

Findings of Morgan in chicken: are they real?

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Abstract. The genetic sex determination of Gallinaceae was explained in literature on the chromosomal level by the existence of the male sex, homogametic ZZ, and of the female sex, heterogametic ZW, as well as by the existence of genes within the chromosome Z and by the absence of genes within the chromosome W (Morgan 1919). In this paper we present the experimental results of direct and reciprocal genetic recombination. The experimental design allows the identification of the dominant sex gene linked to the gene that determines the plumage color in the first generation females. Both these genes are located within the chromosome W. In the same generation the recessive sex gene was identified within the chromosome Z. The second generation was obtained by cross of the males and females of the first generation. In each category of genotypes of the second generation males and females are displayed equally. Three categories of genotypes were produced, namely dominant homozygous, heterozygous, and recessive homozygous. The experimental results demonstrate that within the chromosome W both the dominant sex gene and the gene transmitting the plumage color are located. Our results are not in accordance with the hemizygotic theory of Morgan (1919).

Key words: genetic sex determination, chicken, ZZ, ZW, poultry, Morgan findings.

Introduction. The increasing demand for high quality protein in the developing world is expected to be one of the most important trends in the future of agriculture (Rosegrant et al 2001). Beside other important products (Bud & Mireșan 2008; Pentelescu 2009; Dărăban et al 2009; Carșai 2009; Petrescu-Mag 2009), chicken meat and eggs are likely to be the major contributor to meeting this demand. Moreover, the chicken is increasingly becoming of great interest as an intermediate evolutionary model organism, ideally placed between mammals and more distant vertebrates as fishes (Groenen et al 2000; International Chicken Genome Sequencing Consortium 2004).

The chicken is also a very good model for studies concerning color patterns, sex chromosomes, sex-determining genes and sex-determination in vertebrates. Sex is determined genetically in birds, having a ZZ-ZW sex chromosome system characterized by female heterogamety: a large Z chromosome and a smaller W chromosome (Ohno 1967). Sex is supposed to be determined in this group by the dosage of a Z-linked gene (two in males, one in females) or by a dominant ovary-determining gene carried on the W sex chromosome, or both (Smith et al 2007).

Sex and plumage color inheritance of Gallinaceae was explained so far using the two levels of organization of the genetic material: the chromosomal level and the gene level respectively. The chromosomal determinism starts from the premise that the genes responsible for plumage color inheritance are located within the chromosome Z and that they do not have any correspondent genes within the chromosome W (Morgan 1919). The chromosomal theory of sex determination by heterosomes is still cited, mainly, because of lack of new investigations. Well known scientists in poultry genetics (Groenen et al 2000; Fridolfsson & Ellegren 2000; Ellegren 2001; Kerje et al 2004) always begin their studies assuming the conclusion of the hemizygotic theory mentioned earlier.

The investigations presented in this paper were started due to the existence of major discrepancies between the experimental data from own research (Pricop 2005) and the chromosomal theory of sex determination by heterosomes, which is why this paper relates to the paper of Morgan (1919). We applied the method of the direct and reciprocal cross of Gallinaceae using two different breeds in order to monitor the phenotypic expression of the heterosomal genes responsible for the gene determinism of the

plumage color and of the sex. The cross of parent males and females produced generation F1, while the cross of the males and females from generation F1 produced generation F2.

Direct Cross: Barred Marans Male × Red Rhode-Island Female. The cross of barred Marans males with red Rhode-Island females produced in generation F1 a number of 3218 day-old genetic recombinants which were sexed using the cloacal method. The generation F1 contained heterozygous barred males and heterozygous barred females (see Plate 1).

The heterozygous barred males received from the father the chromosome Z together with the recessive sex gene (sdw) linked to the barred gene (B) and from the mother the chromosome Z together with the recessive sex gene (sdw) linked to the gold gene (b). The recessive homozygous genotype sdwsdw determines the male sex, while the heterozygous genotype Bb determines the plumage color.

The heterozygous barred females received from the father the chromosome Z together with the recessive sex gene (sdw) linked to the barred gene (B) and from the mother the chromosome W together with the dominant sex gene (SDW) linked to the gold gene (b). The heterozygous genotype sdwSDW determines the female sex while the heterozygous genotype Bb determines the plumage color.

We examined a number of 1601 heterozygous (Bb) day-old males and 1617 heterozygous (Bb) day-old females. Both sexes had black down with a white spot of variable size on their head.

The day-old chicks were sexed using the cloacal method. The plumage color of a number of 2840 birds of age 18 weeks was examined. From the 1378 males 34.9% had barred plumage and 13.6% had barred plumage on the body with red feathers on the neck and head. From the 1462 females 51.4% had barred plumage and 0.1% had barred plumage on the body with red feathers on their neck and head. The sexually mature genetic recombinants from generation F1 were crossed to produce the generation F2.

According to the sex chromosomes segregation, the genetic recombinants from generation F1 should contain four expected categories of genotypes in generation F2, differing by sex and plumage color as follows: homozygous barred males (sdwsdw BB), heterozygous barred males (sdwsdw Bb), heterozygous barred females (sdwSDW Bb) and homozygous gold females (sdwSDW bb).

According to our experimental data the progeny of generation F2 (Plate 1) contained two more unexpected genotypes, detected for the first time worldwide, together with the four expected ones: homozygous barred females (sdwSDW BB) and homozygous gold males (sdwsdw bb).

The homozygous barred females should have received the barred gene from the heterozygous barred females of the generation F1 but instead, they displayed the gold gene linked to the dominant sex gene (SDW) rather than the barred gene within the chromosome W. The homozygous gold males should have received a gold gene from both parents together with chromosome Z. In Plate 1 is shown that the F1 females displayed the barred gene linked to the recessive sex gene (sdw) rather than the gold gene within the chromosome Z.

The observed features in the inheritance of plumage color show that the last two categories of genotypes that were detected should not be present since they do not respect the pattern of sex chromosomes segregation in the genetic recombinants of generation F1 and of their recombination in generation F2.

In a similar experiment, Morgan (1919) obtained in the generation F2 only barred males, whereas half of the females were barred and the other half of females were black. In our experiments we produced in generation F2 three categories of genotypes. The ratio males:females within each category of genotypes was 1:1. These results can be explained as follows:

a) in generation F1 the gold gene is located within the chromosome W of the heterozygous females (Bb); it determines the red feathers on the neck and on the head in 0.1% of the heterozygous barred females and represents a particular way of action of this gene within the chromosome W;

- b) the barred gene is located within the chromosome Z of all F1 subjects and is transmitted to the progeny as any autosomal dominant gene;
- c) the cross of F1 heterozygous males with F1 heterozygous females shows that plumage color inheritance in generation F2 by the heterosomal genes is similar to the inheritance of the traits determined by genes located within an autosomal locus;
- d) the existence of 25% dominant homozygous females and males, of 50.1% heterozygous females and males and of 24.9% recessive homozygous females and males in generation F2 shows clearly that the F1 females are heterozygous rather than hemizygous.

Reciprocal Cross: Red Rhode-Island Male × Barred Marans Female. Plate 3 shows the results of the reciprocal cross between red Rhode-Island males and barred Marans females.

The day-old progeny included 50% heterozygous males, genotype Bb, with black down and a white spot of variable size on their head and 50% heterozygous females, genotype bB (trade name Robar SL-2001) with black down on the body and head. Day-old chicks sexing by the down color was explained by the existence of a heterosomal epistatic gene located on chromosome W.

A number of 2633 birds of 18-weeks were examined. From the 1342 males 36.6% had barred plumage and 14.4% had barred plumage on the body with red feathers on their neck and head. All 49% heterozygous (bB) reddish-black females had black plumage on the body with reddish-black feathers on their neck and head.

Correlating the results of plumage color inheritance of day-old chicks with the results observed for those of 18-weeks old birds one can notice that the phenotype of the F1 heterozygous females (bB) is different from that of their parents and from that of the heterozygous males. Based on the macroscopic examination Pricop (2005) reasoned that the heterosomal gene noticed previously within the chromosome W is the dominant sex gene (SDW) which plays two roles:

- a) as a dominant sex gene in relation to its recessive allele, sdw, located within the chromosome Z;
- b) as an epistatic gene that interacts with the gene determining plumage color, located within the chromosome W.

The non-allelic interaction (E) of the dominant sex gene of the barred gene occurs only in the W linkage group and modifies the allelic interaction of the genes from the heterozygous genotype that determines the plumage color. The plumage color of the F1 heterozygous reddish-black females was the phenotypic marker that allowed the identification of the dominant sex gene. The cross of a recessive homozygous males sdwsdw with a heterozygous females sdwSDW produced 50% recessive homozygous males sdwsdw and 50% heterozygous females sdwSDW. This explains the genetic determinism of sex inheritance and the equal number of males and females obtained in the cross.

Following sex chromosomes segregation in the genetic recombinants from generation F1, one would have expected four categories of genotypes in generation F2 differing by sex and plumage color:

- a) homozygous barred females (sdwSDW BB);
- b) heterozygous barred males (sdwsdw Bb);
- c) heterozygous reddish-black females (sdwSDW bB);
- d) homozygous gold males (sdwsdw bb).

In generation F2 we evidenced four more unexpected genotypes, detected for the first time ever, worldwide, together with the four expected ones:

- a) homozygous barred males (sdwsdw BB);
- b) heterozygous barred females (sdwSDW Bb);
- c) heterozygous reddish-black males (sdwsdw bB);
- d) homozygous gold females (sdwSDW bb). The unexpected four genotypes do not respect the pattern of sex chromosomes segregation in the genetic recombinants from generation F1 and of their recombination in generation F2 and thus should not appear.

The homozygous barred males should have received the barred gene from the heterozygous reddish-black females of generation F1 but instead of this they displayed the gold gene linked to the recessive sex gene (sdw) rather than the barred gene within the chromosome Z. The heterozygous barred females should have received the gold gene together with chromosome W from the heterozygous reddish-black females of generation F1 but instead of this they displayed the barred gene linked to the dominant sex gene (SDW) rather than the gold gene on chromosome W.

The heterozygous reddish-black males should have received the barred gene from the heterozygous reddish-black females, but instead of this they displayed the gold gene linked to the recessive sex gene (sdw) rather than the barred gene within the chromosome Z. The homozygous gold females should have received the gold gene from the heterozygous reddish-black females, but instead of this they displayed the barred gene linked to the dominant sex gene (SDW) rather than the gold gene within the chromosome W.

Morgan (1919) crossed the generation F1 progeny resulting from Langshan males × barred Plymouth Rock females and obtained two phenotype categories in generation F2: 50% barred males and females and 50% black males and females.

In our experiments we obtained in generation F2 four categories of phenotypes and three categories of genotypes which, together with the ratio males: female equal to one for each category of genotype, reveal the following:

a) in generation F1 the barred gene is located within the chromosome W of the heterozygous females (bB); it determines genetically the black plumage of the heterozygous reddish-black females and represents a particular way of action of this gene within the chromosome W;

b) the gold gene is located within the chromosome Z of all F1 subjects and is transmitted to the progeny as any autosomal recessive gene. However, the red color appears only on the neck and head due to the modified allelic interaction between it and the barred-hypostatic gene located within the chromosome W;

c) the cross of generation F1 heterozygous males with generation F1 heterozygous females shows that the plumage color inheritance in generation F2 by the heterosomal genes is similar to that of the autosomal genes. One exception has to be noticed, namely that the 49.8% heterozygous progeny are displayed in two phenotypic categories of plumage color summarizing (24.7% heterozygous barred females and males and 25.1% heterozygous reddish-black females and males);

d) in generation F1 the females are heterozygous and not hemizygous because of the following distribution: 24.7% dominant homozygous females and males, 49.8% heterozygous females and males and 25.5% recessive homozygous females and males.

The existence of the unexpected categories in generation F2 both in the direct and reciprocal cross might be explained by the presence of a pseudoautosomal region in chicken (Berlin & Ellegren 2004; Wahlberg et al 2007), similar with those observed in mammalian (Petit et al 1988; Henke et al 1993; Rappold 1993; Chandra 1994; Blaschke & Rappold 2006) and fish sex chromosomes (Traut & Winking 2001; Petrescu-Mag & Bourne 2008), where the genes determining the plumage color inheritance are located. In that pseudoautosomal region the genes are recombining by crossing-over just like in the autosomal regions, although this area is located in the heterosomes.

The hypothetical SDW gene could be HINTW gene, described by Smith (2007) as an intriguing candidate for a dominant female-determining gene on W chromosome. HINTW gene encodes an aberrant form of a hydrolase enzyme. In chicken embryos, HINTW is strongly expressed in the gonads and other tissues of ZW embryos (Smith 2007). In the same paper is indicated that in vitro biochemical data show the fact HINTW gene can interfere with the action of a Z-linked orthologue: HINTZ, which could be our hypothetical sdw gene. Smith (2007) underlines HINTW is conserved among flying birds, and recent molecular analysis indicates that it has undergone positive selection over evolution.

The Cross of Red Rhode-Island Males with Heterozygous Barred Female. The generation F1 heterozygous barred females produced in the direct cross was crossed with

red Rhode-Island males and produced genetic recombinants that can be sexed by the down color when day-old. The heterozygous males' genotype Bb had black down with a white spot of variable size on their head, while the homozygous females' genotype bb (trade name Robar SL-2002) had red plumage.

The color of the heterozygous barred males down is due to the barred and gold genes from the heterozygous genotype Bb. The color of the homozygous gold females is due to the gold gene located both within the chromosome Z and within the chromosome W.

The color differences of Robar SL-2001 and Robar SL-2002 females show that they can be heterozygous, respectively homozygous for this trait. These results are in contradiction with the hemizygotic mechanism: 36% of the heterozygous males have barred plumage and 14.1% of them have red feathers on the neck and head. 49.9% of the homozygous gold females have red plumage and a recessive homozygous genotype (bb). Down color inheritance of day-old Robar SL-2002 chicks is due to the action of the heterosomal genes barred (B) and gold (b). Day-old Robar SL-2002 chicks sexing by the down color is determined by the allelic interaction between the barred and gold genes from the heterozygous genotype Bb that determines the black down color of the heterozygous barred males. They have a white spot of variable size on the head. The recessive homozygous genotype (bb) for the gold gene (b) determines the red down color of the homozygous females that can easily be screened from the males.

Similar Results Contradicting Morgan's Findings. Similar experiments were made by crossing the white Rhode-Island (SS) cocks and red Rhode-Island hens (ss). The results led to the same conclusions (see Plate 2). The reciprocal cross is presented in Plate 4.

The Chromosomal Theory of Sex Determination – Morgan (1919). Morgan explains the sex determination at chromosomal level. The male represents the homogametic sex (ZZ) whereas the female heterogametic sex (ZW).

The homogametic sex ZZ (males) is crossed with heterogametic sex ZW (female).

Males are producing only one category of gametes containing one chromosome Z; females are producing two categories of gametes Z and W.

The result of the crossing are homogametic sex (males) and heterogametic sex (females), sex ratio being 1:1.

This theory is not explaining the experimental results in similar trials, as it could be seen in slide 5 and 6; the color of plumage has been analyzed as a phenotype marker.

The Gene Theory of Sex Determination – Pricop (2005). We have identified for the first time the sex dominant gene (SDW) in W chromosome and the recessive sex allele (sdw) in Z chromosome, explaining thus the experimental data of the previous described field trials. The gene theory of sexuality in *Gallinaceae* is based on these two genes.

The homozygous recessive genotype sdwsdw (males) is crossed with heterozygous genotype sdwSDW (female).

Males are producing only one category of gametes containing one recessive allele of the sex (sdw); females are producing two categories of gametes, having one recessive sex allele (sdw) and one dominant sex gene (SDW).

The results of the crossing are homozygous recessive genotypes sdwsdw (males) and heterozygous genotypes sdwSDW (females), sex ratio being 1:1.

The chromosomal theory of sex determination based on the hemizygotic mechanism: Morgan T. H. considers that the gene responsible for the plumage colour inheritance is located only in Z chromosome, whereas in W chromosome there is no such a correspondent gene. The female transmits the colour only by the gene located in Z chromosome (see comparative presentations in Plates 5-6).

Our new gene theory of sex determination based on the gene mechanism explains all the experimental results and demonstrates that the females have the gene responsible for the inheritance of plumage colour located simultaneously in chromosome Z but also in chromosome W. This gene determinism of plumage colour inheritance leads to consistent results of all experiments.

The plumage colour of the females in F1 obtained by cross bb/ss with BB/SS is the phenotype marker of the sex dominant W gene (SDW) (Plates 3-4).

Similar experiments led us to totally different results in generation F2 compared to Morgan, who did not obtain heterozygous in F2.

Thus we conclude that the hemizygotic mechanism does not explain evident experimental data in plumage colour inheritance.

Conclusions. The identification of the gene that determines the down color linked to the dominant sex gene within the chromosome W and of the recessive sex allele within the chromosome Z allowed, for the first time, a gene approach of sex inheritance and the development of a new theory, "The Gene Theory of Sexuality of Gallinaceae". The experimental results obtained by us require the revision and amendment of Morgan's chromosomal theory of sex inheritance through heterosomes. Consequently we propose the following amendments of the heterosome map modified by Hutt (1936), based on the above described experiments:

1. the simplification of the heterosome map; We propose to replace the two loci (barred-nonbarred and silver-gold) by one polyallelic locus, where the silver (S), barred (B) and gold (s/b) genes should be located;
2. the introduction of the polyallelic locus for the genes within the chromosome W, where the genes silver (S), barred (B) and gold (s/b), responsible for the inheritance of the plumage color should be located. This locus should be similar to the polyallelic locus located within the chromosome Z;
3. the introduction in the heterosome map, both in chromosome Z and in chromosome W, of the locus for the gene determining sex inheritance; thus, the dominant sex gene, SDW, has been identified on chromosome W, while its recessive allele, sdw, was identified on chromosome Z.

The hypothetical SDW gene could be HINTW gene, described by Smith (2007) as an intriguing candidate for a dominant female-determining gene on W chromosome. HINTW gene encodes an aberrant form of a hydrolase enzyme. In chicken embryos, HINTW is strongly expressed in the gonads and other tissues of ZW embryos (Smith 2007). In the same paper is indicated that in vitro biochemical data show the fact HINTW gene can interfere with the action of a Z-linked orthologue: HINTZ, which could be our hypothetical sdw gene. The author underlines HINTW is conserved among flying birds, and recent molecular analysis indicates that it has undergone positive selection over evolution.

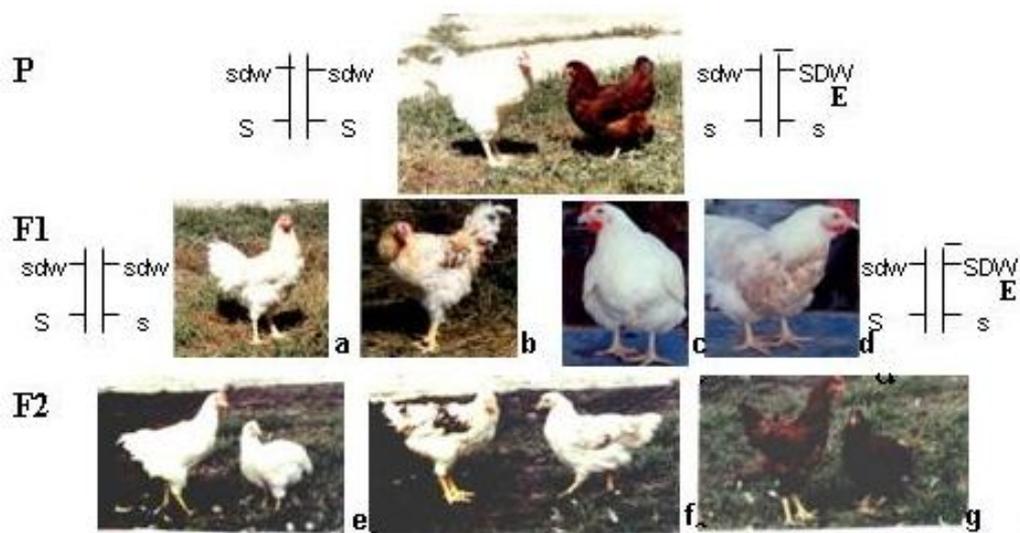
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Cross between white *Rhode-Island* (SS) cocks and red *Rhode-Island* hens (ss)

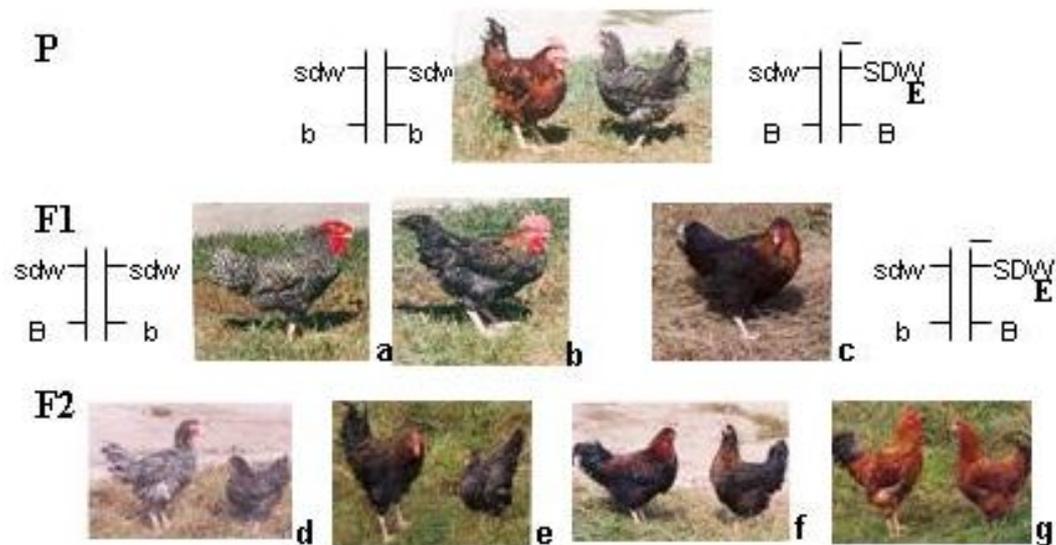


Genotype: sdwsdw SS sdwSDWSS* sdwsdw Ss sdwSDW Ss sdwsdw ss* sdwSDWss
Frequency (%): 24.8 50 25.2
F1 and F2 at 18 weeks (Pricop, F. 2003)

Legend:

P- parents, **F1** - first generation, **F2** - second generation, **SDW** - dominant sex gene, **sdw** - recessive sex allele, **S** - silver gene, **s** - gold gene, **E** – epistasis, **a** and **b** - silver heterozygous males, **c** and **d** - silver heterozygous females, **e** - silver homozygous males and female, **f** - silver heterozygous males and female, **g** - gold homozygous males and female,
 * Unexpected subjects in F2

Cross between red *Rhode-Island* cocks (bb) and barred *Marans* hens (BB)



Genotype/Frequency (%):

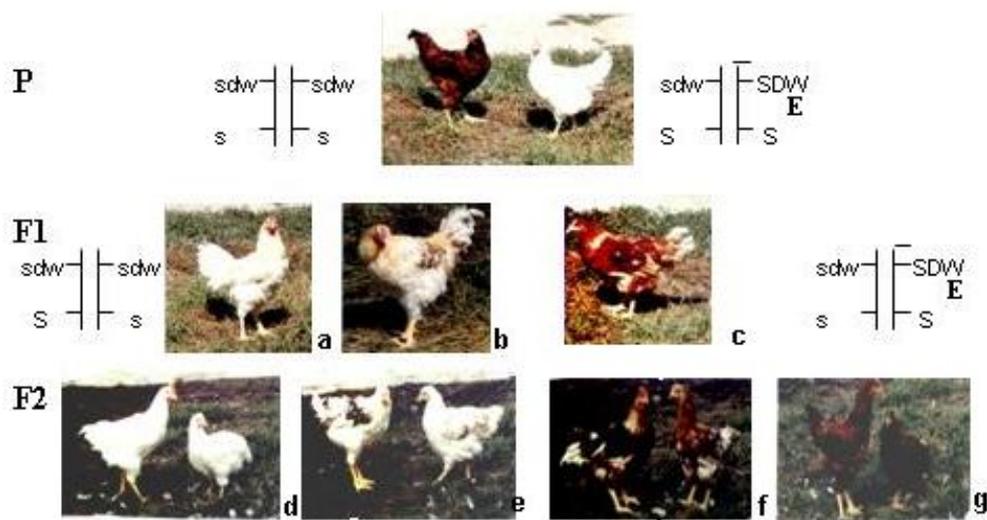
$sdwsdw BB$	$sdwSDWBB^*$	$sdwsdw Bb$	$sdwSDWBb$	$sdwsdwbb^*$	$sdwSDWbB$	$sdwsdwbb^*$	$sdwSDWbb$
24.7		24.7		25.1		25.5	

F1 and F2 at 18 weeks (Pricop, F. 2003)

Legend:

P- parents, **F1** - first generation, **F2** - second generation, **SDW** - dominant sex gene, **sdw** - recessive sex allele, **B** - barred gene, **b** - gold gene, **E** – epistasis, **a** and **b** - barred heterozygous males, **c** – redish black heterozygous females, **d** - barred homozygous males and female, **e** – barred heterozygous male and female, **f** - redish black heterozygous males and female, **g** - gold homozygous males and female, * Unexpected subjects in F2

Cross between red *Rhode-Island* cocks (*ss*) and white *Rhode-Island* hens (*SS*)



Genotype/Frequency (%):

sdwsdwSS	sdwSDWSS^*	sdwsdwSs	sdwSDWSs	sdwsdwS^*	sdwSDWsS	sdwsdwss^*	sdwSDWss
24.8		25.2		24.9		25.1	

F1 and F2 at 18 weeks (Pricop, F. 2003)

Legend:

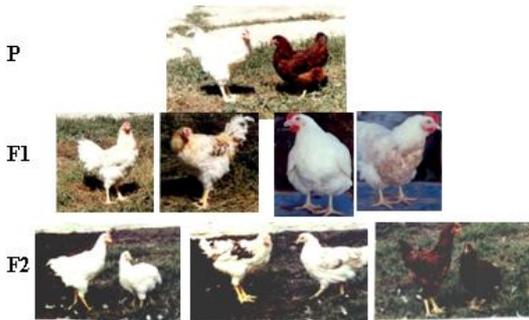
P- parents, F1 - first generation, F2 - second generation, SDW - dominant sex gene, sdw - recessive sex allele, S - silver gene, s - gold gene, E – epistasis, a and b - silver heterozygous males, c - gold heterozygous females, d - silver homozygous males and female, e - silver heterozygous males and female, f – gold heterozygous male and female, g - gold homozygous males and female,

* Unexpected subjects in F2

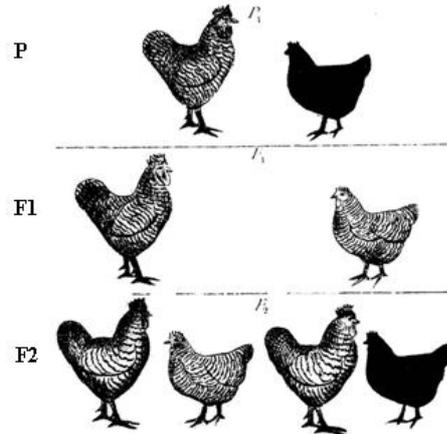
Experimental data I: Pricop (2003) vs. Morgan (1919)



Cross between barred *Marans* cocks (BB) and red *Rhode-Island* hens (bb)



Cross between white *Rhode-Island* cocks (SS) and red *Rhode-Island* hens (ss)



Cross between barred *Plymouth Rock* cocks (BB) and *Langshan* hens (bb)

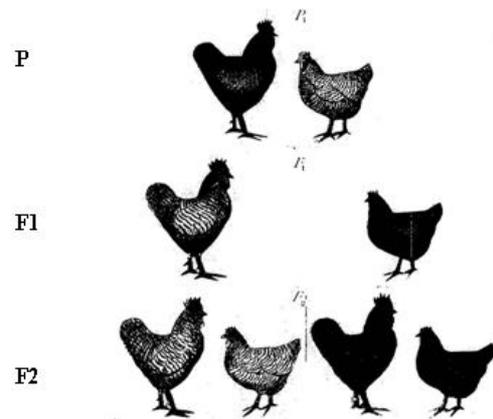
Experimental data II: Pricop (2003) vs. Morgan (1919)



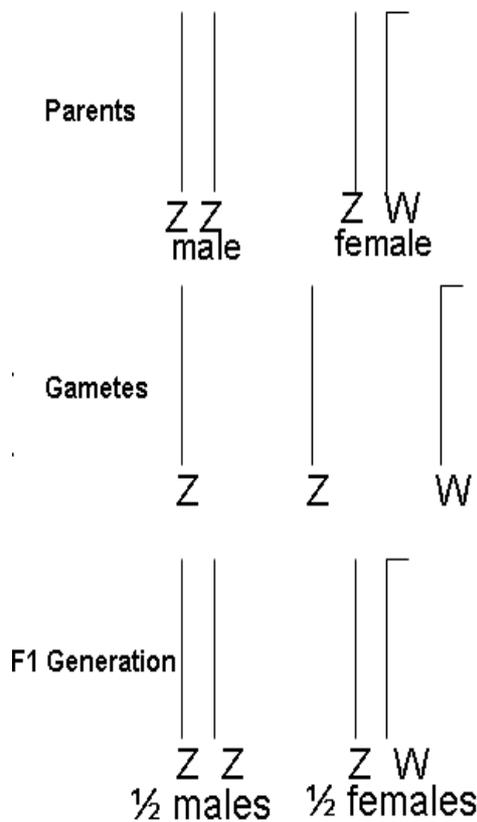
Cross between red *Rhode-Island* cocks (bb) and *Marans* barred hens (BB)



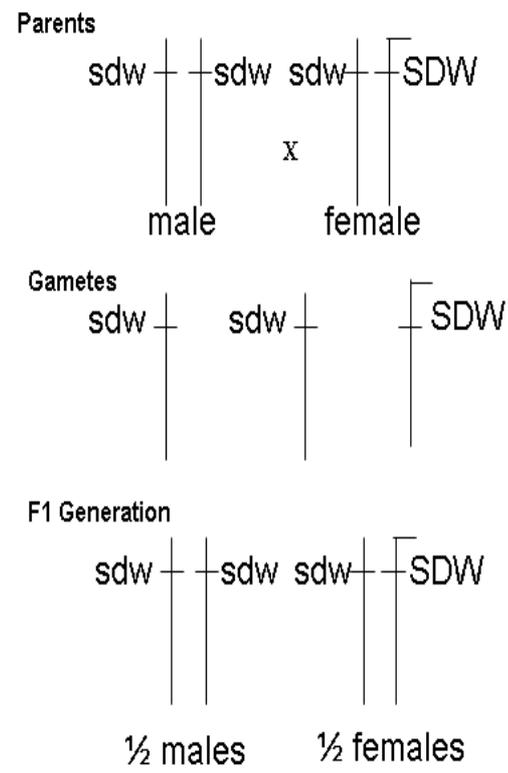
Cross between red *Rhode-Island* cocks (ss) and white *Rhode-Island* hens (SS)



Cross between *Langshan* cocks (bb) and barred *Plymouth Rock* hens (B-)



The chromosomal theory of sex determination – Morgan (1919)



The gene theory of sex determination – Pricop (2005)

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