Man" and "Investigations of Gas and Heat Exchange in Fevers," both by A. Likhachev and P. Avroroff. Finally, two articles by Dr. Kartaschefsky reporting experiments with the small Pashutin respiration apparatus have been translated. They are entitled "The Influence of a Lack of Oxygen on the Exchange of Matter and the Heat Production in Animals" and "On the Influence of the Surrounding Temperature upon Animals in a Gas-Atmosphere poor in Oxygen."

These articles were translated in part by Mr. Alexander Rose, of Boston, Mr. Michel Groosenberg and Miss Anna Monossowitch, who is at present engaged in Russian translation at the Nutrition Laboratory.

Thus it is hoped to keep American workers in nutrition in more intimate contact with the admirable Russian researches that have as yet been practically inaccessible. Arrangements have been made with Professor Likhachev whereby all articles dealing with problems of metabolism can be sent to this laboratory for translation. From time to time the titles and short abstracts of these articles will be published in some scientific journal.

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SPECIAL ARTICLES

A MENDELIAN VIEW OF SEX-HEREDITY

Two important contributions have recently been made to the discussion of sex-inheritance. In each a somewhat different view is presented, yet the two, I believe, are not irreconcilable, and if coordinated, will give us a truer conception of the whole matter than we have had before. I refer, on the one hand, to the recent vice-presidential address of Professor Wilson,[1] and, on the other, to the combined work of Bateson, Punnett, Doncaster, Durham and Marryat, published in Report IV. to the Evolution Committee of the Royal Society.

In 1903[2] I advocated the view that sex is inherited as a Mendelian character. The idea was not original with me. The suggestion came from the now famous Report I. of Bateson and Saunders. The fact has since come to light through Mendel's posthumously published letters[3] that Mendel himself had been impressed by the parallelism between the phenomena of sex-inheritance and those of ordinary Mendelian inheritance. Indeed, the parallelism is so complete and striking that we can scarcely question the existence of a like basis for the two sets of phenomena.

Professor Wilson, to be sure, argues against what he terms "Mendelian theories" of sex-heredity and advances a somewhat different theory of his own. In reality, however, his theory, while an improvement upon its predecessors, is no less Mendelian than they, but rather more so, as I shall attempt to show.

Great advance has been made since 1903 in our knowledge of Mendelian inheritance in general, as well as of sex-inheritance, and it is noteworthy that in restating our knowledge in the two fields similar changes must be made in both. For example, we formerly said regarding crosses between rodents of different colors that "gray is dominant over black" and that "black is dominant over yellow," meaning that the contrasted characteristics were antagonistic and one excluded the other in crosses. As we now look at the matter, gray is not antagonistic to black, but contains an additional element which is wanting in black. The correctness of this view is shown by the fact that black can be changed to gray by a cross which introduces that additional element. A similar relation holds between black and yellow; black is yellow plus something else, and this something else may actually be added to yellow (by a cross with brown, for example) converting it into black.

Similarly as regards sex, in 1903 I expressed the view that male and female are antagonistic members of a Mendelian pair, one excluding the other. Such a view is inadmissible in the light of our present knowledge. What we should say is that the female is the male condition plus something else. Male-

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[1] SCIENCE, January 8, 1909.

[2] *Bulletin, Mus. Com. Zool.*, Vol. 40, p. 189.

[3] *Abh. math.-phys. Klasse d. k. Sachs. Gesellsch. d. Wiss.*, Bd. 29, p. 185, Leipzig, 1905.

ness is not, then, the Mendelian allelomorph to femaleness, but a differential factor between male and female is allelomorphic to absence of that factor. Presence of that factor means femaleness, absence of it means maleness. This differential factor is inherited as a Mendelian character dominant over its absence.

Such a statement will, I believe, bring into harmony the seemingly discordant results of Wilson, of Correns, and of Bateson and his associates. For Correns urges the view, as I did in 1903, that the male and female sex-characters as such are inherited. He believes further that the female organism is a homozygous recessive (♀♀) and the male a heterozygous dominant (♂♀), for he finds that the egg-cells of *Bryonia dioica* all transmit a female sex-tendency, whereas the pollen cells transmit, half of them the female tendency, half the male tendency. His facts are unquestionable. I question only the supposed recessive nature of the female sex-character.

Wilson cautions us against the view that sex as such is inherited, believing that the difference between the two sexes is in reality a quantitative one. He finds the female characterized by the possession of two X-chromosomes, the male by one, and regards a second x-chromosome as the differential factor between male and female. In the view that the essential difference between the sexes is a quantitative one, Wilson makes general an assumption made earlier by Morgan[4] for a particular case.

This suggestion seems to me very helpful. Among other things, it clears up fully the long mysterious matter of sex-determination in the honey bee, of which I gave in 1903 an interpretation since proved to be wrong. But though we regard the distinction between male and female as quantitative, we must not forget that it is discontinuous. *The female is the male condition plus a distinct unit-character Mendelian in heredity.*

We must also not follow Professor Wilson too closely in his assumption "that a single X-element in itself causes or determines the male tendency, while two such elements in association create, or at least set free, the female tendency." For we shall presently see reasons for believing that in certain cases *one* X-element may determine the female tendency, while *no* X-element may determine the male tendency. But in both categories of cases alike the essential difference between male and female would seem to be one X-element, which the female possesses over and above the male.

We may leave open the question whether or not the "X-element" of Wilson is the actual material basis of this differential Mendelian unit-character of sex. The X-element at least behaves in cell-division as we must suppose that the basis of a Mendelian character would behave, and it will be convenient in what follows to treat it as actually representing such a basis.

Wilson's hypothesis will account satisfactorily for the experimental results of Correns, for it necessitates the production in gametogenesis of eggs all alike in sexual tendency, bearing X, but it calls for the production of spermatozoa of two different sorts, half of them bearing X, half of them without X. Eggs fertilized by the former should produce females (XX), those fertilized by the latter should produce males (X). Correns's observations accord with this interpretation.

But the Wilson hypothesis breaks down if we attempt to extend it to the cases discovered by Bateson and his associates. For in these it is evident that the eggs, not the spermatozoa, are dimorphic in sex tendency, whereas the spermatozoa are all alike. We can not reconcile such a condition with the hypothesis that XX produces a female, X a male. But the condition in question does harmonize with the assumption, X = a female, no-X = a male, and this condition, no less than that described by Correns for Bryonia, agrees with the more general assumption that the female possesses one more X-element than the male.

The cases to which reference has been made in which the female produces eggs with different sex-tendencies, but spermatozoa all with

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[4] Science, Vol. 21, 1905; *Am. Naturalist*, Vol. 41, p. 715, November, 1907.

the same sex-tendency, are, first, the moth, *Abraxas grossulariata,* and, secondly, the canary-bird. The two cases appear to be similar, but as the former has been more fully worked out, we may confine our attention to that. The case of *Abraxas* has already been presented in part to the readers of SCIENCE by Bateson and Punnett.[5]

This moth has a rare variety, *lacticolor,* known originally only in the female sex. For brevity in description we may call the typical *grossulariata* condition G, and the *lacticolor* condition L. The latter is a Mendelian recessive to the former.

Cross 1.—The cross L♀ × G♂ gives only G offspring in both sexes, but of course all bearing L as a recessive character. See Table I.

Cross 2.—Heterozygotes (produced by cross 1), when bred inter se, produce G♀, G♂ and L♀, but in no case L♂ offspring.

Cross 3.—A heterozygote G♂, mated with L♀, produces all four possible combinations, G♀, G♂, L♀ and L♂. "The L♂s thus produced were the first that had ever been seen." Now comes the most remarkable part of the whole story.

Cross 4.—When the newly produced L♂s were mated either with heterozygous G♀s produced by cross 1, or with wild G♀s, the offspring were all G in the male sex, all L in the female sex.

Cross 1 establishes beyond question the recessive nature of the color character L. Cross 4 shows that the G♀, whether cross-bred or wild in origin, is heterozygous in color-character, bearing L as a recessive character. No homozygous G♀s have been found. Crosses 1 and 3 show that the male may be, as regards character G, either homozygous, GG, or heterozygous, GL, and cross 3 shows that it may also be homozygous in L, that is, LL. In other words, there is no correlation between the male sex-character and either color-character. There does, however, clearly exist repulsion between the female sex-character and the color-character G, so that, whenever an alternative is offered, femaleness and L go into one gamete, maleness and G into another. But such alternatives manifestly occur only in oogenesis, not in spermatogenesis. In no other way can we account satisfactorily for either the difference in result between the reciprocal crosses, 1 and 4, or the failure of cross 2 to produce the group L♂.

Bateson completes the explanation by offering the further suggestion that there is no disjunction of the sex-characters in spermatogenesis because the male does not carry the female sex-determiner at all, but is homozygous, ♂♂. Consequently, when the L character once gets into a male individual, as by cross 1, where heterozygous GL♂s are produced, then in the spermatogenesis of such an individual gametes are sure to be formed in which the male character is associated indifferently either with G or with L. This, however, permits of the production of (homozygous) L♂s only in cases where the egg bears the ♂ character associated with L, a condition realized in cross 3, but not in cross 2 or cross 4. Doncaster summarizes the case in a table, which is here reproduced as Table I.

TABLE I

Abraxas crosses, Doncaster's interpretation

	Parents	Constitution	Gametes	Offspring
Cross 1	*Lact.* female *Gross.* male	LL ♀ ♂ GG ♂ ♂	L ♀, L ♂ G ♂, G ♂	GL ♀ ♂ = *gross.* female GL ♂ ♂ = *gross.* male
Cross 2	Heterozygous female Heterozygous male	GL ♀ ♂ GL ♂ ♂	L ♀, G ♂ G ♂, L ♂	GL ♀ ♂ = *gross.* female LL ♀ ♂ = *lact.* female GL ♂ ♂ = *gross.* male GG ♂ ♂ = *gross.* male
Cross 3	*Lact.* female Heterozygous male	LL ♀ ♂ GL ♂ ♂	L ♀, L ♂ G ♂, L ♂	GL ♀ ♂ = *gross.* female LL ♀ ♂ = *lact.* female GL ♂ ♂ = *gross.* male LL ♂ ♂ = *lact.* male
Cross 4	Heterozygous female *Lact.* male	GL ♀ ♂ LL ♂ ♂	L ♀, G ♂ L ♂, L ♂	LL ♀ ♂ = *lact.* female GL ♂ ♂ = *gross.* male

If, in Table I, we substitute X for the symbol ♀, discarding the symbol ♂ altogether, and consider all individuals bearing X to be

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[5] Vol. 27, p. 785, May 15, 1908.

females, we get no change in the character of the results shown in the column headed "offspring." See Table II. That is, the facts agree with the hypothesis, X = ♀, no-X = ♂, quite as well as with the Bateson-Doncaster hypothesis. But if we apply Wilson's XX = ♀, X = ♂, hypothesis to the case, the expectations for crosses 3 and 4 will be exactly interchanged; cross 3 should produce only L♀s and G♂s, whereas cross 4 should produce all four possible combinations. This fact is decisive against the Wilson hypothesis and for that of Doncaster, or for such a modification of it as I have attempted to present.

TABLE II

Abraxas crosses, an alternative interpretation

	Parents	Constitution	Gametes	Offspring
Cross 1	*Lact.* female *Gross.* male	LLX GG	LX, L G, G	GLX=*gross.* female GL=*gross.* male
Cross 2	Heterozygous female Heterozygous male	GLX GL	LX, G G, L	GLX=*gross.* female LLX=*lact.* female GL=*gross.* male GG=*gross.* male
Cross 3	*Lact.* female Heterozygous male	LLX GL	LX, L G, L	GLX=*gross.* female LLX=*lact.* female GL=*gross.* male LL=*lact.* male
Cross 4	Heterozygous female *Lact.* male	GLX LL	LX, G L, L	LLX=*lact.* female GL=*gross.* male

We may, it seems to me, summarize our present knowledge of sex-inheritance under one consistent scheme, somewhat as follows:

1. Sex is not directly controlled by the environment, but is determined by internal (gametic) factors.

2. The determination of sex depends upon the presence in the zygote of a factor or factors which are inherited in accordance with Mendel's law.

3. Femaleness, that is, the capacity to produce macrogametes (eggs) depends upon the presence of some factor wanting in the male.

4. The presence of this factor is in heredity dominant over its absence.

5. As regards the transmission of this factor we can recognize two distinct categories of cases:

A. Femaleness is attained only when the differential factor is doubly represented in the individual. In such cases the female is a homozygote (XX), and the egg invariably transmits the differential factor. Sex determination then rests with the male parent, for half the spermatozoa possess the differential factor and half lack it. The female is a homozygous dominant, not, as Correns supposed, recessive; whereas the male is a heterozygous dominant, pure recessives being unknown.

B. Femaleness is attained whenever the differential factor is present in one only of the conjugating gametes which produce the individual. The gamete which transmits the differential factor is of course the macrogamete (egg), since this factor is not possessed by the male parent. The female is a heterozygous dominant, the male a pure recessive; homozygous dominants are unknown.

The experimental proof for the existence of these two categories of cases has been produced for class A by Correns, and for class B by Doncaster and others. Cytological evidence which strongly supports the interpretation given to class A has been produced by McClung, Stevens, Morgan and especially by Wilson. This evidence is fully corroborated by the work of many others. Direct cytological evidence for the existence of class B is not known at present, but may confidently be looked for.

6. The hypothesis which I advanced in 1903, that both sexes are in the same species sex-heterozygotes, is not supported by the considerable body of evidence since accumulated.

If, as seems probable, the differential sex-character has its cytological basis in the "X-element," as Wilson designates it, it becomes an interesting question, what is the cytological basis of those numerous morphological characters possessed by the male, but wanting in the female. For it is a well-known fact that such secondary sexual characters are in general both more numerous and more striking in the male than in the female. For this reason the male has been called the "progressive" sex, which takes on new or striking characters, that may or may not later be shared with the female. Can we reconcile these facts with the idea that the female is a male plus something else? I think so, but we must concede also the possibility that the male may possess certain qualities not merely not manifested by the female, but even not possessed by it. I would offer the suggestion that we have a mechanism suitable for the transmission of characters exclusively male in the Y-element described by Wilson, the "synaptic mate" of the X-element, which takes the place in the gamete of a lacking X-element, and which would not be borne by a gamete possessing that element. If the primary difference between male and female is a defect in the male, the lack of something present in the female, that very defect would constitute a likely place in the germ-cell for new structures to find lodgement, which, behaving as the "synaptic mate," the material counterpart of the X-element would pass only into gametes lacking X, and so would produce structures peculiar to the male, and unrepresented in the female.

If this idea should prove to be correct, then we should have to revise the generalization to which Wilson gives expression "that so far as the eggs are concerned (and also those spermatozoa that contain the X-element) . . . every gamete contains factors capable of producing both the male and female characters, and that this is also true of all the zygotes." If the Y-element should prove to be the basis of characters purely male, then such characters would not be represented at all in gametes containing X, and cases like that described by Darwin, in which the hen-pheasant transmits to its hybrid male offspring in crosses characters of the male of its own species, could have but one interpretation, viz., that the hen-pheasant produces gametes lacking the X-element, as well as those which possess it. In other words, the hen-pheasant would seem to be a sex-heterozygote and so to fall in the same category of cases as the moth, *Abraxas grossulariata*, category B already mentioned. If so, the male pheasant should be incapable of transmitting in crosses characters peculiar to the female pheasant, if such exist.

This line of thought emphasizes the importance of reciprocal crosses in unraveling the mysteries of sex-inheritance and of the inheritance of secondary sexual characters. If the two categories of cases A and B really exist, there should be this difference between them. In A the male may transmit recessive characters peculiar to the female, but the reverse relation does not hold. In B, the female may transmit recessive characters peculiar to the male, but the reverse relation does not hold.

Further, there should be a difference in the two categories of cases in the Mendelian nature of fixed sexually dimorphic conditions. In category A, male secondary characters must be dominant in order to be fixable, *i. e.,* they must be represented in the Y-element by something not found in the X-element, but which will manifest itself even in the presence of the X-element. In category B, male secondary characters must be recessive in order to be fixable, *i. e.,* they must have their basis in the absence from Y of some element present in X, which absence will not be manifested if even a single X-element is present. For example, in *Abraxas* the pale *lugens* character is manifestly a defect character, due to lack of something found in *grossulariata* individuals, L being recessive to G. The gametic coupling of the female character with the *lugens* character, whenever a doubly differential cell division occurs, is doubtless due to the fact that the *grossulariata* character acts as the "synaptic mate" to the X-element, leaving absence of G (*i. e.,* L) associated with X. If in this cell-division G were associated with X, instead of with Y, then it would be possible to produce a stable sexually dimorphic race, with L♂s and G♀s, but the relation being what it is, no stable race can be formed in which the two sexes are G and L, respectively, but only races purely G or purely L in both sexes.

On the hypothesis suggested in this paper, accordingly, we can account for the fact that secondary sexual characters are more common in the male, if not its exclusive possession, even though the male is, as compared with the female, a defect race, or regressive variation. Transference to the female of characters originally possessed by the male alone could be accounted for by the duplication of the Y-element in a heterozygous (XY) germ cell. In this case Y would become the "synaptic mate" of Y, and X would be left once more (as originally) without synaptic mate, fit instrument for the origin of new progressive variations, the characters determined by Y now being the common property of both sexes.

A clue to phylogenetic histories would thus be afforded us, giving point to such variations as the *lugens* variety of *Abraxas*. Thus it is possible (though nothing but pure speculation in the light of our present knowledge) that *lugens* may be the phylogenetically older form, characteristic originally of both sexes, and that the *grossulariata* character may have had its beginning in gametes lacking the X-element, *i. e.,* in a Y-element formed as the "synaptic mate" of X. Thus would arise *grossulariata* males, but the new character being dominant over its antecedent (*lugens*) would quickly be transferred to the females, since these contain a no-X (*i. e.,* a Y) element, in common with the males. But the X-element, as shown by Doncaster's experiments, is still unassociated in a gamete with the new *grossulariata* character, and so the fixing of that character upon the species is not yet complete.

How now may the occasional reappearance of *lugens* females be accounted for? Simply by reduction divisions, in spermatogenesis, in which the two Y-elements fail to segregate as normally, forming in consequence a sperm-cell which lacks Y (the *grossulariata* character). If such a sperm-cell fertilizes an egg of the constitution LX, a *lugens* female is certain to result.

If, as has been suggested, the presence in one gamete and absence from another produced by the same cell-division, of an "odd chromosome" (or other X-element, whether chromosome or something else) is itself a circumstance which favors the origin of new characters in the defective (male-forming) gamete, then we shall perhaps come to attach less importance than has sometimes been done to the supposed influence of sexual selection in evolution. For sexual selection, as has often been pointed out, can in no case account for the origin of new characters, and it is extremely doubtful whether it plays any part even in their preservation.

Striking new characters produced by internal causes doubtless persist unless suppressed by external causes, *i. e.,* unless they disqualify their possessor for competition in the struggle for existence. There is no more reason for supposing that males gain their gay colors and markings from choice on the part of the females, than that females owe their modest colors to choice on the part of the males. But if, as suggested, the very mechanism of gametogenesis is adapted for the production of new characters in the male, then we are afforded a basis for their explanation, without invoking external causes. Recent investigations tend strongly to show that variations of evolutionary significance are primarily internal. This is unmistakably so in the matter of sex. Even in cases where sex is subject to control by environmental factors, as in aphids and daphnids, the environment acts indirectly apparently through the control of the same internal factors which govern sex in other animals. If the mechanism which I have suggested is not their true source, then we may well look for other possible internal mechanisms.

Orthogenesis also, the persistent tendency of an organism to vary in a particular direction, irrespective of the action of natural selection (if indeed orthogenesis be a reality, which, however, I do not assert), orthogenesis then would find an explanation along similar lines to those which I have suggested. For if a Y-element arose because of the very lack of X, then it would be natural for it to continue to grow until it became the full complement of X.

I make no apology for offering the hypothesis, or hypotheses, contained in this paper. I would have every reader recognize as fully as I do that they are hypotheses, and I shall be quite content if they suggest lines of investigation which will further elucidate the nature of sex and the manner of its inheritance.

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