

**A STUDY OF THE SPERMATOGENESIS
OF TWENTY-TWO SPECIES OF THE
MEMBRACIDÆ, JASSIDÆ,
CERCOPIDÆ
AND FULGORIDÆ, A DISSERTATION**

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A Study of the Spermatogenesis of Twenty-two Species of the Membracidae, Jassidae, Cercopidae and Fulgoridae, a dissertation by Alice M. Boring

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ALICE M. BORING

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FULGORIDÆ

A DISSERTATION
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ALICE M. BORING

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A STUDY OF THE SPERMATOGENESIS OF TWENTY-TWO SPECIES OF THE MEMBRACIDÆ, JASSIDÆ, CERCOPIDÆ AND FULGORIDÆ, WITH ESPECIAL REFERENCE TO THE BEHAVIOR OF THE ODD CHROMOSOME¹

BY
ALICE M. BORING

WITH NINE PLATES

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¹A dissertation presented to the Faculty of Bryn Mawr College for the degree of Doctor of Philosophy.

INTRODUCTION

The purpose of this investigation is to extend, to some families of the Hemiptera Homoptera, the studies of McClung, Stevens, Wilson and others on the relation of the accessory or odd chromosome to sex determination. Except for the aphids, which have been extensively worked out by Stevens ('05a, '06a), *Cicada tibicens* (Wilcox '95) and *Aphrophora quadrangularis* (Stevens '06b) are the only species of this group whose spermatogenesis has been previously described. This study covers eight species of the Membracidae, six of the Jassidae, four of the Cercopidae and four of the Fulgoridae.

My work was begun at the suggestion of Dr. N. M. Stevens at Woods Hole in the summer of 1905, continued under Prof. E. G. Conklin, at the University of Pennsylvania, in the year 1905-06, and completed under Dr. Stevens, at Bryn Mawr College, in the year 1906-07. To both Dr. Stevens and Professor Conklin I wish to express my appreciation of their valuable suggestions and constant help and inspiration. I wish also to thank Dr. Herbert Osborn of Columbus, Ohio; Mr. E. P. Van Duzee, of Buffalo; Mr. H. C. Barber, of New York City, and Dr. H. Skinner, of Philadelphia, for the identification of material.

HISTORICAL REVIEW

Most of the work on the spermatogenesis of the tracheate arthropods has been done since 1890. Such studies as those of Bütschli ('71), La Valette St. George ('85), Platner ('86), Verson ('89), and Sabatier ('85) were concerned only with the formation of the spermatozoa, the arrangement of the cells of the testis into cysts, and the general mechanics of karyokinesis. The work of van Beneden ('84), Boveri ('87) and O. Hertwig ('90) on *Ascaris*, and Mark ('81) on *Limax*, turned the interest in the study of the sex cells to the chromosomes, while Weismann's daring hypothesis ('87) as to equational and reducing divisions added to the interest. By 1890, practically all investigations on spermatogenesis centered around the chromosomes in the spermatocyte divisions, and in

that year we find the first statement that one chromosome behaves differently from the others (Henking '90). Unfortunately there is the greatest confusion in the results for the next decade; but since Montgomery's suggestion ('01a) that synapsis means the conjugation of homologous maternal and paternal chromosomes, and its confirmation by Sutton's work on *Brachystola* ('00, '02, '03), there has been greater accord. As a consequence of this, certain fundamental theories are coming to rest on a firm foundation. The chromosomes are shown to keep their individuality from one cell generation to another. The real reduction in number is proved to be brought about by the joining of each paternal to a corresponding maternal chromosome in synapsis. It is found to make no difference whether the reducing or equational division comes first, but the distinction between these two divisions is constant, the one being the separating of the individual spermatogonial chromosomes, the other a simple splitting of these univalent chromosomes. In addition to this, recent work indicates that there is usually present throughout the Tracheata an odd chromosome in the spermatogonia, which behaves differently from the other chromosomes throughout its history. Still later work seems to establish the fact that this chromosome has no paternal mate, does not join any other chromosome in synapsis, divides in only one spermatocyte division, and enters only half of the spermatozoa. In some forms, a small chromosome is present as the paternal mate of this odd chromosome, but dimorphism of the spermatozoa results in either case.

The following review takes up the different observations on the Tracheata since 1890, and attempts to show how each helps to establish, or differs from, the above mentioned theories.

Arachnida

Wallace ('05) finds an even number of spermatogonial chromosomes, 40, two of these being larger than the others and different in behavior. They are condensed in the spermatogonial rest stage, and take an eccentric position in the equatorial plate. They remain separate from each other in the spermatocyte growth

period and do not divide in either spermatocyte division, as the other 19 chromosomes do, thus appearing in only one quarter of the spermatozoa. Wallace concludes that all the spermatozoa degenerate except those with the two odd chromosomes.

Montgomery in *Lycosa* ('05) finds an even number of chromosomes in the spermatogonia. Two of these he calls heterochromosomes, although the only characteristic that justifies this name is that they remain condensed in the growth period. They conjugate like the other chromosomes and divide in both divisions, all of the spermatozoa receiving one-fourth of the heterochromosome tetrad.

The results of neither of these investigators agree with the more recent work on the odd chromosome in spiders and other forms. If, as Wallace states, no spermatozoa develop except those containing the two odd chromosomes and the nineteen ordinary chromosomes, the eggs must all contain only 19 chromosomes, as the spermatogonial number is 40. Suppose each egg to have 19 chromosomes; fertilization by a spermatozoön with 19+2 chromosomes would give all the offspring 38+2 (19+2 in the reduced number), whether male or female; but according to Wallace's contention, the egg can have only 19; therefore it is impossible that all the spermatozoa, except those with the two odd chromosomes, degenerate. According to Montgomery, the heterochromosome in the spermatocyte is bivalent and divides in both divisions. Berry's work ('06) brings the odd chromosome in the spider into line with the odd chromosomes in other forms; it is a single chromosome in the spermatogonia, and divides in only the second division of the spermatocytes, resulting in dimorphism of the spermatozoa.

Myriapoda

Blackman ('05a, '05b) finds in *Scolopendra heros* and *S. subspinipes* an uneven number of spermatogonial chromosomes. Synapsis takes place in the late anaphase of the last spermatogonial division, all of the chromosomes uniting in pairs except the odd one. The odd chromosome divides only in the second spermatocyte division. The peculiarity here is that the other chromosomes

seem to undergo their reducing division when the odd chromosome is dividing equationally, but this is only a further mark of the individuality of the chromosomes, and does not furnish any evidence against Montgomery's theory of synapsis. Medes ('05) finds a similar condition in *Scutigera* forceps.

Orthoptera

Neither vom Rath ('91, '92) nor Wilcox ('95) noticed an odd chromosome in *Gryllotalpa* or *Caloptenus*, although both mention a nucleolus in the spermatocyte growth period which may be the same structure. They both insist that there are two reducing divisions; that is, two divisions that separate whole chromosomes from each other. This is probably due to a confusion in the use of the word chromosome. If we use the terminology suggested by McClung ('00), univalent chromosome in the spermatogonium, bivalent chromosome in the spermatocyte, and chromatid for each unit of the tetrad, the discrepancies in the work of vom Rath and Wilcox are cleared up. Vom Rath finds 12 spermatogonial chromosomes. In the growth period, the spireme splits into six rods, each of which forms a tetrad, or divides into four "chromosomes," as he expresses it. As he calls each chromatid a chromosome, he considers that he has two divisions which separate chromosomes from chromosomes; and therefore must be reducing; while in terms of the original spermatogonial chromosomes, one division is reducing and one equational. Wilcox falls into the same difficulty; he finds 12 spermatogonial chromosomes, and then the spireme divides into 24 "chromosomes," which form 6 tetrads. He had, in reality, 24 chromatids, and only one reducing division.

McClung ('00, '02a) has described the odd chromosome in the *Acrididæ* and *Locustidæ*. He worked on a number of forms and obtained uniform results. In the *Orthoptera*, this chromosome can be traced back into the spermatogonial rest stages. It divides only in the first spermatocyte division, giving dimorphism of the spermatozoa. In 1901, McClung suggested the theory which has since that time received substantial corroboration, that the dimor-

phism of the spermatozoa corresponds to the dimorphism of sex. McClung considers that the longitudinal division always precedes the reducing division, and thinks that this is important on account of the failure of the second polar body to be extruded in parthenogenetic eggs; but the work in the other groups of insects shows that the reducing division probably comes first as often as the equational.

Sutton's careful work ('00, '02) on *Brachystola magna* offers convincing evidence for the individuality of the chromosomes. Each pair of spermatogonial chromosomes becomes enclosed in a separate compartment of the nucleus, while the odd chromosome is in a vesicle shut completely off from the others. He suggests the application of Montgomery's theory of the union of maternal and paternal chromosomes in synapsis to Mendelian inheritance.

The observations of de Sinéty ('01) on the odd chromosome in one of the Acrididæ and in several Phasmidæ are entirely in accord with those of McClung; this chromosome divides in only one spermatocyte division, producing dimorphic spermatozoa. In one of the phasms, he finds a chromosome complex similar to that described later by McClung ('05) for *Hesperotetrix*, where the odd chromosome attaches itself to one end of a tetrad, forming a hexad which divides along the transverse axis of the tetrad, thus sending the odd chromosome and two chromatids of the tetrad to one cell, and two to the other. Unfortunately de Sinéty interprets both of the spermatocyte divisions as longitudinal, but on this point he is in the minority among the workers on Orthoptera.

Baumgartner ('04), in *Gryllus domesticus*, finds the odd chromosome in a separate vesicle as Sutton did for *Brachystola*, but he finds it dividing in the second division instead of the first. Stevens ('05a) in *Stenopelmatus* and *Blatella germanica*, and Otte ('06), in *Locusta viridissima*, find that the odd chromosome divides in the second division instead of the first. Evidently there is no fixed rule as to where the odd chromosome shall divide.

Voinov ('03), Montgomery ('05) and Zweiger ('06) all hold a different view as to the valence of the orthopteran odd chromosome; but as each has studied only one species of the order, while