Text-figures.)

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I. INTRODUCTION.

The pelvis in different races of domestic poultry exhibits considerable variability, extending over a whole series of characters. Indications of the hereditary nature of many of these exist, and there is no doubt about the genotype of the pelvis of the domestic fowl being very complicated. The structure of the pelvis as a whole constitutes a morphological expression, the phenocomplex of the whole genotype of a given individual; the different characters of the pelvis being correlated with one another both genetically and physiologically, and the pelvic structure of one kind or another being the result of a whole series of genes.

In the present paper, special attention has been paid to the structure of the anterior vertebrae of the pelvis, i.e. of its dorsosacral part. This region of the spine shows sharp and distinct differences of structure, and is therefore better suited for genetical analysis. However, here also, in spite of a comparatively clear morphological picture of the types, we find a number of modifications which are perhaps of a fluctuating character. Nevertheless, a great many crosses among poultry confirm the hypothesis we have drawn up of the genetical factors for a given character, and allow us to regard the genetic scheme presented further on as corresponding fairly closely with reality.

The genetical analysis of anatomical characters presents a number of difficulties. Chief among them, in our researches, was the impossibility
Dorsosacral Types in Poultry

of knowing the phenotype of the individual before its death. Only after
the death of the parents did the series of their dissected offspring acquire
positive value. In this way many crosses could only be utilised post
factum, or had to be made according to the supposed structure of the
individual. Hence suppositions as to the structure of the pelvis, made
on the basis of the genetical working hypothesis, on realisation became
of importance. Many chicks from still living poultry could not be
completely utilised as the structure of the parental pelvis was entirely
unknown.

The materials used for these researches were the adult poultry and
chickens of the Anikovo Genetical Station near Moscow. The total
number of individuals dissected was about 4000. The crosses principally
employed were those of Orloff and Pavloff poultry with Minorcas,
Faverolles, Indian Game, etc. Adult fowls and chickens of later embryonic
stages were dissected.

The first part of these researches, carried out under the direction of
Professor A. S. Serebrovsky, was printed in the Memoirs of the Anikovo
Genetical Station of Moscow\(^1\) under the title "The genetical analysis of
the structure of the pelvis in the domestic fowl." The second part
"Types of structure of the sacral region of the pelvis in the domestic
fowl and their inheritance," also printed in Russian\(^2\), presented a continu-
ation and a further development of the first part. It introduced some
slight alterations in the details of the genetical scheme already put
forward, resulting from the study of a larger quantity of material as
well as from the completion of various pedigrees through the death of
the parents. The present article covers the ground of the earlier ones
with some additions.

II. Description of the Pelvic Types.

Normally, domestic poultry have 14 ribless cervical vertebrae and
seven pairs of ribs, belonging to V. 15-21. This last is the first
vertebra belonging to the synsacrum. According to Gadow\(^1\) V. 21 is
the beginning of the dorsosacral region of the pelvis.

The pelvis of a "normal" fowl has four dorsosacral vertebrae (21-24),
characterised by well-developed transverse outgrowths (processus trans-
versi). The proc. transv. ventrales of V. 24 are especially well developed.

\(^2\) Russian Journal of Experimental Biology (edited by Professor N. K. Koltsoff), Serie
sides of the vertebrae to the os inominatum (Fig. 1, p). Sometimes V. 23 also bears such outgrowths (Fig. 4 a), but for the most part they are somewhat less developed. In the majority of poultry with four dorsosacral vertebrae V. 23 resembles V. 22 in structure. It bears comparatively thin and concrescent proc. transv. ventrales and dorsales, which seem to bend inwards towards the back if the pelvis be looked at from the ventral side (Fig. 1). These variations in the degree of development of the proc. transv. of V. 23 exist in many families (series) of poultry and will be spoken of later on (Section v).

![Fig. 1.](image_url)

With V. 25 in a normal pelvis the lumbosacral region starts, with vertebrae of an entirely different structure. There are no proc. transv. ventrales and the proc. transv. dorsales are thin, rising sharply towards the back and directed somewhat backwards (Fig. 1). After the lumbosacralia, the proc. transv. ventrales begin for the most part from V. 30, but this character presents a certain variation, and is not taken into account in this article.

Thus the pelvis of a normal fowl is characterised by four vertebrae of dorsosacral structure, there being a very sharp difference between V. 24 and V. 25. Nearly 75 per cent. of the entire material at my disposal belonged to this type. The changes in structure of the pelvis, when compared with the generally accepted anatomical norms, are as follows.
A pelvis with *five dorsosacral* vertebrae is rather frequent in some races of poultry (1000 out of 4000 in our material). V. 25 acquires the same broad proc. transv. ventrales as those of V. 24, and if one looks at the pelvis from the ventral side, the eye is struck at once by *two pairs* of broad flat proc. transv. (Fig. 2, p1, p2) going from the spine to the bones of the pelvis, and in front of them three more vertebrae (21–23) with feeble proc. transv. The lumbosacral vertebrae begin with V. 26,

![Diagram of pelvis with labels](image)

*Fig. 2.*

and this backward homoeosis of the dorsosacral region often extends to those parts of the synsacrum which are situated behind (the first pair of proc. transv. ventrales after the lumbosacralia begins at V. 30). Frequently V. 23 bears an eighth pair of thin ribs.

This type of pelvis differs sharply from the one described above (having four dorsosacralia), and from its general correlation of the pelvic bones with the synsacrum, creates the impression of a removal backwards along the spine of the different anatomical regions of the synsacrum and of the pelvic bones.

For this reason I have already called it (21) "a type of a backward removal of the pelvic bones" (plus-type, Fig. 2).

The dissection of Bantam chickens and adults has revealed a third
type of pelvic structure, differing sharply from the two types already described in the number of the dorsosacral vertebrae. For in many Bantams the pelvis has only three dorsosacral vertebrae (21–23). V. 24 has no proc. transv. ventrales, but from its structure belongs to the lumbo sacralia (see Fig. 3). Broad flat proc. transv. (p) are also developed here on the last dorsosacral vertebra, viz. V. 23 (not V. 24). Minute dissections made in 1919–20 by A. S. Serebrowsky (at the Tolia Genetical Station), and later on by myself, showed only 13 ribless cervical vertebrae in many Bantams. C.V. 14 often had a short rib, and the vertebrae

14 to 20–21 had seven or eight pairs of ribs. This diminution in the number of the ribless cervical vertebrae considerably obscured the morphological and genetical relations between the Bantam pelvis and that of other types, making their comparison by no means easy. Looking at such a pelvis from the ventral side (Fig. 3), one sees at once, on comparing with a normal pelvis (Fig. 1), and particularly with the type possessing 5 ds. vertebrae (Fig. 2), that the anatomical regions of the synsacrum, and to some extent the bones of the pelvis, seem to have been moved forward. This displacement I named (in the first paper) a "forward removal."

Therefore, according to the number of dorsosacral vertebrae, three principal types can be established in the structure of the pelvis (see Table I).

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TABLE I.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of dorsosacral vert.</td>
<td>3</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Dorsosacral vert. (accounted from the cranium)</td>
<td>21-23</td>
<td>21-24</td>
<td>21-25</td>
</tr>
<tr>
<td>Broad proc. transv. (p) (see Figs. 1-3)</td>
<td>Constantly on the 23rd vert.</td>
<td>On the 24th or on the 23rd and 24th vert.</td>
<td>Constantly on the 24th and 25th vert.</td>
</tr>
</tbody>
</table>

To elucidate the inheritance and genetical nature of these three types is the object of the present paper. But before attempting to do so it is necessary to make a brief study of the variability within the limits of each type. A general examination of my material showed a somewhat considerable variation in the normal 4-da. type, manifested by a greater or lesser development of the proc. transv. on V. 23. In my first paper, the 4-da. type of structure was even divided into two types, viz.

(1) The so-called "typical structure" (N 4 da., see Section v) where the proc. transv. of V. 23 are like those of V. 22, and much less developed than on V. 24 (Fig. 1 or 4 c).

(2) The so-called "incomplete removal forward" (M 4 da., Section v) where the proc. transv. of V. 23 are of the same size as those of V. 24 (Fig. 4 a).

These two types of structure are united by a chain of transitions which, conventionally, can be thus expressed:

\[ \text{proc. transv. of V. 23} = \text{of V. 24} \ldots 23 \leq 24 \ldots 23 < 24 \ldots \ldots 23 \leq 24 \ldots 22 = 23 \leq 24 \ldots \text{"the typical structure."} \]

The structures placed to the left of the vertical line, I considered as the "removal forwards" (Fig. 4 a, b), that to the extreme right as the typical structure (Figs. 1 and 4 c, d). More extensive material and a more minute examination, however, have now led me to the conclusion that the common fundamental character is the presence of four dorsosacral vertebrae, the variability in size of the proc. transv. of V. 23 (causing the differences described above) being a character of secondary importance, with evidently some phenotypical variation. (Some indications of this hereditary character will be mentioned later in Sections III and v.) Hence in the subsequent course of my work cases of "incomplete forward removal" were united with those of typical structure, owing to the presence of four dorsosacral vertebrae, into one and the same 4-da. type, as being genetically and morphologically a distinct one.
The identity of these two structures is also manifest by the fact that the proc. transv. of V. 23 and V. 24 are not very apparent, and present but slight differences in embryos and newly-hatched chickens. Only through later ossification and concrescence of the vertebrae do the relative sizes of the proc. transv. of these vertebrae become quite evident.

Besides those in V. 23 there are other variations in this type of pelvis found in V. 25. This vertebra, the first of the lumbar-sacralia, has usually no proc. transv. ventrales in this type, thus differing distinctly from the preceding vertebra, the last of the dorsosacral ones (24). However, in a few cases (about 1 per cent.) small conical protuberances are noticeable on V. 25—the rudiments of the proc. transv. ventrales, which do not reach the os innominatum, and are free at the end. Sometimes these protuberances only exist on one side (see 2 on Fig. 4 c, d). The feeble development of these rudimentary formations compels us to class such structures among the 4-ds. type.

The type with 5 dorsosacral vertebrae (5 ds.) varies very little, as
V. 24 and V. 25 are nearly always very much alike, both in structure and in the degree of development of the proc. transv. ventrales. Owing to the presence of two pairs of broad proc. transv. (p), this type seems, at first sight, to be very like the variation of 4 ds., where the proc. transv. of V. 23 are as strongly developed as those of V. 24 (comp. Figs. 2 and 4 a). But they belong to different vertebrae (23–24 and 24–25). What is of importance, is that in spite of the morphological resemblance in the structure of the vertebra possessing p-outgrowths (see Figs. 2 and 4 a), and although the position of V. 24 is analogous to that of V. 23 in the 4-ds. type (viz. in front of the last vertebra of the dorsosacral structure), in this (24th) vertebra (in the 5-ds. type) the degree of development of the proc. transv. does not show the slightest variation, and also all the individuals of the 5-ds. type have two, almost equal, pairs of broad proc. transv. ventrales, belonging to V. 24 and V. 25 (about 1000 individuals). This absence of variation in the proc. transv. of V. 24 (for the type given) finds its explanation in the genetical interpretation of the character investigated (see end of Section v, and Section viii). On the whole, the type with 5 ds. vertebrae is very constant and well defined.

Variation in the 3-ds. type is likewise small. V. 22, which precedes V. 23 with broad proc. transv. (p), never bears such proc. transv. but always ones of a distinct type—narrow and situated deeply inwards (Fig. 3). The only rare deviations found were pointed excrescences on V. 24—the rudiments of proc. transv. ventrales of the dorsosacral type. These outgrowths do not acquire the shape of the proc. transv., and there is therefore no difficulty in referring this structure to the 3-ds. type. These changes are very like those already described for V. 25 in the normal pelvis (Fig. 4 c, d).

In concluding this descriptive part I may state briefly the correlations existing between the types of pelvis described and the number of the ribs. The normal number of ribs in poultry is seven pairs but not infrequently there is found an extra pair. This eighth pair can have two modes of origin, appearing either anteriorly on C.V. 14 or posteriorly on V. 22. The first mode occurs in Bantams, leading to the formation of 13 ribless vertebrae in the cervical section. In other races the extra ribs are nearly always found posteriorly on V. 22 and then show a close correlation with the 5-ds. pelvic type. This connection can be illustrated as follows:

1. In 386 chickens, possessing 14 cervical vertebrae and eight pairs of ribs (the extra one on V. 22), the distribution of the pelvic types was as shown in Table II.
TABLE II.

<table>
<thead>
<tr>
<th>Types of pelvis</th>
<th>Number of chickens</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 ds.</td>
<td>106</td>
</tr>
<tr>
<td>5 ds.</td>
<td>280</td>
</tr>
</tbody>
</table>

(2) In seven-ribbed chickens the proportions were as in Table III.

TABLE III.

<table>
<thead>
<tr>
<th>Types of pelvis</th>
<th>Number of chickens</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 ds.</td>
<td>290</td>
</tr>
<tr>
<td>5 ds.</td>
<td>102</td>
</tr>
</tbody>
</table>

A correlation is very evident. The elongation of the dorsosacral region from 4 to 5 vertebrae is frequently accompanied by an extra pair of ribs. 106 chickens of the 4-ds. type (see Table II) all had V. 23 resembling V. 22 (Fig. 1) and there was not a single modified chicken that had a V. 23 like V. 24 (Fig. 4 a). It is difficult to decide the nature of such correlation and the question is evidently one for further research.

III. ILLUSTRATIONS OF THE HEREDITARY NATURE OF THE CHARACTERS STUDIED.

The hereditary nature of the types described is apparent even after a most superficial examination of the data derived from crosses. I give the following examples:

(1) 20 crosses of the type 4 ds. × 4 ds. have given 324 chickens, viz. 252 of the 4-ds. type, and 72$^1$ of the 5-ds. type (= 77.8 : 22.2 %).

(2) 20 crosses of the type 4 ds. × 5 ds. gave 316 chickens, viz. 220 of the 4-ds. type and 96 of the 5-ds. type (69.6 : 30.4 %).

(3) 3 crosses of the type 3 ds. × 4 ds. gave:
   24 3 ds. : 25 4 ds. : 0 5 ds.

(4) 3 crosses of the type 4 ds. × 5 ds. gave:
   0 3 ds. : 16 4 ds. : 15 5 ds.

There are a few crosses of the type 4 ds. × 4 ds. which gave only chicks of the 4-ds. type.

The data in the column to the right in Table V (p. 43) may serve as examples of the numerical relations for the different pairs of parents. The existence of a genetical segregation in the offspring is distinctly manifested by the following data. Among the material there are fowls—sisters and brothers—which, when respectively crossed with the same

$^1$ Further on in the formulae the 4-ds. type will be written first, the 5-ds. type second; and in the crossings with the 3-ds. type, this pelvic type will be placed first.
cook (or with the same hen) give a progeny differing in respect of
the numerical proportions of the pelvic types. The differences are marked,
and there can be little question of their showing that the sisters (or
brothers) we are comparing belong to different genotypes. Thus two
sister hens 3837 and 3838 (daughters of Bantam-Pavloff $\varphi F_1$ 2338 4 ds.
and Paduan $\varphi$ 1302 M 4 da.) were crossed with one and the same cock 4949 (Bantam hybrid; pelvic structure unknown) and produced different
series of chickens:

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>$\varphi$ 4949 $\Omega$ 3837 4 : 17 : 2 or 17-4 : 73-9 : 8-7 %</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b)</td>
<td>$\varphi$ 4949 $\Omega$ 3838 14 : 15 : 3 or 45-7 : 46-9 : 9-4 %</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The real deviation of these series from each other is more than three
times as great as the sum of the probable errors of the classes, thus
showing with certainty that the hens 3837 and 3838 belong to different
genotypes. The comparison between the two series led one to suppose,
in the hen 3838, the presence of a M 4-ds. type (see Section v, Fig. 4 a)
and this was confirmed by a post mortem dissection of this hen.

As a second example we may take the two brothers, F$_1$ Indian Game-
Pavloff, which when mated with the same two hens (their sisters) gave
entirely different series:

<table>
<thead>
<tr>
<th></th>
<th>M 4 da.</th>
<th>N 4 da.</th>
<th>5 da.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>$\varphi$ 3123 with two of his sisters gave 14-5 : 71-0 : 14-6 %</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b)</td>
<td>$\varphi$ 3124 with the same sisters gave 32-7 : 57-7 : 7-5 %</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$\varphi$ 3123 had the normal 4-ds. pelvic type. It was supposed that the
cock 3124 had the M 4-ds. type (Section v) and so it turned out after
his death.

Such cases unquestionably point to the hereditary character of the
types of pelvic structure described. If a fluctuation does exist, it does
not markedly overshadow the genetical tendencies, and we may now
discuss the possibility of framing a genetical scheme of inheritance.

Structurally the 3-ds. type is more sharply marked off from the two
other types, being found only in Bantams and their hybrids. Its genetical
relation with the others will be examined further on in Section vi. We
may now trace the genetical relations of the 4-ds. and 5-ds. types.

IV. INHERITANCE OF PELVIC TYPES WITH FOUR AND FIVE
DORSOSACRAL VERTEBRAN.

A general examination of all the material obtained in dissecting
chickens from parents of known pelvic structure brought out the following
points:
The very great frequency of chickens of the 4-ds. type (in all about 3000 out of 4000).

2. Crosses of the 4-ds. × 4-ds. type gave either all the chickens of the 4-ds. type, or else up to 40-60 per cent. (in separate families) of chickens of the 5-ds. type.

3. Crosses of the 5-ds. × 5-ds. type (unhappily but few in number) gave, for the most part, a small number of individuals of the 4-ds. types, the rest being like the parents.

4. Crosses of the nature 4 da. × 5 da. nearly always gave both types, sometimes in equal proportion, or else not less than \( \frac{1}{2} \) of the 5-ds. type.

On comparing points (2) and (3) one can at once see that the genetical relations of the 4-ds. and 5-ds. types are rather complex. Two apparently contradictory results, viz., (a) 4 da. × 4 da. gives 5 da. and (b) 5 da. × 5 da. gives 4 da., do not admit of a simple Mendelian relation between these two types. The high proportion of the 4-ds. type in the general population suggests that it is not recessive. I pointed out the dominant nature of this type in my first paper, where the regular appearance of chickens of the 5-ds. type from individuals of the 4-ds. type was shown.

The study of the genealogy and of the entire progeny of 4-ds. type individuals has revealed in some of them a difference of behaviour on crossing with the same cock, or the same hen. It appeared possible to isolate two groups of individuals with a pelvic structure of the 4-ds. type.

The majority of hens (Group I) in crosses with the 5-ds. type transmit the 4-ds. type in marked degree, but a few (Group II), even in crosses with the 4-ds. type, show in their progeny a definite preponderance of the 5-ds. type. For example:

1. Osoff hen 709 (4 da.) with cock Osl. 708 (5 da.) has given 11 4 da. : 4 5 da. (Group I).
   Osoff hen 710 (4 da.) with the same cock (708) has given 11 4 da. : 22 5 da. (Group II).
2. Hen 3297 (4 da.) with cock 3123 (mupp. 4 da.) has given 11 4 da. : 0 5 da. (Group I).
   Hen 1950 (4 da.) with the same cock (3123) has given 36 4 da. : 8 5 da. (Group II r).
3. Plymouth Rock hen 609 (4 da.) with English Game cock 605 (4 da.) has given 4 4 da. : 3 5 da. (Group I).
   Hybrid English Game hen 1227 (4 da.) with the same cock (605, her father) has given 1 4 da. : 6 5 da. (Group II).
4. The three 4-ds. hens 15, 3836, 2454 in crosses with cocks of the 5-ds. type gave only chickens of the 4-ds. type (homozygotes 4 da.?).

These examples show that the 4-ds. type evidently possesses several different genotypes. Individuals of the 4-ds. type derived from 5 da. × 5 da. matings are clearly genetically distinct from those which, when crossed with the 5-ds. type (example 4, above), give chickens of the 4-ds. type only. We have also the following crosses:
(a) 4 ds. × 5 ds. (15:57) gave 6 4 ds.: 0 5 ds.
(b) 4 ds. × 5 ds. (3215:3437) " 5 " : 7 "
(c) 5 ds. × 5 ds. (57:3337) " 5 " : 8 "
(d) 5 ds. × 5 ds. (3246:3337) " 7 " : 8 "

In (a) the 4-ds. type seems to have been completely dominant over 5 ds. In (b) there is approximately an equal number of each type, and the 4-ds. type of the mother behaves like a heterozygote (?). In (c) and (d) we appear to obtain chickens of the 4-ds. type as extracted recessives from 5-ds. parents. There would seem to be both a dominant and a recessive type of 4-ds. pelvis.

We may suppose the existence of two different factors not allelo-

morphic to one another, viz. A, for the 4-ds. type, and B, for the 5-ds.
type of pelvic structure. From the sample crosses given above (e.g.
4 ds. × 4 ds. giving 4 ds. and 5 ds.) we may further suppose that A is
epistatic to B, so that aB individuals will have the 5-ds. structure, and
AB (and Ab) individuals the 4-ds. structure.

In an earlier paper I suggested that the genotype aabb is of the 4-ds.
type, regarding it as a normal recessive. The appearance of 4-ds. indi-

viduals in the cross 5 ds. × 5 ds. (aB × aB) is evidently possible only if
both parents are heterozygous for B, for these "extracted" individuals
must be bb. Also they cannot contain A, since this, on our hypothesis,
is epistatic to B. Hence the recessive 4-ds. type must be aabb. Possibly
there may be another factor, hypostatic to A and B, which in their
absence stimulates the 4-ds. phenotype, though it is simpler to suppose
that a, in the absence of B, brings about the 4-ds. type of pelvis.

The following individuals may serve as examples of aabb genotypes:
(1) Orloff # 710 (4 ds.) with # Orlt. 708 (5 ds.) gave 11 4 ds.: 22\textsuperscript{1} 5 ds.
(2) Orloff # 6957 (4 ds.) × 5 ds. × 5 ds. His genetical behaviour when
mated with 5-ds. # suggests that he is a recessive 4-ds. bird; for with
# 6797 (suppos. 5 ds.) he gave 3 4 ds.: 3 5 ds.; with # 3317 (suppos. 5 ds.)
he gave 3 4 ds.: 2 5 ds. Unfortunately the numbers are very small as
the cock died early.

Hence for these two types of pelvis we suggest the following genetical
scheme:

**A**, a factor stimulating a pelvic structure with 4 ds. vertebrae, i.e.
inhibiting the action of **B**.

**a**, a recessive gene for the pelvic structure with 4 ds. vertebrae.

**B**, a factor stimulating a pelvic structure with 5 ds. vertebrae.

\textsuperscript{1} In this case there is evidently a lack of aabb (4-ds.) chickens, possibly owing to their
lower viability. However, the data are not yet sufficient to test this supposition.
A. N. Pertooff

Table IV.
Pedigree of the fundamental crossings.
The living individuals are framed by one line.
b, its recessive allelomorph (participates perhaps in the modification of the 4-ds. type; see Section v).

A is almost completely epistatic over B.
a is hypostatic to B.

Individuals AaBb, Aabb = 4-ds. type\(^1\) (including the modifications); aaBB, aaBb = 5-ds. type; aabb = 4-ds. recessive type.

This genetic scheme fits closely the actual data derived from the crosses. The possibility of a successful forecast of the pelvic structure and a very close coincidence of the numbers presupposed by the scheme with those obtained (see pedigree, Table IV), show that the scheme accords well with the facts.

Examples of genetical segregation and of inheritance of the 4-ds. and 5-ds. types in different families and pedigrees are given in Tables IV and V. Table V contains the greater part of the data derived from crosses of parents whose pelvic structure is known. Of crosses where at present the structure of only one parent is known, we have a much greater number, but I shall not give them as one cannot employ them with absolute certainty. Also there are many dissections of chickens which cannot be utilized since both parents are still alive. The many post mortem confirmations of forecasts of structure made on our hypothesis allow of our pronouncing with definite probability on the pelvic structure of a living individual from the progeny results on crossing; e.g. the birds 2001, 2003, 2044, 2046, 2123, 2302 in Table IV were, when still alive, placed in the 4-ds. type, and 2437 in the 5-ds. type; and this was confirmed after death. The individuals 2303, 2306 are still alive and are considered as belonging to the 4-ds. type (see pedigree).

The following cases may serve as examples of the method of assigning formulae:

A 4-ds. structure was presupposed for \(\exists\) 2302 from the numerous crossing results taken altogether. With 4-ds. individuals there were rather numerous crossings on the 3:1 scheme, and some large series which gave a small number of 5-ds. type, very close to a 7:1 ratio.

\(^1\) In my first researches referred to above I isolated the extreme modification and the development of the proc. transv. of Y. 23 in the 4-ds. type, into a separate type (the so-called "incomplete forward removal," Fig. 4 n) with the genetical formula AbB. This formula has now been confirmed for such a variation (see Section v), but the structure itself is classed with my earlier "typical" structure (Fig. 1) to form one common 4-ds. type (the number of the dorsoanal vertebrae, being the fundamental character). Hence A must be regarded as the gene for the 4-ds. type, and not only for the "removal forward" (Ab is not only a "removal forward," but the 4-ds. type in general). For the rest, the genetic scheme remains the same (concerning Bantams, see Section v).
### TABLE V.

**Examples of the inheritance of 4-ds. and 5-ds. types.**

<table>
<thead>
<tr>
<th>Crossing</th>
<th>Expected according to the scheme</th>
<th>Obtained</th>
<th>Expected</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Genetical formula</td>
<td>4 ds.</td>
<td>5 ds.</td>
<td>4 ds.</td>
</tr>
<tr>
<td>4 ds. x 4 ds.</td>
<td>1:1 aabb x AaBB</td>
<td>4 pairs</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>All 4 ds. Homozygotes AA</td>
<td>64</td>
<td>—</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>3:1* AaBb x AaBB</td>
<td>6 pairs</td>
<td>64</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>7:1 AaBb x Aabb</td>
<td>6 pairs</td>
<td>140</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>13:3* AaBb x AaBb</td>
<td>4 pairs</td>
<td>133</td>
<td>31</td>
</tr>
<tr>
<td>4 ds. x 5 ds.</td>
<td>All 4 ds. Homozygotes AA</td>
<td>16</td>
<td>—</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>1:1 AaBb x aabb or AaBB x aabb</td>
<td>3 pairs</td>
<td>22</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>5:3 AaBb x aabb</td>
<td>4 pairs</td>
<td>33</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>3:1 Aabb x aabb</td>
<td>9 pairs</td>
<td>77</td>
<td>24</td>
</tr>
<tr>
<td>5 ds. x 5 ds.</td>
<td>1:3 aabb x aabb</td>
<td>3 pairs</td>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>All 5 ds. Homozygotes BB</td>
<td>There are no crossings</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* The examples for the schemes 3:1 and 13:3 are approximate, as with a small numerical quantity and incomplete pedigrees, one cannot be sure which of these schemes we have for a given family. (The calculation of the probable error for separate families often does not give here any definite indications.)

Hence 3 2302 cannot be homozygous for A since in that case he would give only chickens of the 4-ds. type. Nevertheless he must carry A since his behaviour is not that of the recessive aabb. Again, one must suppose that he also carries B for the following reason. In some of his crosses with 4-ds. 32 carrying B the number of 5-ds. offspring chickens nearly approaches one-quarter. On our hypothesis such a result is given by the following three types of cross, viz.

- AaBb x AaBB
- AaBb x aabb
- AaBB x AaBB.

All individuals here, except the recessive aabb, have the factor B. Now suppose for a moment that 3 2302 is a 5-ds. bird. The cross 4 ds. x 5 ds. only gives a 3:1 ratio when it is of the nature Aabb x aabb, i.e. where the individual of the 4-ds. type does not carry B. But the females of the 4-ds. type crossed with 3 2302 all carried B. Therefore the appearance of a 3:1 ratio when they were crossed with 3 2302 shows
that he must contain B, and consequently belong to the 4-ds. type. And the existence of modified 4-ds. individuals in his offspring points to his being heterozygous for B. On these grounds he was supposed in my first paper to be constitutionally AaBb, a supposition that has lately been confirmed post mortem.

Again, ♀ 2437 came of two 5-ds. parents (see pedigree) and when crossed with ♀ 2015 (4 ds.) gave a large number of 5-ds. chickens. Consequently she could not have been aabb, and hence presumably belonged to the 5-ds. type, a presumption that was confirmed after her death. Further the approximate equality of the 4-ds. and 5-ds. types from the cross with ♀ 2015 (Aabb) suggests that she was BB rather than Bb (with Bb 3 : 1 was the expected ratio).

The calculation of a formula for an individual whose pelvic structure is known is much simplified by crossing with many different hens (or cocks).

For example, ♀ 3879 (see pedigree on Table IV) of the 5-ds. type came from ♀ 2123 (4 ds. AaBb) and ♀ 1985 (4 ds. AaBb), who gave between them 36 4-ds. and 8 5-ds. chickens—a close approach to the expected 13 : 3 ratio.

♀ 3879 with certain of his sisters gave the following results:

(1) With ♀ 3851 (4 ds.) he gave 11 4 ds. : 6 5 ds.
(2) With ♀ 3864 (4 ds.) he gave 20 4 ds. : 6 5 ds.
(3) With ♀ 3877 (supp. 4 ds.) he gave 16 4 ds. : 9 5 ds.

Families (1) and (3) are much alike and suggest the type of mating AaBb × aaBb giving a 5 : 5 ratio.

Family (2) suggests a 3 : 1 ratio from the mating Aabb × aaBb.

All three results agree with the supposition that ♀ 3879’s formula is aaBb.

V. HEREDITARY MODIFICATIONS OF THE PELVIS WITH FOUR DORSOSACRAL VERTEBRÆ.

The modifications of the 4-ds. type, as regards the development of the proc. transv. ventrales of V. 23 (Fig. 4 a, b), have been described in Section II. A series of transitions, apparently of a fluctuative character, exists between the structures represented in Figs. 1 and 4 a. One of them is shown in Fig. 4 b.

Nevertheless, the pelvis with strongly developed proc. transv. on V. 23 (p V. 23 = p V. 24, Fig. 4 a) often differs genetically from the normal structure (Fig. 1). As I have already pointed out, this structure was previously regarded as a separate type, and in my first paper(3) definite data were given as to its hereditary nature, and a formula
was devised for it in terms of \( A \) and \( b \). When subsequent work cleared up the genetical nature of the differences between the various pelvic types it was classed with those of normal structure, both having 4-ds. vertebrae. In the examples discussed above I did not separate this subtype, as these examples were intended to illustrate the inheritance of the number of vertebrae in the dorsoossal structure.

We may now discuss the genetical nature of this modification in terms of the scheme already put forward.

On this scheme the 4-ds. type can have seven genotypes, viz.

(1) \( AABB \); (2) \( AABb \); (3) \( AAbb \);

(4) \( AaBB \); (5) \( AaBb \); (6) \( Aabb \);

(7) \( aabb \);

and we suppose that of these (3) and (6) show the modified structure in most cases while the rest show a normal one. There are many examples in our material which make this hypothesis probable. In agreement with it is the fact that in crosses between two modified 4-ds. individuals (\( Ab \)), 5-ds. chickens are very rarely seen. But the modified structures show considerable phenotypical variation, especially in the transitional cases, and are difficult to classify. Only individuals of the structure shown in Fig. 4 \( a, b \) were classed as those of modified structure, the other forms, presenting transitions towards the normal type, being classed with the latter (Fig. 1).

As examples illustrating the hereditary nature of this modification of the 4-ds. type, we may take the following cases (4 4 ds. being the normal, 5 4 ds. the modified structure):

(1) \( M 4 \text{ da.} \times \) \( M \text{ da.} 2834 \times N \text{ da.} 1202 \) gave 5 \( M : 7 \) \( N \) (all 4 ds.).

(2) \( M \text{ da.} 2124 \times N \text{ da.} 2001 \) gave 5 \( M : 6 \) \( N \) (all 4 ds.).

(3) \( N \text{ da.} 2309 \times N \text{ da.} 2301 \) gave 3 \( M : 11 \) \( N \) and 6 5 ds.

The differences in the results of (2) and (3) illustrate the different genetical behaviour of \( M \text{ da.} 2124 \) and \( N \text{ da.} 2302 \) when mated with the same hen.

The pedigrees in Table IV illustrate the following cases of matings of the type \( N \text{ AaBb} \times N \text{ AaBb} \) where the expected ratio is 3 \( M : 10 \) \( N : 3 \) 5 ds.:

\[
\begin{array}{ccc}
\text{M 4 da.} & \text{N 4 da.} & \text{5 da.} \\
\hline
\text{expected} & \text{4} & : & 17 & : & 4 \\
\text{47} & : & 15 & : & 6 \\
\text{5} & : & 17 & : & 5 \\
\text{6} & : & 21 & : & 11 \\
\text{9} & : & 25 & : & 4 \\
\text{9} & : & 23 & : & 6 \\
\end{array}
\]
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In all of these the actual results accord closely with expectation.

In several families from $\text{AaBb} \times \text{AaBb}$ (see Table V, under ratio 13 : 3) 164 chickens were obtained, distributed as follows:


Here the deficiency of modified individuals and the excess of normal ones together with the close approach to expectation of the numbers for 5 ds. suggest that for the $\text{Ab}$ combination the modification is not always complete, and that some of the more weakly modified individuals have been classified as normals.

The 1 : 1 ratio expected on hypothesis from the mating $\text{AaBb}$ (N) $\times \text{AAbb}$ (M) is illustrated by examples 1 and 2 on p. 45.

Crosses of the types $\text{aaBB}$ (5 ds.) and $\text{Aabb}$ (4 ds. modif.) should give 4-ds. and 5-ds. types in equal numbers. From $\varphi$ 2437 (cf. pedigree), known to be $\text{aabb}$, we should expect all the 4-ds. chickens to be normal on crossing with a $\text{M}$ 4 ds. $\varphi$. Crossed with $\varphi$ 2015 (M 4 ds. $\text{Aabb}$) she gave 5 4-ds. and 7 5-ds. chicks, all of the former being unmodified normal ones as expected.

The 5-ds. bird heterozygous for B ($\text{aaBb}$) when crossed with a modified 4-ds. bird of the constitution $\text{AAbb}$ should give only 4-ds. chicks, half being modified and half normal. $\varphi$ 3879 (see pedigree, Table IV) known to be $\text{aabb}$ was crossed with $\text{M}$ 4 ds. $\varphi$ 3838 (AA), and all the chickens obtained were of the 4-ds. type, M and N being represented in equal numbers.

We may take it therefore that B does actually restrain a strong development of the proc. transv. on V. 23 in the 4-ds. pelvic type.

The $\text{Ab}$ combination is for the most part, but not always, a modified 4-ds. type, either entirely or feebly.

The combination $\text{AB}$ is almost always of the normal 4-ds. type. It is possible that the heterozygous or homozygous state of B is also of importance for the modification of the 4-ds. type, but the material in hand is insufficient for an analysis of this point. The mutual relations of A and B explain the absence of variations in V. 24 of the 5-ds. type, as no antagonism between these two factors exists here.

VI. Inheritance of the Pelvic Type with Three Dorsosacral Vertebrae.

Many Bantams have a specific structure of the pelvis with 3 ds. vertebrae (Fig. 3). This structure is often accompanied by changes throughout the spine. Normally domestic fowls have 14 ribless cervical
vertebrae and 7 pairs of ribs, the first pair being borne by V. 15. In all
the races of poultry that I have dissected individuals with 7 or 8 pairs
of ribs were met with. These changes in the number of vertebrae also
exist in Bantams (about 50 per cent. are 8-ribbed), but are much more
complicated, owing to the fact that here the eighth pair makes its
appearance in a manner different from that usual for the other races of
poultry. A normal individual (not a Bantam) with 14 cervical vertebrae
and 7 ribs carries these ribs on V. 15–21; in an individual with 8 pairs the
extra rib develops on V. 22 and is generally rudimentary. The extra
rib appears here behind whereas in Bantams I never found an eighth
pair on V. 22. Eight-ribbed Bantams had always 13 cervical vertebrae
with ribs on V. 14–21; the eighth rib appearing here in front.

The study of the pelvis of adult Bantams, and of their chickens in
which the anterior limit of the synsacral region was already quite clear
of well marked, and where the concrescence of the synsacral vertebrae
was complete or beginning, showed that there was not a single pelvis
with 5 ds. vertebrae, though 3 ds. vertebrae were not infrequent. In
nearly all cases V. 21 was the first one concrescent with the synsacral
one, i.e. in numerical order counting from the cranium the same one as
in individuals with 14 cervical vertebrae. In the 8-ribbed individuals
with 13 cervical vertebrae only the last pair of ribs belongs to a pelvic
vertebra, viz. V. 21, and in this respect such a pelvis is similar to the
7-ribbed pelvis of the 3-ds. type shown by individuals with 14 cervical
vertebrae, there being one pair of pelvic ribs in each case. The extra
pair of ribs always appears in front on C.V. 14. Hence the 3-ds. and 4-ds.
types in the Bantams can be compared with the types of other races
as regards their different elements (number of pelvic vertebrae, last
pelvic ribs, etc.).

Though the Bantam material is not very extensive (about 300 dissec-
tions including 114 pure-bred Bantam chickens) it nevertheless allows,
of some definite conclusions as to the genetical nature of the 3-ds. type.

The pelvic types were distributed as follows in the 114 pure Bantam
chickens: 3-ds. type, 50 individuals; 4-ds. type, 64 individuals; 5-ds. type,
none.

Genetically Bantams of the 4-ds. type behave like 4-ds. individuals
homozygous for A. Many of them show the modified form of structure
as in Fig. 4 a, and one can suppose these to be bb birds.

The following cross between Pavloff F₁ hybrids and Bantams may
serve as examples of 4 ds. × 4 ds. matings. Three hens (modif. 4-ds.
type), crossed with ♂ 2328 (norm. 4 ds.), gave 40 chickens of the 4-ds.
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type: 21 modified and 19 normal, i.e. the expected equality if the hens were $AABB$ and the cock either $AABb$ or $AaBb$.

As an example of a cross between pure-bred Bantams of the 3-ds. type and a 4-ds. individual we may take the case of $\delta$ 618 (4-ds.) which with $3\,\varnothing\,\varnothing$ gave 24 3 ds. : 25 4 ds.

The 1 : 1 ratio occurred also in the separate families. Unfortunately there were no 3 ds. $\times$ 3 ds. crosses with both parents known. From 4 ds. $\times$ 4 ds. crosses among Bantams the 3-ds. type did not occur, 4-ds. individuals do not apparently give the 3-ds. type, but I cannot affirm this with perfect certainty as the material studied has not been large.

Of great interest and value is the recently realised cross of the big Orloff fowl with Bantams which has been successful when the Bantam was used as the mother, though the number of chickens studied has been small.

The Orloff cock 708 (5-ds. type) was crossed with a Bantam hen 3223 (3-ds. type) and gave several chickens, 3 of which died and were dissected. One was a 3-ds. type (!) and two were of the 4-ds. type. The appearance of a 3-ds. type in crossing with an Orloff cock, must point to the dominant nature of this type, as it cannot be supposed that a pure-bred Orloff could be heterozygous in a factor for the 3-ds. type, a form of pelvis never found in pure-bred Orloffs or in other large races of poultry. Nor does the possibility of a fluctuation from 5 ds. to 3 ds. seem at all likely.

The dominant nature of the 3-ds. type is also probable from the following data:

Bantam cock 618 (4 ds.) $\times$ Bant. hen 3223 (3 ds.) gave 1 3 ds. : 2 4 ds.

Orloff cock 708 (5 ds.) $\times$ Bant. hen 3222 (3 ds.) gave 1 3 ds. : 2 4 ds.

We suppose therefore that there is a factor (C) for the 3-ds. type epistatic to the factors for the other pelvic types\(^1\) and this is in agreement with the case of the 4 ds. $\delta$ 618 above which gave practically equal numbers of 3-ds. and 4-ds. chicks from three different hens. Constitutionally the $\delta$ 618 must have been $cc$, and each of the hens $Cc$.

VII. CONCLUDING REMARKS.

From the data we have given some general conclusions can be drawn as to the distribution of the genotypes of the pelvis in different races of poultry.

In the first place it is evident that pure-bred poultry are scarcely ever homozygous for the factors analysed. This one can understand since

\(^1\) My earlier hypothesis as to the 3-ds. type being hypostatic is ruled out by the result of the 3 ds. $\times$ 5 ds. cross.
the structure of the pelvis, being an internal character, could not be
selected on external appearance. Only indirectly could selection be
applied to structure of the pelvis through correlations between pelvic
structure and external characters of some kind or other amenable to
selection.

In the 3-ds. type the acetabulum is shifted forwards along the spine,
frequently as far as the level of V. 28, whereas in the 5-ds. type it is
shifted backwards to the level of V. 31, and it is reasonable to suppose
that these osteological differences react on the position of the body.
A forward displacement of the point of support of the body must
mechanically result in a more horizontal position, and a backward
displacement in a more vertical one. Taking the extreme types of
structure (3 ds. and 5 ds.) one can see that in Bantams the body has, as
it were, an almost horizontal position, whilst an Orloff cock of the 5-ds.
type holds himself more erect. But this can only be perceived in extreme
cases and no difference in posture is as a rule perceptible in individuals
of the 4-ds. and 5-ds. types, where the displacement of the acetabulum
is not considerable.

There is a large proportion of 4-ds. individuals in all the races of
poultry dissected, whereas there are marked differences in the distri-
bution of the 5-ds. and especially of the 3-ds. type. The 5-ds. type is
most often found in races of big poultry (Faverolles, Cochins); the 3 ds.
type belongs specifically to the small races of Bantams, or to those nearly
related to them in size (Paduans, etc.).

The Orloff race shows a rather high proportion of individuals with
the 5-ds. pelvic type. Among 178 pure-bred chickens examined there
were 101 N 4 ds. individuals and 77 5 ds. individuals.

Not a single individual of the 4-ds. type had a modified structure.
These data show that the combination Ab (stimulating the modified
4-ds. type) is very rare among the Orloff poultry owing to the common
occurrence of B in this breed.

Bantams. Outwardly this type of poultry presents many diverse
races characterised by small size and the possession of a whole series of
anatomical modifications in their skeleton, but they appear to be
generally characterised by possessing C. Apparently there are not many
homozygous CC Bantams, but the heterozygous state Cc ensures the
spreading of this factor among the small races of poultry. The absence
in Bantams of the 5-ds. pelvic type shows that they are homozygous
for A (or else it makes one suppose the existence of a special inhibiting
factor).

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Faverolles, Brahmas and Wyandottes resemble the Orloff in the frequency of the 5-ds. type. The highest proportion of 4-ds. individuals would appear to be found in Indian Game, Orpingtons and Pfulliffs, but there are so far only very scanty data for these races.

The various structural types of pelvis show no correlation either with the shape or the weight of the egg. Nor is there any genetical correlation with certain of the colour factors discovered in poultry, e.g. that for black pigment in the feathers (tifa), or with the factor for leg feathering (asuse) (4).

The genetical relations of the factors and their phenotypes may furnish some indications as to their appearance in the phylogeny of poultry. The factor C of the Bantams is certainly the "youngest" among the three factors A, B and C. There exists a hypothesis that the Bantams are derived from other races through the fixing of a mutation (or series of mutations) which altered the general size of the body. Along with this, doubtless, the proportions in the skeleton also changed. The shortened 3-ds. type which appeared could in the Bantams be selected on external appearance, because in this race the body has a more horizontal position (a character evidently correlated with the 3-ds. type).

One may suppose the pelvic structure with 5 ds. vertebrae to have been the oldest. The aB genotypes (5 ds.) dominated over ab (recessive 4-ds. type), and the recessive nature of the 4-ds. type existed until the appearance of the A gene, epistatic to B. In this way the 4-ds. type became dominant (AB), and the relations between the 4-ds. and 5-ds. types became altered in the general population, inclining toward an increase of the number of "new" genotypes AB and Ab.

It is not of course supposed that peculiarities in pelvic type are the result of only three pairs of factors. Even if the modification of the 4-ds. type described in Section v is not entirely hereditary in nature, there may be other structural modifications dependent upon factors not yet determined.

VIII. Summary.

(1) In domestic races of poultry there are three principal hereditary types of pelvic structure with 3, 4 and 5 dorsosacral vertebrae respectively (see Figs. 1, 2 and 3).

(2) The inheritance of these three types is dependent upon three pairs of factors.

A, a factor stimulating a pelvic structure with 4 ds. vertebrae. In the
absence of \( B \) it generally leads to a modified form of the 4-ds. type (large proc. transv. of V. 23, Fig. 4 a).

\( a \), recessive to \( A \), leading to a 4-ds. type in the absence of other dominant factors.

\( B \), a factor stimulating a pelvic structure with 5 ds. vertebrae; hypostatic to \( A \), but epistatic to \( a \) (\( aB = 5 \) ds.; \( AB = 4 \) ds. norm.); inhibitory to certain modifications of the 4-ds. type (Fig. 4 a, b).

\( b \), allelomorph to \( B \) in the majority of the modified 4-ds. individuals.

\( C \), a factor stimulating the 3-ds. type of pelvis (Fig. 3). Apparently epistatic to \( A \) and \( B \) (a certain incompleteness of the epistasis can be observed in the modifications of V. 24 described in Section II, p. 36; the rudiments of proc. transv. on the 24th vertebra).

\( c \), recessive to \( C \) in individuals of 4-ds. and 5-ds. types.

Genotypes with \( ABC \), normal 4-ds. type (Fig. 1); with \( Abc \), modified 4-ds. type (Fig. 4 a, b); with \( AaBB \) (possibly), a specially modified 4-ds. type (Fig. 4 c, d; see \( x \)); with \( aBc \), 5-ds. type, with little variation owing to the absence of mutual interaction (antagonism) between \( A \) and \( B \).

Genotypes \( aabb \), recessive 4-ds. type; genotypes with \( C \), 3-ds. type.

(3) Different pure races of domestic poultry are never uniformly of any given pelvic type. In all races there is a rather high proportion of individuals with 4 ds. vertebrae (the "typical" or normal pelvic structure). Small sized races often show a 3-ds. structure; large ones a 5-ds. one.

REFERENCES.


