NOTES ON THE ACCESSORY CHROMOSOME

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July 21, 1901

McClung, C. E. 1901. Notes on the accessory chromosome, *Anatomischer Anzeiger*, 20: 220–226.

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ESP Foundations Reprint Series: Classical Genetics

Series Editor: Robert J. Robbins

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Bibliographical Note

This ESP edition, first electronically published in 2000, is a newly typeset, unabridged version, based on a reprint of the original paper as it appeared in Křiženecký, J. 1965. *Fundamenta Genetica, The Revised Edition of Mendel's Classic Paper with a Collection of 27 Original Papers Published during the Rediscovery Period.* Prague: Publishing House of the Czechoslovak Academy of Sciences

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INTRODUCTION

That most organisms occur as two fundamental types—male and female—has been a commonplace observation since antiquity. However, the actual mechanism of sex determination was unknown until the early part of the 20th Century, when it was shown that sex of progeny was determined by the chromosomal makeup of the zygotes from which they developed.

In 1891, Henking noted that some insects (*Pyrrhocoris apterus*) showed sexual differences in karyotype and in meiosis. Females had 24 chromosomes that behaved as 12 pairs of homologs during meiosis, whereas males had 23 chromosomes that behaved as 11 pairs of homologs and one solitary chromosome. This lone chromosome became known as an ACCESSORY CHROMOSOME.

Based on his own findings, and a review of the work of others, in 1901 C. E. McClung concluded that the accessory chromosome was responsible for determining sex, and he submitted a long paper[1] laying out his reasoning behind that conclusion. Recognizing that the long paper would not appear until the next year, McClung also prepared this short note outlining the main observation and conclusion:

> Being convinced … of the primary importance of the accessory chromosome, and attracted by the unusual method of its participation in the spermatocyte mitoses, I sought an explanation that would be commensurate with the importance of these facts. Upon the assumption that there is a qualitative difference between the various chromosomes of the nucleus, it would necessarily follow that there are formed two kinds of spermatozoa which, by fertilization of the egg, would produce individuals qualitatively different. Since the number of each of these varieties of spermatozoa is the same, it would happen that there would be an approximately equal number of these two kinds of offspring. We know that the only quality which separates the members of a species into these two groups is that of sex.

In the present note, McClung is putting the scientific community on notice about his bold conjecture that the accessory chromosome might represent the long-sought mechanism of sex determination. In other words, McClung is asserting that a difference in chromosome

[1] McClung, C. E. 1902. The accessory chromosome—Sex determinant? *Biological Bulletin*, 3:43-84. (available in digital form from the Electronic Scholarly Publishing project: http://www.esp.org)

number is the *cause*, not an effect, of sex determination. This analysis represents the first effort to associate the determination of a particular trait with a particular chromosome.

Although McClung made some errors in the details of his proposal, his general suggestion of a CHROMOSOMAL MECHANISM OF SEX DETERMINATION has proven to be true for many different organisms. This demonstration of a link between chromosomes and a fundamental aspect of phenotype—an organism's sex—provided the first key support for the chromosome theory of inheritance.

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NOTES ON THE ACCESSORY CHROMOSOME

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ALMOST ALL RECENT PAPERS upon insect spermatogenesis have contained more or less definite references to a chromatic element which differs in a marked way from the ordinary chromosomes. Early observers of this structure noted it as a variety of nucleolus, but lately its true chromatic nature has been recognized. In pursuing a study of the spermatogenesis of *Xiphidium fasciatum,* I discovered this element to be a prominent and striking member of the germinal mitoses and, after careful study, became convinced of its importance. Its history in the testes of this animal, I described in a preliminary paper under the title "A Peculiar Nuclear Element in the Male Reproductive Cells of Insects", *Zool. Bull.,* Vol. 2, No. 4. Further work upon the complete spermatogenesis of Xiphidium was later postponed upon discovering that the male cells of the Acridian genus Hippiscus are larger and better adapted to a study of the finer details of the maturation mitoses. The results of my investigations upon this and other genera of the Acrididae indicated that the importance of the element observed in the Locustid cells had not been overestimated. The conclusions derived from this second investigation were embodied in a paper entitled "The Spermatocyte Divisions of the Acrididae", *Kans. Univ. Quart*., Vol. 9, No. 1.

My own work had been concerned almost exclusively with the spermatocyte mitoses and, feeling the need of information concerning the nature of the element in the spermatogonia, I induced one of my students, Mr. W. S. Sutton, to undertake an investigation which might supply the desired knowledge. His results may be found in an article: "The Spermatogonial Divisions of *Brachystola magna*", in the *Kans. Univ. Quart.*, Vol. 9, No. 2.

Meanwhile the work of Paulmier and Montgomery had shown that Henking's observations upon Pyrrhocoris were largely true of the Hemiptera in general, and further confirmed many facts that I had noted in the Orthopteran families. With the accumulating observations, it seemed desirable, for the purpose of attaining some uniformity, to bring together the work of the different investigators for comparison. This I have attempted to do, and the results of my labors will be found in a paper, "The Accessory Chromosome—Sex-determinant?", the MS. of which is in the hands of the editor of the *Journal of Morphology*. Since it may be some time before this will be printed, I have thought it best to make preliminary announcement of some of my more important results.

The purpose for which the original article was written may be gathered from the following quotation: "From these different observations, I hope 1) to bring out the essential features which characterize the accessory chromosome, 2) to show the extreme probability of its universal occurrence among insects, 3) to outline its history in the different cell generations of the testis, and 4) to suggest a theory in explanation of its function."

Before taking up a discussion of these points, a few words regarding the name to be applied to this element may not be out of place. Henking who first noted it, calls it a "nucleolus" during the early stages of the spermatocytes, and later a "chromatin element". Montgomery, who next observed it in the Hemiptera, prefers to call it a "chromatin nucleolus", while Paulmier, working upon the same order of insects, designates it the "small chromosome". I, myself, early chose the name "accessory chromosome" and still consider it preferable to the others suggested. My reasons for this are as follows: All observers are agreed that the element is composed of chromatin and that it divides in mitosis like all other chromatin elements. The only essential feature wherein it differs from other chromosomes is that during the prophase of the first spermatocyte it fails to lose its identity in the spireme; and further, that during one of the spermatocyte mitoses it remains undivided.

It is therefore a chromosome and never, in any sense, a nucleolus, which would invalidate the names used by Henking and Montgomery.

In a recent paper, “A Study of the Germ Cells of Metazoa”, Montgomery refers to the question of a name for the unusual chromosome and objects to “accessory chromosome” because it is indefinite. He prefers to continue the use of “chromatin nucleolus”, although he admits that the structure is not a nucleolus but is a chromosome, for the very poor reason that it sometimes has the form of a nucleolus. The choice between the two terms is merely that between inaccuracy and indefiniteness when the latter quality is really desirable in the face of the unsettled character of the element. Morphologically, the term “accessory chromosome” is definite and exact, in that it classes the object to which it is applied with the formed chromatin elements while, on the other hand, the name “chromatin nucleolus” is inexact as well as indefinite since it places the structure with the nucleoli, a class of bodies to which it often has not even a resemblance in form. Moreover, Paulmier’s designation, “small chromosome”, is an absurd misnomer in the case of the Locustid cells where the accessory chromosome is as large as five or six ordinary ones. In view of the general recognition of the element as a chromosome and its still unsettled character, the term “accessory chromosome” is both suggestive and non-committal, and its use is therefore continued.

According to the results of most investigators the accessory chromosome “is characterized l) by a remarkable uniformity in staining power, similar to that exhibited by chromosomes in the metaphase; 2) by a continuous peripheral position during the spireme stage, at least; 3) by an isolation from the chromatin reticulum and a nonparticipation in its changes; and 4) by fission during metakinesis after the manner of chromosomes”. These observations are generally to be made in the first spermatocyte where the element is most plainly manifest. Its identity with a chromosome of the spermatogonia and its failure to divide in one spermatocyte mitoses are facts less easily demonstrated, and which have, therefore, less general acceptance.

An outline history of the accessory chromosome as reported by the different observers would read somewhat as follows: It is first observed in one of the early generations of the secondary spermatogonia and thenceforth it is noted as a regular participant in the spermatogonial mitoses. It differs from the other chromosomes principally in having a separate vesicle during the prophase (Sutton). At the end of these divisions, it may be seen persisting in the form of a more or less clearly defined chromosome, while the remaining chromatin elements break down to form the spireme, or equivalent structure (Montgomery, Paulmier, Sutton, McClung).

During the long continued prophase of the first spermatocyte, it may be found lying at the periphery of the nucleus in the form of a sharply defined, darkly staining body. On the establishment of the mitotic figure, it takes its place, with varying degrees of conspicuousness, in the equatorial place of chromosomes and there divides (Henking Paulmier, Montgomery).

When the elements of the second spermatocyte arrange themselves ready for division, the accessory chromosome, is again noted, but in this instance it fails to divide, and is thus apportioned to but half the resulting spermatids (Henking, Paulmier). As a result of this, we have two forms of spermatozoa in equal numbers.

Regarding the general distribution of the accessory chromosome among insects, it may be said that, aside from its precise identification in the Hemiptera and Orthoptera, the work of many other insect spermatologists tends to show the presence of such a structure in the spermatocytes of other orders. I have personally observed it in the Orthoptera, Hemiptera, Neuroptera, Coleoptera, and Lepidoptera so that I do not question that it is a constant element in the male germ cells of all insects.

It may be noted further that it has been identified in the spiders (Wallace), which would seem to indicate its general occurrence in the Arthropods. I have examined the cells of Cambarus but have not been able to identify it there. Owing to the small size and great number of chromosomes in the cells of these Crustaceans, however, it would be very difficult indeed to distinguish an individual element of this kind, so that failure to find it would by no means prove its absence.[1]

Also Montgomery in his paper upon "The Spermatogenesis of *Peripatus balfouri*" describes a structure which I think must be the accessory chromosome. His reasons for thinking that it is not so are by no means conclusive. The first objection, that it can not be distinguished in the first spermatocyte mitotic figure, holds good for many insects; the second, that the number of these bodies is indefinite, may be met by the statement that the accessory chromosome undergoes fragmentation in the Orthopteran cells where its genesis is clear; the third, that these bodies in Peripatus are early peripheral in position upon the nuclear membrane, is a fact in strict accordance with the behavior of the accessory chromosome in the Orthopteran cells; and the fourth, that there is a clear space ("perinucleolar") around the bodies, is

[1] Since the completion of the paper of which this is an abstract, another of my students, Mr. M. W. Blackman, has made a preliminary study of Myriapod spermatogenesis (see *Kans. Univ. Quart.*, Vol. 10, No. 2). In Scolopendra he is able to recognize the accessory chromosome in a strongly modified form. This departure from the typical appearance of the element in insect cells is correlated with a like divergence in all particulars from the ordinary form of spermatogenesis, so that an explanation of the one must wait upon the other.

of little weight when it is known that the chromosomes of the Orthopteran cells are thus set off from the achromatic substance. The spermatogenesis of Peripatus would seem to be atypical enough throughout to suggest extensive deviations in details.

While my work has been done principally on the Arthropods, I have examined representatives of other phyla, and in a tentative study of the mouse testis have clearly distinguished a structure which so closely resembles the accessory chromosome of the insect cells that I am convinced of its identity.

From the results so far obtained, I was assured that we had to do with a structure of great importance and one which would repay most careful study. I have therefore devoted my attention almost exclusively to it, and together with my students, have collected over a thousand testes from nearly a hundred species for study. It is only by an extensive comparative study, as I suggested in my first paper, that any reliable conclusion may be hoped for.

The theoretical portion of the large paper was written with much reluctance. The small amount of undisputed information at hand made generalization a difficult matter: but a working hypothesis is necessary, and in view of the fact that others have been published, I decided to include mine with the observations. Before presenting this, however, the view advanced by Paulmier, and adopted with more or less reservation by Wilson and Montgomery, may well be considered.

Because the accessory chromosome fails to divide in the second spermatocyte, Paulmier considers that it is a chromosome in the process of disappearing from the species. As evidence against this assumption, I would point out that the history of the element in the spermatogonia, where it is raised to the rank of a nucleus by separate inclusion in its own vesicle and where it normally divides in each mitosis; its regular and constant behavior in the first spermatocyte, where it is remarkable for its unvarying position and staining reaction; and finally the uniformly undivided condition itself in one of the spermatocytes all show that the element is a normal one. Degenerate structures are always irregular and uncertain in their manifestations, while in the case of the accessory chromosome we have the greatest degree of regularity and certainty of behavior.

Paulmier’s theory, however, breaks down completely when the true character of the accessory chromosome is considered. Nearly all observes are agreed that the element is a spermatogonial chromosome which passes over entire into the spermatocytes. The appearances in the Orthoptera are, I think, conclusive proof of this. It will be noted further that the element retains its form as a chromosome unvaryingly from the anaphase of the last spermatogonial division unfit it is apportioned to two of the four spermatids arising from each first spermatocyte. So far as I can learn, we have no knowledge of an ordinary chromosome regularly dividing more than once without going into a resting stage between divisions. Why, then, should we expect this spermatogonial chromosome which has passed over into the spermatocytes to divide more than once?

Paulmier makes his theory possible by considering the accessory chromosome a tetrad, but in this he is certainly mistaken. The accessory chromosome may, and sometimes does, divide into its two chromatics during the telophase of the last spermatogonial division and thus comes over into the first spermatocyte double, but the chromatics are the halves of an ordinary spermatogonial chromosome, and are not comparable to the elements of a tetrad. It is to be noted in this connection that the evidence afforded by Orthopteran material is much clearer and more definite than that derived from the spermatogonia of the Hemiptera, so that Paulmier's error is not remarkable.

Being convinced from the behavior in the spermatogonia and the first spermatocytes of the primary importance of the accessory chromosome, and attracted by the unusual method of its participation in the spermatocyte mitoses, I sought an explanation that would be commensurate with the importance of these facts. Upon the assumption that there is a qualitative difference between the various chromosomes of the nucleus, it would necessarily follow that there are formed two kinds of spermatozoa which, by fertilization of the egg, would produce individuals qualitatively different. Since the number of each of these varieties of spermatozoa is the same, it would happen that there would be an approximately equal number of these two kinds of offspring. We know that the only quality which separates the members of a species into these two groups is that of sex. I therefore came to the conclusion that the accessory chromosome is the element which determines that the germ cells of the embryo shall continue their development past the slightly modified egg cell into the highly specialized spermatozoon.

It would not be desirable in a preliminary paper of this character to extend it by a detail of the discussion by which the problem was considered. Suffice it to say that by this assumption it is possible to reconcile the results of many empirical theories which have proved measurably true upon the general ground that the egg is placed in a delicate adjustment with its environment, and in response to this, is able to attract that form of spermatozoon which will produce an individual of the sex most desirable to the welfare of the species. The power of selection which pertains to the female organism is thus logically carried to the female element.

Numerous objections to this theory received consideration, but the proof in support of it seemed to overbalance them largely, and I was finally induced to commit myself to its support. I trust that the element here discussed will attract the attention which I am convinced it deserves, and can only hope that my investigations will aid in bringing it to the notice of a larger circle of investigators than that now acquainted with it.