

**THE CHROMOSOMES IN RELATION TO THE
DETERMINATION OF SEX IN INSECTS**

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INTRODUCTION

In this short note, Wilson (a leading cell biologist of his time) offers his endorsement of the idea that there is a relationship between specific chromosomes and the determination of sex in insects:

Material procured during the past summer demonstrates with great clearness that the sexes of Hemiptera show constant and characteristic differences in the chromosome groups, which are of such a nature as to leave no doubt that a definite connection of some kind between the chromosomes and the determination of sex exists in these animals. These differences are of two types. In one of these, the cells of the female possess one more chromosome than those of the male; in the other, both sexes possess the same number of chromosomes, but one of the chromosomes in the male is much smaller than the corresponding one in the female (which is in agreement with the observations of Stevens on the beetle *Tenebrio*).

Wilson's contribution is the observation that the various cases all seem to fall cleanly into one of two types — those in which the male seems to be missing a chromosome, and those in which the male is carrying a pair of mis-matched chromosomes.

Wilson's goes on to note that he does not believe that the 'accessory chromosomes' are actual sex *determinants* as conjectured by McClung¹, but rather that they probably act in a quantitative, not qualitative manner.

Wilson's endorsement of the idea that chromosome make-up is related to sex determination greatly facilitated the later general acceptance of the notion that individual chromosomes might be related to individual traits. Of course, sex is not a simple Mendelian trait, such as round or wrinkled peas, but nonetheless the evidence that some aspect of phenotype (sex) was related to some aspect of genotype was an important initial step in bringing genetics together with cytology.

This paper also provides an interesting example of the importance of symbology and terminology in the presentation of ideas. It is clear from the paper that Wilson has a firm grasp of the relationship between chromosomal complement and sex, but his presentation to a modern

¹ McClung, C. E. 1902. The accessory chromosome — Sex determinant?. *Biological Bulletin*, 3:43-84. Available from the ESP project at: <http://www.esp.org/foundations/genetics/classical/cem-02.pdf>

eye seems labored and awkward. Wilson illustrates the process using an algebraic presentation, which is accurate but not especially clear.

In fertilization

$$\text{Egg } \frac{n}{2} + \text{spermatozoan } \frac{n}{2} = n \text{ (female).}$$

$$\text{Egg } \frac{n}{2} + \text{spermatozoan } \frac{n}{2} - 1 = n - 1 \text{ (male).}$$

A later approach—the Punnett square—expresses the same information in a much more immediately apparent format, showing how the random combination of two different classes of spermatozoa with one class of eggs yields two classes of progeny.

		sperm	
		σ^r A	0
e g g s	φ A	AA, φ	A0, σ^r
	A	AA, φ	A0, σ^r

Here “A” = the presence and “0” = the absence of an accessory chromosome. “AA” = two accessory chromosomes = a female, “A0” = one accessory chromosome = male.

Genetics, like all other sciences, advances first through conceptual innovation, then later consolidates those gains through improved presentation and symbology.

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Material procured during the past summer demonstrates with great clearness that the sexes of Hemiptera show constant and characteristic differences in the chromosome groups, which are of such a nature as to leave no doubt that a definite connection of some kind between the chromosomes and the determination of sex exists in these animals. These differences are of two types. In one of these, the cells of the female possess one more chromosome than those of the male; in the other, both sexes possess the same number of chromosomes, but one of the chromosomes in the male is much smaller than the corresponding one in the female (which is in agreement with the observations of Stevens on the beetle *Tenebrio*). These types may conveniently be designated as *A* and *B*, respectively. The essential facts have been determined in three genera of each type, namely, (type *A*) *Protenor belfragei*, *Anasa tristis* and *Alydus pilosulus*, and (type *B*) *Lygaeus turcicus*, *Euschistus fissilis* and *Coenus delius*. The chromosome groups have been examined in the dividing oogonia and ovarian follicle cells of the female and in the dividing spermatogonia and investing cells of the testis in case of the male.

Type *A* includes those forms in which (as has been known since Henking's paper of 1890 on *Pyrrhochoris* [*sic*]) the spermatozoa are of two classes, one of which contains one more chromosome (the so-called 'accessory' or heterotropic chromosome) than the other. In this type the somatic number of chromosomes in the female is an even one, while the somatic number in the male is one less (hence an odd number) the actual numbers being in *Protenor* and *Alydus* ♀ 14, ♂ 13,

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and in *Anasa* ♀ 22, ♂ 21. A study of the chromosome groups in the two sexes brings out the following additional facts. In the cells of the female all the chromosomes may be arranged two by two to form pairs, each consisting of two chromosomes of equal size, as is most obvious in the beautiful chromosome groups of *Protenor*, where the size differences of the chromosomes are very marked. In the male all the chromosomes may be thus symmetrically paired with the exception of one which is without a mate. This chromosome is the 'accessory' or heterotropic one; and it is a consequence of its unpaired character that it passes into only one half of the spermatozoa.

In type *B* all of the spermatozoa contain the same number of chromosomes (half the somatic number in both sexes), but they are, nevertheless, of two classes, one of which contains a large and one a small 'idiochromosome.' Both sexes have the same somatic number of chromosomes (fourteen in the three examples mentioned above), but differ as follows: In the cells of the female (oogonia and follicle-cells) all of the chromosomes may, as in type *A*, be arranged two by two in equal pairs, and a small idiochromosome is not present. In the cells of the male all but two may be thus equally paired. These two are the unequal idiochromosomes, and during the maturation process they are so distributed that the small one passes into one half of the spermatozoa, the large one into the other half.

These facts admit, I believe, of but one interpretation. Since all of the chromosomes in the female (oogonia) may be symmetrically paired, there can be no doubt that synapsis in this sex gives rise to the reduced number of symmetrical bivalents, and that consequently all of the eggs receive the same number of chromosomes. This number (eleven in *Anasa*, seven in *Protenor* or *Alydus*) is the same as that present in those spermatozoa that contain the 'accessory' chromosome. It is evident that both forms of spermatozoa are functional, and that in type *A* females are produced from eggs fertilized by spermatozoa that contain the 'accessory' chromosome, while males are produced from eggs fertilized by spermatozoa that lack this chromosome (the reverse of the conjecture made by McClung). Thus if n be the somatic number in the female $n/2$ is the number in all of the matured eggs, $n/2$ the number in one half of the spermatozoa (namely, those that contain the 'accessory'), and $n/2 - 1$ the number in the other half. Accordingly:

In fertilization

$$\text{Egg } \frac{n}{2} + \text{spermatozoan } \frac{n}{2} = n \text{ (female).}$$

$$\text{Egg } \frac{n}{2} + \text{spermatozoan } \frac{n}{2} - 1 = n - 1 \text{ (male).}$$

The validity of this interpretation is completely established by the case of *Protenor*, where, as was first shown by Montgomery, the 'accessory' is at every period unmistakably recognizable by its great size. The spermatogonial divisions invariably show but one such large chromosome, while an equal pair of exactly similar chromosomes appear in the oogonial divisions. One of these in the female must have been derived in fertilization from the egg-nucleus, the other (obviously the 'accessory') from the sperm-nucleus. It is evident, therefore, that all of the matured eggs must before fertilization contain a chromosome that is the maternal mate of the 'accessory' of the male, and that females are produced from eggs fertilized by spermatozoa that contain a similar group (*i.e.*, those containing the 'accessory'). The presence of but one large chromosome (the 'accessory') in the somatic nuclei of the male can only mean that males arise from eggs fertilized by spermatozoa that lack such a chromosome, and that the single 'accessory' of the male is derived in fertilization from the egg-nucleus.

In type *B* all of the eggs must contain a chromosome corresponding to the large idiochromosome of the male. Upon fertilization by a spermatozoon containing the large idiochromosome a female is produced, while fertilization by a spermatozoon containing the small one produces a male.

The two types distinguished above may readily be reduced to one; for if the small idiochromosome of type *B* be supposed to disappear, the phenomena become identical with those in type *A*. There can be little doubt that such has been the actual origin of the latter type, and that the 'accessory' chromosome was originally a large idiochromosome, its smaller mate having vanished. The unpaired character of the 'accessory' chromosome thus finds a complete explanation, and its behavior loses its apparently anomalous character.

The foregoing facts irresistibly lead to the conclusion that a causal connection of some kind exists between the chromosomes and the determination of sex; and at first thought they naturally suggest the conclusion that the idiochromosomes and heterotropic chromosomes are actually sex determinants, as was conjectured by McClung in case of the 'accessory' chromosome. Analysis will show, however, that great, if not insuperable, difficulties are encountered by any form of the assumption that these chromosomes are specifically male or female sex determinants. It is more probable, for reasons that will be set forth hereafter, that the difference between eggs and spermatozoa is primarily due to differences of degree or intensity, rather than of kind, in the activity of the chromosome groups in the two sexes; and we may here find a clue to a general theory of sex determination that will accord with the facts observed in Hemiptera. A significant fact that

bears on this question is that in both types the two sexes differ in respect to the behavior of the idiochromosomes or 'accessory' chromosomes during the synaptic and growth periods, these chromosomes assuming in the male the form of condensed chromosome nucleoli, while in the female they remain, like the other chromosomes, in a diffused condition. This indicates that during these periods these chromosomes play a more active part in the metabolism of the cell in the female than in the male. The primary factor in the differentiation of the germ cells may, therefore, be a matter of metabolism, perhaps one of growth.