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ANIMAL CYTOLOGY
&
EVOLUTION

BY

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PREFACE

During the twenty years which have elapsed since E. B. Wilson's great work, *The Cell in Development and Heredity*, was written the science of animal cytology has advanced so much that a general text-book covering all branches of the subject would have to be three or four times the size of the present volume. Moreover, it is doubtful if any living cytologist is fully conversant with cell-physiology as well as with genetical and evolutionary cytology.

This book deals, therefore, with only one aspect of animal cytology, namely the evolution of the chromosomes. Since these bodies are themselves the material basis of evolution, when we study the changes which have taken place in them in the course of phylogeny we are, in fact, studying the evolution of the evolutionary mechanism itself. Thus the book might have been called 'The Evolution of Evolution', but such a title might have appeared ambiguous to some and pompous to others.

Such a large amount of genetical and cytological work has now been carried out on the flies of the genus *Drosophila* that 'Drosophily' has almost become a separate branch of biology. In one way this is all to the good, but in practice it often leads to a division between *Drosophila* workers and general cytologists or geneticists working on other groups of organisms. Thus the former are frequently ignorant of the not inconsiderable amount of cytological work which has been carried out on Orthoptera, Vertebrates, etc.; while, conversely, those who have worked on the cytology of grasshoppers or mammals are often woefully ignorant of *Drosophila* genetics.

There can be no doubt that this separation has had unfortunate consequences. For example, it was not realized until 1934 that the salivary gland chromosomes could be used for cytogenetical analysis in *Drosophila*, although these relatively enormous chromosomes had been studied in other dipterous flies as early as 1880. Had the first generation of *Drosophila* workers known of the work of Balbiani, Carnoy, Alverdes and others on the salivary chromosomes of *Chironomus* it is probable that they would have made use of the salivary chromosome technique in their own work twenty years earlier. If the present book helps to close up the cleavage between *Drosophila* workers and general cytologists it will have served one important purpose.

Any book written in war-time, when libraries are difficult of access, must suffer in some respects. If any cytological work of importance was carried out in enemy or enemy-occupied countries in the years 1940–4 it does not figure here because the author was unable to obtain continental journals after the fall of France. Moreover, certain rare journals were evacuated from London

at the outbreak of war and were not available for reference. More serious was the fact that almost the entire book was written in North Wales, with only occasional visits to Oxford or London to visit libraries.

I am greatly indebted to a number of persons who read the manuscript and pointed out errors or made suggestions for its improvement. In particular I should like to thank Prof. Th. Dobzhansky, Prof. J. B. S. Haldane, Dr S. Hughes-Schrader, Dr J. S. Huxley, Dr U. Philip, Prof. Franz Schrader and Dr H. Spurway.

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M. J. D. W.

1945

CHAPTER I

INTRODUCTION—THE NATURE OF THE EVOLUTIONARY PROCESS

The object of this book is to discuss the bearing of animal cytology upon the problem of the mechanism and processes of evolution. By cytology we mean nuclear cytology, since the evolution of the cytoplasmic constituents of the cell is an entirely different subject.

Most recent discussions of evolution have included both animals and plants within their scope. Thus in Darlington's *Recent Advances in Cytology*, Dobzhansky's *Genetics and the Origin of Species* and Huxley's *Evolution, the Modern Synthesis*, the evidence from botany and zoology is interwoven on nearly every page. Although it must be admitted that this 'synthetic' method of treatment has certain advantages, it is gradually becoming clear that the evolutionary processes of animals and plants differ in certain broad features, so that for many purposes they are best discussed separately. For this reason, and also for considerations of space, the present volume deals exclusively with animal chromosomes and animal evolution, work on plant cytology being only referred to when it has a direct bearing upon the principles of chromosomal evolution in animals.

The cytology of the Protozoa has been omitted for a different reason. While not denying the excellence of much recent work on the nuclear cycle in unicellular organisms (e.g. that of Bělař (1926) and the more recent work of Geitler (1942), Chen (1940 *a*, *b*) and others), it must be doubted whether the time is yet ripe for a general discussion of chromosome structure or of the mechanism of evolution in the Protozoa and Protophyta.

The problem of how and why related species of organisms have acquired visibly different chromosome sets is one that has occupied the minds of cytologists for many years. On the other hand, it is an aspect of organic diversity which has been very much neglected by those who have written on the general theory of evolution. Yet as long ago as 1905 McClung spoke of advances in fundamental knowledge coming about 'by a comparison of the germ cells and body characters in nearly related species, by observing the differences in germ cells of individuals that vary from the type of the species, or finally by experimentally disturbing the normal conditions in the germ cells and observing the effects upon the body'. What McClung had in mind was clearly a somewhat premature hope that it would be possible to establish direct correlations between visible differences in chromosome morphology and the external structural characters used in distinguishing species. This expectation has been realized in part, but it is now evident that the architecture of the chromosomes is so

complex that many of the evolutionary changes which occur in them are on a molecular scale and hence far below the limit of resolution of the microscope.

It is now generally agreed that all evolutionary transformations have had their origin in the chromosomes, and that these bodies which constitute the physical basis of heredity also furnish the material for the evolutionary process. Although Lamarckian or near-Lamarckian theories are still occasionally met with, particularly in the writings of some palaeontologists and bacteriologists, they are not put forward by persons who are well acquainted with modern work in the fields of genetics and cytology.

So far as we know at present there are only two kinds of events which are capable of giving rise to heritable changes and hence to evolutionary transformations: gene mutations and 'structural' chromosomal changes which involve alterations in the sequence of the genes. Cytoplasmic inheritance, which seems to play a role though a very minor one in some plants, is almost and perhaps completely absent in animals above the level of the Protozoa; it can safely be neglected in a general discussion of animal evolution.*

McClung's three lines of investigation: (1) comparison of chromosome sets in related species, (2) comparison between the chromosome sets of aberrant individuals and the normal set which is characteristic for the species, and (3) the experimental alteration of chromosome morphology, have all proved to be fruitful methods of inquiry, and have occupied the attention of many investigators. As early as 1914, Metz, in a series of classical papers (1914, 1916 *a*, *b*; Metz and Moses, 1923), was comparing the chromosome sets of different species of *Drosophila* and classifying them into groups according to the number and shapes of their chromosomes. Even before this, Wilson and other American workers had studied chromosomal variation in natural populations of Orthoptera, Heteroptera and Coleoptera (McClung's second line of investigation). It was not until 1927, however, that a reliable means of inducing chromosomal changes by experimental means was found. The discovery that irradiation by X-rays would produce both gene-mutations and structural changes (Muller, 1927) opened up vast new fields in both genetics and cytology. It made possible the formulation of precise 'laws' and principles governing the processes of chromosomal evolution. Until then it was hardly possible to relate the data of comparative cytology to the species problem. Before about 1930 most animal cytologists were more concerned with facts about chromosome numbers, sizes and shapes and with hypotheses about the mechanisms of mitosis and meiosis than with building their results into the general fabric of evolutionary thought. Thus for a time it appeared as if McClung's three lines of work had failed to yield results of general importance. For this reason chromosome cytology tended for a time to become an esoteric subject, the details of which seemed to

* 'Maternal effects', i.e. an influence of the maternal genes on the cytoplasm of the egg, are quite common in animal genetics, but they have nothing to do with true cytoplasmic inheritance.

be of little interest to workers in other fields. Even to-day this tendency still exists to some extent, and many biologists seem to think of evolution almost entirely in terms of gene-mutations, neglecting the structural changes, or relegating them to a very subordinate part in their theories of evolution.

The rediscovery of the salivary-gland chromosomes in the Diptera (Painter, 1933; Heitz and Bauer, 1933) has entirely changed this situation. Once again, as in the time of Weismann, the chromosomes are coming to occupy the central place in physiological and evolutionary thought, only this time we know vastly more about their detailed structure and genetical behaviour in a great variety of animals and plants. By studying salivary-gland chromosomes it is possible to make direct comparisons between the gene-sequences of different individuals and species with an ease and precision previously undreamed of. It is now more than ever apparent that it is quite impossible to analyse the mechanism of evolution without taking into consideration structural rearrangements of chromosome parts. Theoretically, one might suppose that nearly related species might differ in a few genes, but that the sequences of their genes would be the same. In fact, this is not so, at any rate in the Dipterous genera *Drosophila*, *Chironomus* and *Sciara*, where the most closely related species always seem to differ, even if only slightly, in their gene-sequences.

The general view of evolution which is accepted by most modern biologists, and especially by geneticists, may be described as neo-Darwinian, since it lays considerable stress on the role of natural selection. It is sometimes objected that selection is merely a 'destructive' force, and hence cannot be expected to produce anything 'new'. But, as Huxley (1942) points out, all evolution is the result of an interplay between chromosomal changes and selection, in which the latter may be regarded as playing a 'directive' part, building up combinations of genes and gene-sequences which would not come into existence by mere chance.

The formulation of the mathematical theory of natural selection has been carried out in the past two decades by R. A. Fisher, Sewall Wright and Haldane. The examples worked out in their papers relate mainly to gene-mutations, but the same general principles apply, with few modifications, in the case of structural changes. One result of this theoretical work was to focus attention on the need for more precise data on the distribution of genetical and cytological variation in wild species, the size of natural populations, their fluctuations from month to month and year to year and other similar problems of *gene-ecology* and *population-dynamics*. In this book we shall not deal with gene-mutations, except incidentally, since our concern is with the cytological (as distinct from the genetical) aspects of evolution. It is, to be sure, almost impossible to draw any hard and fast line between cytological and genetic phenomena, but since the more strictly genetical side of evolution has been dealt with very fully from the neo-Darwinian standpoint in the recent books of Dobzhansky and Huxley it does not seem desirable to cover this ground once more.

It may be convenient at this stage to recapitulate the main elements in the neo-Darwinian position:

(1) Mutations and structural rearrangements are 'physico-chemical accidents' which are non-adaptive in origin (the various hypotheses as to the causation of these 'accidents' lie outside the scope of this book).

(2) Natural selection acts as a filter which eliminates mutations and rearrangements which are disadvantageous and favours those which are advantageous. The number of mutations and rearrangements which become incorporated in phylogeny is only a minute fraction of the total number which occur, the majority being disadvantageous.

(3) The probable effects of selection can be calculated mathematically if the physiological effects of the mutation or rearrangement and the population-dynamics of the organism (size of individual units of population, rate of reproduction, motility, etc.) are known.

(4) The spread or extinction of mutations which are neither strongly deleterious nor highly advantageous tends to obey the laws of chance. In small populations especially, disadvantageous mutations may spread and advantageous ones become extinct. Adaptation is thus never quite perfect.

(5) As far as we can tell at the present time all evolutionary phenomena can ultimately be interpreted in terms of gene-mutations and chromosomal rearrangements, polyploidy* and hybridization* on the one hand and natural selection and the laws of probability on the other, without dragging in any special principles which cannot be interpreted in terms of the above factors.

(6) No radical difference exists between 'macro-evolution' and 'micro-evolution'—the evolution of species and genera is a consequence of the genetical processes which are going on all the time in natural populations and does not depend on any unknown processes of an entirely different kind, as some authors (e.g. Goldschmidt, 1940) have supposed. Thus, as Mayr (1942) puts it: '...the origin of the higher categories is a process which is nothing but an extrapolation of speciation'.

The detailed evidence for these views has been set out by Dobzhansky and Huxley and will not be recapitulated here. Among the few recent authors who do not accept the neo-Darwinian viewpoint we may mention Robson and Richards (1936), whose discussion of the mechanism of evolution (not written from a genetical standpoint) ends on a note of complete scepticism and uncertainty, and especially Goldschmidt (1940). The latter author regards 'macro-' and 'micro-evolution' as entirely different processes, and believes that true species are formed in an abrupt manner by a mechanism entirely different from that whereby subspecies are produced. He thus rejects one of the fundamental principles of Darwinism, namely, that varieties (or at any rate some of them)

* In animals these seem to play a very minor role, although in plants they are important factors in evolution.

are incipient species. Goldschmidt's views have been strongly criticized by Dobzhansky (1941*a*) and by Mayr (1942). The most complete answer to them comes from recent work on speciation in *Drosophila* (see Chapter VII). In this genus it has been shown that every gradation exists from 'strains' differing in a few quantitative characters only to fully developed species which are sharply demarcated from one another.

There are two main aspects of evolution: (1) the formation of species, and (2) morphological and physiological change. From a cytological standpoint we shall be interested in both of these. The differences in gene-sequence which distinguish one species from its nearest relatives throw a new light on the 'species problem', while the cytological characteristics of whole groups (haploidy of male Hymenoptera, absence of crossing-over in the males of the 'higher' Diptera, etc.) have a bearing on the differentiation of the larger groups and the problem of their evolutionary plasticity.

The term 'speciation' has been introduced into the literature of evolution to designate the process whereby new species come into being. Dobzhansky (1937*d*) has defined speciation as 'the fixation of discontinuity among organisms'. If taken literally, this definition would seem to include all kinds of evolutionary change, but Dobzhansky goes on to explain that by speciation he means the establishment of physiological isolating mechanisms which prevent effective interbreeding. Thus two 'races' which were originally capable of hybridizing freely are assumed to acquire either (1) a reluctance to cross-mating, (2) sterility of the cross, or (3) sterility of the hybrid. Any one of these three types of isolating mechanisms will prevent interchange of genes between the two strains and will initiate a new dichotomy in evolution.

It will be seen that speciation is conceived of as a rather special stage in the evolution of species—the stage during which the isolating mechanism is not yet completely effective, but is spreading through the area occupied by the new 'incipient species' and possibly becoming more efficient by selection of subsidiary 'modifying genes'.

A number of attempts have been made in recent years to define the concept of the species. One difficulty arises from the fact that taxonomists working on different groups do not necessarily have the same standards as to what should be regarded as a 'full' species. In particular, the criteria seem to differ greatly according to whether the group has been thoroughly studied or not. Thus, as Mayr (1942) puts it: 'The student of spiders may still have the species concept which the ornithologist had in 1880, and the student of weevils that of the ornithologist of 1900.' If species were nothing but morphological entities it would probably be impossible to frame a definition of the species which would apply in annelids, insects and mammals, since there would be no way of comparing degrees of structural divergence in groups whose morphology is so radically different. However, since species are, by common consent,

biological as well as morphological entities, we may attempt to frame a biological definition.

It is this question of arriving at a satisfactory definition and applying it in practice that is referred to by museum taxonomists as the 'species problem'. Most of the definitions that have been put forward admit the gradual nature of speciation and adopt a dynamic attitude to the problem, recognizing that species are stages in evolution and not static entities. One of the most generally acceptable of the definitions that have been put forward is that adopted by Dobzhansky (1937*d*, 1941*a*), according to which species represent 'that stage of the evolutionary process at which the actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding'.

One objection to this formulation is that it defines the process of speciation rather than the idea of the species; another is that it is often difficult to decide whether two forms are 'physiologically incapable' of hybridization. Many forms can be crossed in the laboratory that probably never hybridize under natural conditions, and occasionally wild hybrids are encountered between forms that must be regarded as valid species from every other point of view. The present writer would prefer a definition somewhat more general in character: 'A species is a group of individuals which are capable of normally and regularly breeding together, except in so far as they may be separated by geographical isolation.' This formulation implicitly admits that absolute physiological isolation is not the essential criterion—the acid test is whether the two forms are able to interbreed 'normally and regularly'. Mayr (1940) has adopted a somewhat different wording that expresses the same idea: 'A species consists of a group of populations which replace one another geographically or ecologically and of which the neighbouring ones intergrade or hybridize wherever they are in contact, or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.' The general adoption of this viewpoint in ornithology has led to a considerable reduction in the number of species recognized by taxonomists, many forms which were earlier looked upon as full species being now regarded as geographical subspecies. But in many groups of insects the adoption of the new 'biological' outlook in systematics has led to an increase in the number of species, by revealing the existence of 'cryptic' species so similar in outward appearance that the old-fashioned taxonomist would never have regarded them as specifically distinct, although it is now clear that they form entirely different breeding units.

The chief feature that all these definitions have in common is the recognition of the species as a *breeding unit*. Admittedly, this concept is not much use to a museum taxonomist faced with a tray of pinned insects or a drawer of stuffed birds, but it is to be hoped that it will eventually be applied in all cases where

an element of doubt exists as to the specific distinctness of two forms. In cases such as the head and body lice of man (originally described by Linnaeus as distinct species but regarded by modern authors such as Buxton (1940) as races or subspecies) the essential thing is to determine whether one or two breeding units are present.*

Sturtevant (1942) has laid down three criteria for deciding whether a given form should be regarded as a distinct species:

(1) 'Distinct species must be separable on the basis of ordinary preserved material.'

(2) 'Cross-fertility between distinct species is in general absent or so slight as to make unlikely any transfer of genes from one to the other in nature.'

(3) 'Subspecies usually replace one another geographically, species may do so, but are more likely to show extensively overlapping distribution areas.'

The first criterion would be acceptable to most museum taxonomists but probably not to all geneticists. The third one has many exceptions, but may be useful in doubtful instances.

The idea that species are artificial categories created by man out of a disorderly array of intergrading forms is one that is only occasionally expressed, although it occurs in the discussions of some palaeontologists and in the writings of some biologists whose work has been concerned with asexual organisms such as bacteria, in which it is quite possible that true species do not exist. The fact that there is a 'species problem' does not necessarily imply that species are not perfectly real and natural entities; it merely signifies that taxonomists sometimes disagree about the labelling of museum specimens and that the 'species' they create are sometimes artificial. But this artificiality (where it occurs) is not inherent in the material; it is due either to human failings of the taxonomists themselves, or to the small number of specimens available for study, or to the fact that most new species are described on a few morphological characters, without any biometrical, ecological or zoogeographical studies.

In spite of all these difficulties it is really remarkable how much unanimity exists about the delimitation of species in groups that have been adequately studied. The birds are possibly the best example, from this point of view; there are only about 8,500 species known in the world, and it is probable that less than 100 new species remain to be discovered (Mayr, 1940). Moreover, the number of taxonomists who have specialized on birds is relatively very large, and, as a result of the labours of collectors and sportsmen, museum collections of birds are far more complete than is the case in most other groups. This situation may be compared with the lamentable state of affairs in many groups of insects, where the known species represent only a small fraction of the total

* Obviously, none of the definitions of the species quoted above apply in the case of obligatorily parthenogenetic forms. A re-investigation of the 'species problem' in such forms is badly needed.

number existing in the world. Where, however, we are dealing with insects that have been very extensively collected (such as the larger and more decorative butterflies) we find that there is a general unanimity as to the delimitation of the species, which are just as definite entities as in the case of birds.

Mayr estimates that only about 1% of the 8,500 species of birds are 'difficult species' which are so similar that competent authorities have real difficulty in separating them. A considerably larger number, however, seem to have reached a stage in evolutionary differentiation at which it is difficult to decide whether they should be regarded as 'full' species or not. Out of 755 species indigenous to the North American continent Mayr estimates that 94 (12½%) represent 'species in the making'. Some of these forms are readily distinguishable, but in their general morphology they indicate clearly enough that they have only recently broken off the parent species; for the most part they seem to be geographically isolated forms confined to small areas in the Rocky Mountains or to islands off the Californian coast. The existence of these 'incipient species' (which may be compared with the A and B races of *Drosophila pseudoobscura*) is a confirmation of the dynamic view of speciation outlined above and an argument against the view that it will eventually be possible to decide on the delimitation of *all* species with complete certainty and unanimity. The situation is, in fact, just what one would expect if the origin of species is a gradual process. On the other hand, if Goldschmidt's viewpoint, according to which species arise by sudden 'macromutations', were true we should not expect to find all gradations between races and species existing side by side in nature.

If we could represent the exact phylogeny of every group by a diagram in the form of a branching tree, it would be evident that the trees were not all the same shape. Some groups have branched out into a vast number of species while other phylogenetic trees have few branches situated far apart. In many families one large genus includes about 90% of the species, the remaining 10% being placed by taxonomists in a large number of much smaller genera. In some groups the morphological differences between species are relatively slight, while in others they are obvious even to the superficial observer. The evolution of each group may be regarded as a 'pattern', of which the existing species and subspecies represent a cross-section.

With the development of scientific taxonomy the need for a more elaborate terminology than the usual hierarchy of species, genus, family, etc., has gradually become apparent. In groups that have been thoroughly studied by taxonomists such as the birds, mammals and Lepidoptera, many species seem to consist of a number of geographical races or subspecies which replace one another geographically. Rensch (1929) has applied the term *Rassenkreis* to complexes of forms replacing one another in this way. Huxley (1942) uses the term *polytypic species* in almost exactly the same sense. Where a number of entirely distinct species replace one another geographically Rensch speaks of an *Artenkreis*.

Obviously, a Rassenkreis can be thought of as gradually evolving into an Artenkreis by an increase in the differences between the subspecies until they eventually attain the status of full species. On the other hand, discontinuous and overlapping distributions are often found in closely related species, so that the Artenkreis principle is of less general application than that of the Rassenkreis. Mayr uses the term *superspecies* as equivalent to Rensch's Artenkreis.

These concepts have been applied mainly to the higher vertebrates. In insects, where the territory of the individual is so much smaller, ecological replacement is probably more important than in vertebrates, so that 'ecological subspecies' or 'biological races' (see Thorpe, 1930) are relatively more common.

An interesting situation exists where each subspecies of a Rassenkreis is interfertile with those occupying adjacent areas but where the end-members of the series are incapable of interbreeding when brought together, either in the laboratory or as a result of their areas of distribution increasing until they overlap. Numerous examples of this state of affairs have been given by Rensch (1929), Kinsey (1936) and Huxley (1942). These cases present taxonomists with a difficult problem of nomenclature. The differences between *A* and *B*, *B* and *C*, *C* and *D* may not be sufficient to warrant specific rank, but if *A* and *D* are not only very different in appearance but are completely infertile when crossed, what is the taxonomist to do? The only satisfactory solution in most of these cases would be to speak of each 'ring' or 'chain' of races as a Rassenkreis, the end-members of which are recognized to be genetically isolated. Kinsey (1936, 1937*a*), who has made an extremely detailed taxonomic survey of the gall-wasps (Cynipidae) of the U.S.A. and Mexico, has adopted the alternative of calling every morphologically distinguishable form a species, no matter how slightly it differs from its neighbours in the chain. His 'species' are thus not equivalent to those of other authors; they correspond to the geographical subspecies, races or 'strains' of ordinary taxonomic practice.

In a later paper (1942) Kinsey has gone so far as to deny altogether the validity of the species-concept. Thus in one place he speaks of the 'nebulous something which everybody calls a species but which nobody can define, describe or recognize in a fashion which is quite acceptable to the next student in the field', and in another: 'Now we are ready to question the reality of any grouping of local populations, into species or any other category.' What Kinsey is really saying here is that every population has a distinct genetical make-up (a fact fully recognized by genetical writers such as Dobzhansky), and that in the 'chains of races' with which he has been dealing each geographical race intergrades with the next so that no definite discontinuity exists between them. The real gaps are, of course, between the entities which he calls 'complexes', but which we must regard as true species, although perhaps of a special type. When speaking of these Kinsey states that there is no interbreeding between them, and that 'sterility mechanisms have finally entered as primary isolating

factors, at this taxonomic level'. It may be worth remarking, in passing, that the speciation pattern of the Cynipini may have been largely determined by that of the plant genus (*Quercus*) upon which they live. The fact that several species of *Cynips* may live on one oak is not an argument against this view, since the single species of tree may formerly have had a discontinuous distribution.

Although we may agree on a broad general definition of the species-concept it is undeniable that different types of species occur, often in the same group. Huxley (1942) speaks of polymorphic, polytypic and monotypic species (the first consist of sharply contrasted types, the second are differentiated into subspecies, the last are not differentiated). From a genetical and cytological standpoint an equally important distinction is between rare and common species. In general, common species are more variable than rare ones, as was realized by Darwin; but rare species are more likely to be split up into isolated groups between which migration seldom or never occurs. A further separation can be made between 'continental' species (i.e. those which occupy a continuous area of continental dimensions) and 'insular' ones (which occupy limited territories such as islands, mountains rising from a plain or desert, etc.). Kinsey (1937*b*) finds that in gall-wasps the 'insular' species are far less variable than the 'continental' ones (the latter being mostly common species, the former rare ones).

We still know very little about the cytological characteristics of rare versus common or continental versus insular species. Judging from *Drosophila* it rather seems as if the number of different gene-sequences is greater in species with a restricted distribution (such as *D. pseudoobscura*) than in ones which are world-wide (such as *D. melanogaster*, *D. funebris*, *D. simulans*, *D. hydei*, etc.). But the comparison may not be a fair one, since many of the cosmopolitan species owe their present distribution to human agency within the last few centuries. If it should really be the case that cytological variation is greater in rare, insular species than in common, continental ones, that would be extremely interesting, since all the evidence points to the relationship being the other way about in the case of genic variation. It may be that most gene-mutations which undergo fixation do so as a result of selection, while most gene-sequences which establish themselves do so by chance.

The general picture of natural populations that has been built up in the last few years suggests that in most species there is far more genetical than cytological variation; that is to say, the number of different gene-sequences existing at any one time is much less than the number of allelomorphic gene-differences. So great is the number of possible combinations of the latter that in man and domestic animals it is fairly clear that every individual differs genetically from every other one (except in the case of identical twins). Mayr (1940) believes that this conclusion holds true for all other animals (parthenogenetic forms excepted), but as regards the lower animals this is so far unproven.

On the other hand, in most species the number of cytologically distinct types is fairly small, although it may run up to several thousand if we consider all possible combinations of perhaps a dozen or more different inversions or other structural rearrangements. Even so, however, a large number of individuals will be cytologically identical, although they may be all genetically unique, as suggested by Mayr.

The importance of geographical isolation for the fixation of genetical and cytological diversity has been stressed by all modern writers on evolution. The subspecies, races or strains into which most species can be split up nearly always have distinct geographical distributions which may overlap or not, but are seldom completely co-extensive. In the higher vertebrates it is not unusual for a species to be divisible into several distinct geographical subspecies, while in insects we find all gradations between this situation and the one where several 'biological races' inhabit the same area but live on different hosts or food plants. We may infer from this that geographical and ecological isolation play a primary role in the differentiation of species into the lower categories of subspecies, races, strains, etc. While some of the gene-differences between these categories may be non-adaptive, there can be little doubt that the gene-complexes characteristic of geographical races and subspecies are, in general, adaptive to the particular conditions under which these forms live. Crossing between different geographical races or subspecies will necessarily break down these adaptive combinations of genes and will produce individuals less well adapted to their environment than either of the 'pure' forms (unless there is a complete gradation of environmental conditions, which will seldom be the case). Thus any isolation mechanism, whether physiological or cytogenetical, will usually be to the advantage of both forms. The production of new isolating mechanisms from time to time and their perpetuation through selection are thus seen to be essential to the preservation of stable, adaptive combinations of genes.

Before any mutation or structural rearrangement can establish itself in evolution it must first of all make its appearance in the progeny of a single individual and then undergo fixation in a local population or group of individuals. The probability of a mutation or structural rearrangement undergoing fixation, whether by chance or because it has a 'positive selective value', depends on the size of the population or, more precisely, on the *population number*, a concept of Sewall Wright (1931, 1932, 1935) for which he uses the symbol N.* The smaller N is, the greater the chance of a mutation or rearrangement being lost by extinction or reaching 'fixation' as a result of the extinction of alternative

* N has been defined by Wright as follows: 'The conception is that of two random samples of gametes, N sperms and N eggs, drawn from the total gametes produced by the generation in question.... Obviously N applies only to the breeding population and not to the total number of individuals of all ages. If the population fluctuates greatly, the effective N is much closer to the minimum number than to the maximum number. If there is a great difference between the number of mature males and females, it is closer to the smaller number than to the larger.'

allelomorphs or sequences. Wright has, in fact, pointed out that in a population of N breeding individuals $1/2N$ genes will reach 0% or 100% frequency in each generation unless heterozygotes are selected. This process of inevitable change in gene- and sequence-frequencies, even in the absence of a selective mortality, is referred to by Wright as 'drift' and by some other writers such as Huxley as the 'Sewall Wright effect'. Dubinin calls it the 'genetico-automatic process', and has studied it in actual populations.

In the past cytologists have not paid much attention to the size of the populations from which their samples were drawn, the degree of isolation between populations and other factors of a like kind. But the newer evolutionary cytology which is largely concerned with cytological variation in natural populations (see Chapter VI) must take account of all these things if it is to play its part in building up a unified body of evolutionary theory.

In this unavoidably brief sketch of modern ideas on evolution we have only been able to touch on a few of the many aspects of an extremely complex subject. Before we can consider the problems of chromosomal evolution it will be necessary to describe the anatomy of the chromosome body, and the next two chapters are accordingly devoted to this subject. We can then pass on to consider such topics as the cytological heterogeneity of natural populations, the processes of chromosomal evolution in particular groups such as the grasshoppers and the genus *Drosophila*, the evolution of meiosis and of the sex chromosomes. In the last chapter we shall return to some of the wider aspects of evolution and discuss the light thrown upon them by modern cytological work.

CHAPTER II

THE STRUCTURE OF MITOTIC CHROMOSOMES

The general anatomy of the chromosome body is now fairly well known, although the mechanism of mitosis still remains a mystery in many respects.* Even the molecular structure of chromosomes is beginning to be understood, thanks to a co-operative attack by chemists, biophysicists and cytogeneticists. Some of the unsolved problems of chromosome structure will be neglected in this book, since they are not directly relevant to the subject of chromosomal evolution. It is, for example, not known with certainty at what stage in their life cycle the chromosomes first undergo longitudinal splitting into paired threads (chromatids). Some authorities maintain that the split first occurs during the resting stage, in preparation for the next mitosis; others believe that it takes place much earlier, i.e. at some time during the previous division. One author (Nebel) even maintains that chromosomes split two mitoses before the one at which the actual separation of the chromatids takes place. For a presentation of the various views on the time of splitting of chromosomes, the papers of Darlington (1935*a*), Huskins (1937), Mather (1937), Kuwada (1939), Kuwada and Nakamura (1935) and Nebel (1935, 1939) should be consulted; but it seems highly probable that the time of splitting is not the same in all organisms, and that it may even differ in the various tissues of the same organism. General reviews of the morphology of the chromosome body have been published by Heitz (1935) and Geitler (1938*a*, 1940).

The structure of the chromosomes during the so-called resting stage is so variable, according to the type of nucleus studied, that it is impossible to give any satisfactory general account of it. Although the chromosomes undoubtedly have a continuous existence throughout the whole of the nuclear cycle they can usually only be studied with profit during mitosis. In many types of resting nuclei the chromosomes are 'unfixable', that is to say, they cannot be seen in microscopical preparations or, if they can be seen, their appearance bears little or no resemblance to the structure which they are believed to possess in the living cell. This is particularly the case in nuclei in which an irregular network of coagulated material is seen after fixation: it is now clear that all 'networks' seen after fixation are gross artefacts. In some other kinds of resting nuclei filaments can be seen, either during life or after fixation, which undoubtedly represent chromosomes; but usually the structural details cannot be analysed or interpreted. In text-books of histology one often comes across statements that particular types of nuclei contain 'coarsely granular' or 'finely divided'

* See Schrader, *Mitosis* (Columbia University Press, 1944).

chromatin, but it is very doubtful what relationship these appearances bear to the condition during life.

From a chemical standpoint chromosomes are composed of protein and nucleic acid. Their molecular structure has been investigated by staining reactions (Feulgen, 1926; Feulgen and Rossenbeck, 1924; Feulgen and Imhäuser, 1925; Bauer, 1932, 1933), polarization methods (Schmidt, 1937), ultra-violet spectroscopy (Caspersson, 1936, 1940; Caspersson and Schultz, 1938, 1939, 1940) and the micro-incineration technique (Barigozzi, 1937 *a*, *b*). The proteins are apparently globulins and histones which are chemically combined with the nucleic acid (Caspersson, 1941), the linkage between the two types of compounds being salt-like.* Virus particles and many enzymes are also made of nucleo-proteins, so that it is probable that this type of compound is an extremely fundamental one in all living systems.

Both protein and nucleic acid exist in the chromosome as elongated fibres which all lie parallel to one another in the long axis of the system. The earlier view of Wrinch (1936), according to which the nucleic acid molecules were believed to lie at right angles to the protein threads, has now been shown by X-ray analysis to be wrong (Astbury and Bell, 1938 *a*, *b*). The cyclical changes in appearance which the chromosomes undergo during the nuclear cycle are undoubtedly due in the main to differences in the relative amount of nucleic acid and protein, and possibly also to the amount of water present.

The nucleic acid molecules in the chromosomes are formed by the polymerization of many nucleotides (about 2,000 per molecule according to Signer, Caspersson and Hammersten (1938)). Each nucleotide is built up of a molecule of phosphoric acid in combination with a purine or pyrimidine group and a peculiar pentose sugar, desoxyribose. Other kinds of nucleotides are found in the cytoplasm, and in nucleoli (Caspersson and Schultz, 1940); they differ from the nucleotides of the chromosomes in the nature of the sugar molecule, which is *d*-ribose. The extra-chromosomal nucleotides are mostly not polymerized: some of them are possibly concerned with enzymatic systems of the cell, while others may act as raw materials for chromosome growth, a change in the pentose constituent of the molecule taking place at the time it is built into the fabric of the chromosome.

The protein part of the chromosome seems to form a permanent framework which persists throughout the resting stage. As the nucleus passes into mitosis the amount of the nucleic acid in the chromosomes gradually increases, until the latter reach the compact cylindrical form which they exhibit at metaphase, when the amount of nucleic acid is at a maximum. Telophase may, broadly

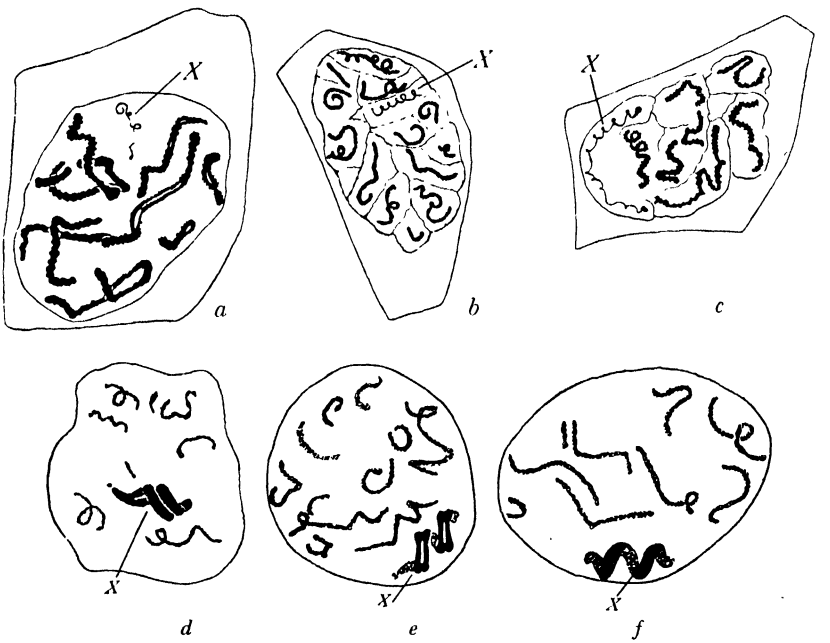
* Stedman and Stedman (1943) claim to have discovered a new type of protein (which they call chromosomin) in cod sperm. They believe that this substance is the essential basis of the gene, but until their detailed results have been published it is not easy to decide how far the classical views on the chemical structure of chromosomes will require modification.

speaking, be regarded as a reversal of prophase, the amount of nucleic acid gradually decreasing. Whether the nucleic acid content of the chromosomes ever falls to zero in the resting stage is unknown, but it is certainly very low in some types of resting nuclei. The whole process by which the nucleotides are polymerized and incorporated into the chromosomes may be spoken of as nucleination, the opposite process that occurs at telophase being referred to as denucleination. The exact role played by the nucleoli in the nucleination cycle is not quite clear, but these bodies are undoubtedly reservoirs of nucleotides that are later utilized in the nucleination of the chromosomes (Caspersson and Schultz, 1940). It is now known that the nucleoli are always attached to particular chromosomes of which they may be regarded as lateral vesicular outgrowths (Dearing, 1934; Kaufmann, 1938). The Feulgen reaction (staining with fuchsin-sulphurous acid after a preliminary hydrolysis with hydrochloric acid) is more or less specific for desoxyribose nucleic acid, and is not given by ribose nucleotides (at any rate when the usual degree of hydrolysis is employed). Thus the Feulgen method of staining has come to be regarded as specific for 'chromatin'; other nuclear dyes, such as haematoxylin and the anilin dyes (e.g. crystal violet, rosanilin, etc.), are less specific and may stain parts of the cell other than chromosomes.

As the nucleination process takes place the protein framework of the chromosome gradually assumes a spiral form, so that by the time metaphase is reached the whole chromosome is coiled like a spring. The first observations of spiral structure were made as early as 1880 by Baranetsky, but it was not realized until recently that all chromosomes assume this form during mitosis. The spirals are not usually apparent, either in life or in fixed preparations, owing to the gyres of the spring being in contact with one another, so that there is no space between them. Moreover, there is possibly a certain amount of accessory nucleic acid covering the whole structure (see p. 17). The two chromatids may be coiled quite separately, so that the chromosome is **8**-shaped when seen in section —or the coils of the two chromatids may be pressed into one another in an alternating manner, so that the chromosome has an oval or circular cross-section. The number of coils in a chromosome depends on its length: some very short chromosomes probably do not form even one complete gyre, while very long ones may have as many as 20–30.

In order to reveal the spiral structure of metaphase chromosomes special technical methods of fixation usually have to be employed. These methods are of many types, chemical (fuming with ammonia vapour, acids, etc.) and mechanical (crushing under a cover-glass, etc.). They all seem to act by slightly separating or relaxing the coils of the spring so as to make the anatomy of the whole chromosome body visible. These methods have been used with great success by botanical cytologists, particularly in some groups of plants with unusually large chromosomes (Liliaceae, Commelinaceae, etc.); in animals they

seem to be less applicable. There can be no doubt, however, that all animal chromosomes possess a spiral structure; in many instances the spirals of one division persist in a semi-relaxed condition through the resting stage so that they are still visible in the early prophase stages of the next mitosis. Much of the work on spiral structure in animal chromosomes has been carried out on



Text-fig. 1. Early spermatogonial prophase nuclei in Acrididae (*a–c*) and Tettigoniidae (*d–f*). Not all the autosomes are shown. *X* chromosome negatively heteropycnotic in *a* (*Schistocerca*), *b* (*Melanoplus*) and *c* (*Chortophaga*); positively heteropycnotic in *d* and *e* (*Platycleis*) and *f* (*Metrioptera*). From White (1940*a*).

these 'relic spirals' (Bonnevie, 1908 *a*, *b*; Mohr, 1916; de Winiwarter, 1931; White, 1940*a*), but true metaphase spirals have also been clearly seen in some material (Makino, 1936).

For some years it was uncertain whether the direction of coiling (right- or left-handed) was constant for particular chromosomes or chromosomal regions. For plants it has been shown by Nebel (1932), Matsuura (1935) and others that the direction of spiralization is not constant, and it has more recently been shown to be at random in the chromosomes of certain grasshoppers (White, 1940*a*). In this last case the 64 or 128 cells of a single cyst (all descended from one cell by successive divisions) may show as many right-handed as left-handed *X* chromosomes, so that there is apparently not even a tendency for the direction of coiling to remain the same for a few divisions.

There has been considerable argument as to whether the whole substance of the chromosome is spirally coiled at metaphase. Like other controversies about chromosome structure this one has become, in part, a debate as to the terminology to be adopted. Some authorities believe that each chromatid consists of a slender thread (which they call the *chromonema*) embedded in a *matrix* which covers the chromonema and conceals its spiral form. Other authorities deny the existence of a matrix altogether; Darlington (1935*c*) in particular has subjected the whole concept to a destructive criticism. It is somewhat difficult to choose between these two viewpoints, since they are largely based on material prepared by different technical methods. The complete invisibility of the spiral in most metaphase chromosomes would seem to be evidence in favour of the presence of some accessory material. On the other hand, many views which have been held at one time or another as to the nature and supposed functions of the 'matrix' clearly go far beyond the evidence at present available. Some workers who do not use the term speak of a *pellicle*, which they seem to conceive as a thin sheath round the metaphase chromosome, rather like the skin of a sausage.

During prophase (but usually not at other stages) it is possible to see that the chromosome is not quite uniform along its length. If the nucleic acid content of a chromosome is low it may appear to have a hairy or 'woolly' surface. This is particularly the case in the meiotic chromosomes of oocytes. The 'lamp-brush' chromosomes seen in the oocyte nuclei of many vertebrates with yolky eggs (Rückert, 1892; Crew, 1933; Duryee, 1941) are merely an extreme example of chromosomes with an irregular outline. Koltzov (1938) has interpreted this 'lamp-brush' structure as evidence for his view that material is being cast out from the chromosomes at this stage to control the metabolic activities of the cells.

In some types of nuclei the prophase chromosomes have a moniliform appearance, like a string of beads on a thread. This kind of structure is particularly characteristic of the meiotic prophase, but is also seen in many somatic divisions. The beads (called *chromomeres*) seem to be localized accumulations of nucleic acid, while the internodes between them are relatively free of staining material, so that they are almost colourless in microscopical preparations. The number of chromomeres may be very large; Belling (1928) estimated their total number in the haploid chromosome set of *Lilium* at 1,500–2,500, and it is by no means certain that he was able to see all the smaller ones. In *Trillium* Huskins and Smith (1935) counted 900–1,000 chromomeres which varied considerably in size. Adjacent chromomeres have a tendency to coalesce during fixation, so that what appears to be a single large granule under the microscope may really be due to the clumping together of a number of smaller chromomeres. In most animal chromosomes the visible chromomeres are almost certainly compound in nature. The frequently quoted work of Wenrich (1916) on the meiotic chromosomes of grasshoppers will be dealt with elsewhere (p. 28), since it is clear that the

'chromomeres' he studied were bodies of an altogether different order of magnitude—namely, large heteropycnotic regions of the chromosomes. In the salivary-gland chromosomes of the Diptera it is possible to study the chromomeric structure in far greater detail than in any other type of chromosome, and the results obtained with this material confirm the view that all chromosomes consist of chromomeres (i.e. localized portions of the protein framework which have a high affinity for nucleic acid) separated by 'internodes' which have a low nucleic acid content. The exact relationship between the visible segmentation of the chromosomes and the genes will be discussed later (p. 48).

Many chromosomes, perhaps all, possess one special region which plays an essential role in connection with the developing spindle at mitosis. This region has been variously called the *achromite*, *spindle attachment*, *primary constriction*, *attachment body*, *spindle-fibre locus*, *fibre attachment*, *kinetochore* or *centromere*. Some of these names are indicative of the functions which have been ascribed to it. We shall use the term centromere in this book, since it is one of the shortest that have been proposed and because it is possible to form adjectives from it (e.g. *acentric*, lacking a centromere, *polycentric*, having many centromeres).

At mitosis the centromeres of all the chromosomes appear to co-operate in producing the spindle, and may be regarded as organizers of the gelation process which converts the fluid nuclear sap and surrounding cytoplasm into the rigid body to which the chromosomes are attached. In the case of long chromosomes it can usually be seen at metaphase that they are only connected to the spindle at one point along their length, and that this point coincides with the position of the centromere. Fragments of chromosomes which have lost their centromeres (i.e. acentric fragments) usually do not become attached to the spindle, but float about freely in the cytoplasm. The fact that spindles can be formed under special circumstances without any chromosomes being present (e.g. in anucleate eggs) does not prove that the centromeres do not act as organizers of the gelation process in all ordinary cell divisions. Although the functional role of the centromeres is most evident at metaphase and anaphase they are permanent and autonomous regions which can be seen at other stages of the nuclear cycle, in suitable material.

Since the centromeres are in any case much smaller than the chromosomes it is clear that even in favourable material they are not easily studied. It is thus hardly surprising that it is rather difficult to reconcile the various published accounts of their detailed structure. In many chromosomes centromeres have not been seen at all, either because they are too small or on account of special technical difficulties which have not yet been overcome. In a few groups of organisms it is even possible that no individualized centromeres exist, the whole length of the chromosome being attached to the spindle (see p. 22).

Most frequently centromeres have the appearance of non-staining gaps in the

substance of the chromosome, not unlike the internodes between chromomeres, only longer. At metaphase and anaphase the chromosomes are very frequently bent at the centromere, so that they appear to consist of two limbs with a slight gap between them. In certain organisms it is possible to detect a small granule or chromomere in the middle of this gap. These bodies were figured by Navaschin (1912) in the chromosomes of the plant *Galtonia*, and by Darlington (1933,' 1937*b*) in a number of other plants. This author introduced the term 'attachment chromomere' (later 'centromere') to designate the granule itself rather than the non-staining region on either side of it, but we shall henceforth use the term centromere in a wider sense, to designate the whole region of attachment to the spindle. In the Urodele *Amphiuma*, Schrader (1936, 1939) has described a similar structure for the 'kinetochore'. His figures show that each chromosome has a pair of granules embedded in a non-staining area which he terms a 'cup'. On the other hand, in many large chromosomes (e.g. those of the plant *Trillium* which have been used in many investigations) the centromere seems to be a simple non-staining gap in the substance of the chromosome with no special chromomere. There is thus reason to believe that the exact structure of the centromere is not the same in all organisms.

It is possible that centromeres with a granule in the middle should really be regarded as compound, consisting of two attachment regions separated by a small chromomere. On the other hand, there is some reason to believe that the granule really does have a structure which is in some way different from the ordinary chromomeres of the rest of the chromosome. Thus in some preparations it shows a special staining reaction, different from that of the other chromomeres.

It is at any rate clear that the granule belonging to the centromere divides at the same time as the body of the chromosome, while the non-staining regions on either side of it probably remain undivided for a much longer period, i.e. up to the anaphase in which the two halves of the chromosome undergo separation. Thus when we observe chromosomes at metaphase we see that each one consists of two chromatids lying closely parallel and only fused at one point which has so far failed to divide. This conception of the region of attachment as one that divides later than the rest of the chromosome receives confirmation from experimental work in which the chromosomes have been caused to split more than once between successive divisions as a result of irradiation or temperature shocks (White, 1935 *a*, *b*; Barber, 1940).

It was formerly believed that centromeres could occupy either an interstitial or a terminal position in the chromosome, i.e. that some chromosomes were divided into two limbs by their centromeres while others consisted of only one limb. Eventually, however, it was shown that a great many chromosomes which had been thought to possess terminal centromeres really had a minute 'second limb' beyond the centromere (Kaufmann, 1934; Prokofieva, 1934, 1937*a*; White,

1935*b*). Even the tiny IVth chromosome of *Drosophila melanogaster* has now been shown to have a two-armed structure (Panshin and Khvostova, 1938; Griffen and Stone, 1940*b*). It is thus probable that chromosomes with strictly terminal centromeres do not exist naturally, although they may be produced by chromosome breakage in laboratory experiments. The minute 'second limbs' of some chromosomes resemble the granules which are found in the middle of some centromeres; they may be similar in nature.

Even if we regard all chromosomes as two-limbed bodies a distinction still exists in practice between those which have the centromere somewhere near the middle and those in which it is very close to one end. The former we shall call *metacentric*, the latter *acrocentric*.*

In acrocentric chromosomes the minute 'second arm' is theoretically important, but since it is usually genetically inert it is often neglected from the standpoint of formal genetics. Thus, although the number of chromosome arms in a complete chromosome set is probably always twice the number of chromosomes, it is frequently convenient to consider only the longer arms, as if each metacentric had two but acrocentrics only one. In those grasshopper species which have all their chromosomes of the acrocentric type the 'second limbs' are not necessarily the same size in all the members of the chromosome set (Coleman, 1943).

Metacentric chromosomes are usually V-shaped at metaphase and anaphase while acrocentric ones are rod-shaped, the little region which forms the second arm being usually invisible. Nearly all chromosome limbs are somewhat club-shaped at metaphase, being slender near the centromere and thicker towards the distal end.

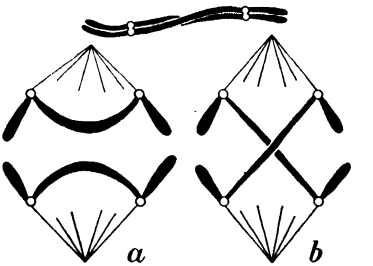
Some species of animals have all their chromosomes of one kind, acrocentric or metacentric, while in others some chromosomes are of one type some of the other. In some whole groups the acrocentric type is completely unknown. There seems to be a general uniformity about the morphology of the centromeres in a given species: although the chromosomes may be of very different sizes the centromeres are all alike in size and appearance.

Some authors have adopted a threefold division of chromosomes into 'V-shaped', 'rod-shaped' and 'dot-shaped', but the latter are merely small acrocentrics or metacentrics. Another point which has caused some confusion is that some chromosome limbs in a metaphase 'plate' may be curved or sickle-shaped while others are straight: it is probable, however, that this is merely an indication that we are dealing with flexible rods and not rigid bodies; thus a

* The term *telocentric* (formerly used by the author in the same sense as *acrocentric*) is best reserved for chromosomes which have been broken through the centromere, so that the latter has become strictly terminal. Such chromosomes have been studied in maize by McClintock (1941*b*) and Rhoades (1940); they are unable to function normally and hence cannot become permanent features of the chromosome set.

particular chromosome limb may be straight in one cell and curved in the next, and no particular importance should be ascribed to these variations in appearance.

Much of our knowledge about the functions of the centromere has been derived from a study of chromosomes which have been exposed to X-rays. It is possible by irradiation to break chromosomes transversely; after fragmentation of several chromosomes in the same nucleus the pieces may spontaneously join up again to produce 'compound' chromosomes, the parts of which are derived from different members of the original set. In this way one can artificially obtain chromosomes which contain more than one centromere. It has been shown by Mather and Stone (1933) and by many subsequent workers that bicentric or polycentric chromosomes produced in this way do not persist indefinitely in a tissue or an organism. Sooner or later a division occurs in which two centromeres in a single daughter chromosome pass to opposite poles at anaphase. The intermediate region of the chromosome is then stretched on the spindle (see Text-fig. 2); either it breaks or the two telophase nuclei are prevented from separating, thus giving rise to a binucleate cell.



Text-fig. 2. Diagram showing two different methods of orientation of a dicentric chromosome on the mitotic spindle. In *b* the daughter chromosomes are being stretched and will probably break at a slightly later stage.

Acentric chromosomes which have been produced by irradiation likewise cannot become permanent members of the chromosome set, since they fail to become attached to the spindle, and there is no mechanism which controls their division or passage to the daughter nuclei. They usually get left in the cytoplasm and eventually degenerate, being probably attacked by proteolytic enzymes from which the other chromosomes are protected by the nuclear membrane and nuclear sap (Mather and Stone, 1933; White, 1935*b*; Carlson, 1938, 1941).

In some groups of animals centromeres have never actually been seen, so that their very existence is still in doubt. In cases where the chromosomes are very small we should hardly expect to see the centromeres; but in certain orders of insects the chromosomes are quite large and yet no centromeres can be observed. This is notably the case in the Heteroptera, Homoptera and Lepidoptera. The chromosomes of these orders seem to be very highly nucleinated, so that at metaphase they are usually short rods or almost spherical and show no detailed structure of any kind. Where chromosomes exist which are longer than their own diameter (the *X* chromosome of the heteropteran *Protenor*, described by Schrader (1935), is an example) they show no point of bending which would indicate the position of the centromere, and even at anaphase the two halves of

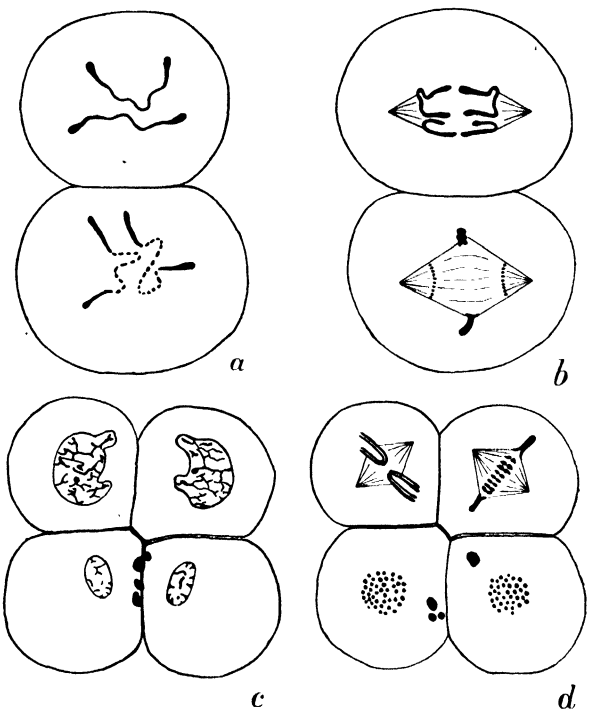
the chromosome keep parallel to one another and to the equatorial plane as they pass to the poles (as if the whole length of the chromosome were attached to the spindle).

Various interpretations of these chromosomes which do not show centromeres have been put forward. On the one hand, we may regard them as monocentric chromosomes which do not differ essentially from those of other groups, but in which the centromeres are obscured by the large amount of nucleic acid or other accessory material. This is the most satisfying attitude to adopt, from the point of view of logical simplicity; on the other hand, it is possible to assume that these chromosomes are polycentric, i.e. that they possess numerous centromeres at intervals along their length. It is now known that this type of chromosome exists in the nematode *Ascaris megalocephala*, and it may of course be found elsewhere. If the longer chromosomes of the Heteroptera were polycentric that would explain why they tend to keep parallel as they pass to the poles at anaphase, but it would not explain why the centromeres are invisible, at any rate in ordinary preparations. Schrader (1935) was led by his observations on *Protenor* to adopt a third hypothesis, namely, that the chromosomes of these groups of insects possess no discrete, individualized centromeres, the function of attachment to the spindle being diffused over the whole surface of the chromosome. It must be admitted that in the Homoptera and Heteroptera the whole body of the chromosome always seems to be attached to the side of the spindle. Geitler (1937, 1938*a*, pp. 21–2) has suggested that one should not assume that the chromosomes of one or more insect orders have a radically different structure from those of all other animals and plants until more definite evidence is forthcoming.

An attempt to analyse the structure of some homopteran chromosomes by experimental means has been made by Hughes-Schrader and Ris (1941). These workers irradiated scale insects of the genus *Steatococcus*; they were able to fragment the chromosomes so that the number of pieces present was much greater than the original number of whole chromosomes. Nevertheless, all portions, however small, formed spindle components at mitosis; moreover, they were apparently able to pass through several cell divisions successfully. These rather surprising results would seem to suggest that the *Steatococcus* chromosomes (and probably those of other Homoptera and Heteroptera) are polycentric or have a 'diffused' centromere activity, as suggested by Schrader. If the chromosomes of the Homoptera and Heteroptera did really lack definite centromeres we should expect them to obey quite different laws from those which govern the evolutionary transformations of other chromosomes. So far, there is no indication that this is the case (see Chapter VIII). It is, of course, possible that the difference in structure between homopteran and 'normal' chromosomes is not as profound as it appears at first sight. Perhaps many chromosomes which we ordinarily think of as having localized centromeres

really have a 'diffused' centromere activity which reaches a maximum, so to speak, at one point along the length of the chromosome.

We have already referred to the case of *Ascaris megalocephala*, in which polycentric chromosomes are undoubtedly present. There are two varieties of this species, in one of which there are two chromosomes in the germ-line cells, while in the other there are four. The haploid numbers of the two forms are thus 1 and 2. It has, however, been known since the time of Boveri (1887, 1892, 1909) that in both varieties a peculiar fragmentation of these chromosomes takes place during certain of the cleavage divisions. At the first cleavage division

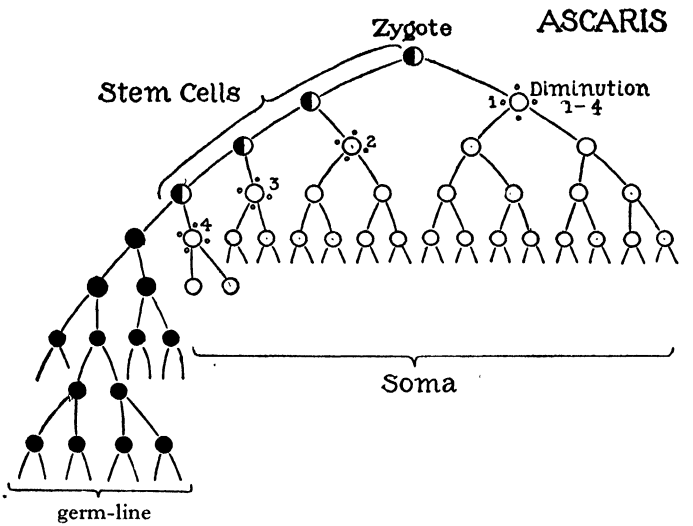


Text-fig. 3. *Ascaris megalocephala* var. *univalens*. Cleavage divisions. *a* = metaphase and *b* = anaphase of second cleavage. In *b* the chromosomes are undergoing diminution in the lower cell, but not in the upper one, which will give rise to the germ-line. *c* = telophase of second cleavage with 'eliminated' chromatin in the two lower cells. *d* = metaphase of third cleavage division; the top left-hand cell will form the germ-line, elimination is taking place in the top right-hand cell. From Boveri, redrawn.

and in all the subsequent divisions of those cells which are destined to give rise to the germ-line the metaphase chromosomes are elongated bodies whose middle region usually forms a characteristic zigzag inside the spindle, while the club-shaped ends project out into the cytoplasm (Text-fig. 3). Sometimes the middle

region can be seen to be made up of stainable segments alternating with non-staining regions that probably represent the centromeres.

In the second to the fifth cleavage mitoses in all those cells which will form somatic tissues each of the 2 or 4 chromosomes (according to the variety) breaks up into a number of portions. The club-shaped end-regions are left in the cytoplasm, where they ultimately undergo degeneration. The behaviour of these end-regions is thus similar to that of acentric fragments which have been produced experimentally; possibly their fate indicates that they are left without centromeres when fragmentation takes place.



Text-fig. 4. *Ascaris megalocephala*: diagram to show the divisions at which diminution takes place. From Wilson (1925).

The short segments derived from the middle parts of the germ-line chromosomes henceforth behave as entirely separate chromosomes. The exact number of these small bodies is not yet known with certainty; it seems that it is different in the two varieties, and it is probably not the same in the two sexes. Thus var. *univalens* is stated to show 52–72 chromosomes in its somatic cells while *bivalens* has 62–144 (Kautzsch, 1912, 1913; Guieysse-Pellissier, 1909; Geinitz, 1915; Walton, 1924). It is highly probable that the observed variations in somatic chromosome number were due to faulty technique.

Whatever the explanation of the fragmentation process it is clear that the germ-line chromosomes are polycentric, with many centromeres distributed at intervals along the middle regions. The zigzagging of these portions of the chromosome is a result of this multiple attachment, the chromosome being bent

at some of the centromeres (Bonnevie, 1913). At anaphase the middle segments of the germ-line chromosomes move bodily apart, keeping parallel to one another, while the end-regions drag behind (Text-figs. 3, 4). As far as is known, all the centromeres of each daughter chromosome always pass to the same pole of the spindle at anaphase; presumably they are so close together that there is no possibility of one chromatid becoming twisted round the other between two successive centromeres.

When the germ-line chromosomes of *Ascaris megalocephala* are fragmented by means of X-rays, any piece from the middle region becomes attached to the spindle at the succeeding division (White, 1936*b*).

The behaviour of the club-shaped end-portions of the chromosomes during cleavage suggests that they may be genetically 'inert' and therefore not necessary for the differentiation of the somatic tissues. If they do contain any active genes, perhaps they are ones which have a special function in the cells of the germ-line.

In *A. lumbricoides*, which has a somatic number of 43 in the male and 48 in the female (Edwards, 1910; Walton, 1924), it has been shown by Bonnevie (1902) that the ends of the chromosomes are cast off in exactly the same way during the cleavage divisions of the somatic nuclei; but in this species there is no fragmentation of the middle part, so that the chromosomes are probably monocentric and the same number of bodies is present in soma and germ-line. Walton (1924) states that in all members of the family Ascaridae an elimination process takes place during cleavage, whereas in other families of nematodes nothing of the kind has been observed. Whether the monocentric or the polycentric type of chromosome is primitive in the group is, of course, unknown—probably the former.

Many chromosomes at late prophase or metaphase exhibit non-staining gaps which are constant in position. It is an open point whether these *secondary constrictions* (as they have been called, to distinguish them from the *primary constriction* associated with the centromere) are merely unusually long interchromomere connections, or whether they are really different from the ordinary 'internodes'. Secondary constrictions may be present in one or both arms of a metacentric, and in some instances more than one may be present in a single chromosome arm. If a secondary constriction is situated very near to the end of a chromosome the small knob-like portion beyond it may be called a 'satellite' or 'trabant' (terms used especially by botanical cytologists).

Many, but not all, secondary constrictions bear nucleoli, and may be regarded as containing nucleolar organizers. Thus in *Drosophila melanogaster* secondary constrictions occur in the proximal part of the *X* chromosome and in the short arm of the *Y*; both these bear nucleoli (Kaufmann, 1933, 1934, 1938; Heitz, 1933 *a*, *b*). On the other hand, the 'left' limb of the IInd chromosome has a secondary constriction which does not bear any nucleolus. Many chromosomes

in Orthoptera bear small vesicular outgrowths which are probably similar to nucleoli; these 'chromomere vesicles' (Corey, 1939) are constant in position and probably arise from internodes of the same kind as the secondary constrictions.

It has long been known that certain chromosomes or chromosomal regions become nucleinated to a greater or less extent than the rest of the chromosome set at particular stages of mitosis and meiosis. This phenomenon has received the name of *heteropycnosis* (differential thickening), and it may be manifested in two different ways; if the region in question remains under-nucleinated we



Text-fig. 5. Negative heteropycnosis of the *X* chromosome in a spermatogonial prophase and metaphase of *Locusta migratoria*. Drawn from irradiated material, hence various translocations present. From White (1935*b*).

may say that it is negatively heteropycnotic, while if it is over-nucleinated we may speak of positive heteropycnosis. Both conditions appear to be due to a particular type of protein framework which is more (or less) active in capturing nucleotide molecules than the rest of the chromosome set. Caspersson (1941) has shown by spectroscopic methods that there really is a chemical difference between the proteins of the heteropycnotic and non-heteropycnotic regions. It should be pointed out, however, that the degree of heteropycnosis of a particular chromosome often varies in a characteristic way throughout its cycle. Thus the same chromosome may be negatively heteropycnotic at one stage and positively heteropycnotic at another.

This is what actually happens to the *X* chromosome in the short-horned grasshoppers (Acrididae) and also in the crickets (Gryllidae). During the early spermatogonial divisions in the testis this chromosome appears as a thin thread which even at metaphase has an irregular 'woolly' outline; it never becomes fully nucleinated like the other chromosomes, and looks like an early or mid-prophase chromosome right through the metaphase stage (Text-fig. 5). In the later spermatogonial divisions this difference between the *X* chromosome and the autosomes disappears, so that by the time the last spermatogonial mitoses are reached the *X* becomes nucleinated to the same extent as the autosomes. During the prophase of the first meiotic division the *X* chromosomes become

strongly positively heteropycnotic. At this period they are great thick sausage-shaped bodies which contrast sharply with the thin and often weakly staining autosomes. Eventually, by the time the metaphase of the first meiotic division is reached, there is little difference between the *X* chromosome and autosomes—indeed, the *X* may have already begun to undergo denucleination, so that it is once more negatively heteropycnotic. During the interkinesis and in the spermatids the *X* is almost always positively heteropycnotic again (Text-fig. 6).

This reversibility seems to be a very general feature of heteropycnosis. Thus Darlington and La Cour (1940) and Darlington (1942) have pointed out that, in many plant chromosomes, regions which are positively heteropycnotic during the resting stage will show up as negatively heteropycnotic segments at metaphase in material that has been kept at a low temperature for some time before fixation, and the same may be true in some groups of animals (Callan, 1942). On the other hand, some heteropycnotic chromosomes do not naturally show a reversal of behaviour, although perhaps they might be made to do so under appropriate experimental conditions. Thus the *X* chromosomes of the long-horned grasshoppers (Tettigoniidae), unlike those of the crickets and short-horned grasshoppers, are always positively heteropycnotic and do not undergo a reversal in the course of spermatogenesis.

There is no evidence that the nucleic acid present in heteropycnotic chromosomes or regions is in any way different from that present in 'normal' regions. Differences in staining reactions have sometimes been reported, but such differences are notoriously unsafe guides to the chemical nature of a cell organ. In most instances variation in the intensity of chromosomal staining reactions can probably be ascribed to differences in the amount of nucleic acid rather than to the presence of more than one kind of acid. It is also probable that the water content (degree of hydration) of the chromosomes varies throughout the nuclear cycle, and this may also affect the intensity of staining.

In some organisms it is clear that more than one type of heteropycnosis exists. Thus in the Acrididae, mentioned above, certain regions of the autosomes always show positive heteropycnosis during the prophase of meiosis; but they differ from the *X* in not being negatively heteropycnotic during the early spermatogonial divisions. There is usually one autosome in these grasshoppers in which the heteropycnotic regions are especially developed so that the chromosome is very conspicuous at meiosis, and may even resemble that *X* in its degree of nucleination. On account of its appearance this autosome has received various special names (*megameric* or *precocious chromosome*). At an early spermatogonial metaphase, however, it is indistinguishable from the other autosomes (Janssens, 1924; McClung, 1928; Carlson, 1936; White, 1940*a*).

We are thus forced to the conclusion that there are two kinds of heteropycnosis in the chromosome set of these grasshoppers—a kind that undergoes reversal in the course of spermatogenesis and a kind that does not. It seems clear that

more than one type of protein framework may give rise to heteropycnosis (White, 1940*a*, 1942*a*).

It will be convenient to use the term *heterochromatic* to describe any chromosomal region which becomes heteropycnotic at some stage in its cycle. Chromosomal regions which never under any circumstances show heteropycnosis may be called *euchromatic*. Most chromosomes probably contain segments of both kinds, the euchromatic ones being longer in the aggregate, although either may predominate in particular chromosomes. Certain sex chromosomes (see Chapter XI) appear to be entirely heterochromatic, although they may perhaps contain euchromatic segments that are too short to be detected by ordinary cytological means.

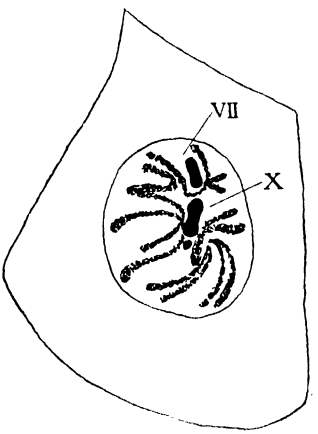
In *Drosophila melanogaster* all the chromosomes have heterochromatic regions round the centromeres, that of the *X* being especially long. It is probable that there are also short heterochromatic segments at the distal ends of the chromosomes, and more minute ones may be distributed at intervals along the rest of the chromosome bodies (Prokofieva-Belgovskaya, 1937*b*, 1938). This alternation of the two kinds of protein framework, with large heterochromatic regions around the centromeres and smaller ones at the other ends of the chromosomes, is also found in most, if not all, orthopteran chromosomes as well as in many other insects. It is therefore of very general and perhaps universal occurrence. The 'chromomeres' studied by Wenrich (1916) in the grasshopper *Phrynotettix* (and rightly interpreted by him as evidence for the individuality of the chromosomes, which was still disputed at that time) were probably heterochromatic segments or 'blocks' rather than true chromomeres.

In *Drosophila* the heterochromatic segments contain few or no active genes. It has long been known that the *Y* chromosome, which is completely heterochromatic, is genetically 'inert', and in recent years it has been found that the other heterochromatic regions are also inert. It should be pointed out, however, that inertness is rarely complete. Thus the *Y* chromosomes of *Drosophila* species are not absolutely necessary to the life of the fly, since males lacking them are viable; but they do contain a number of regions which, together, ensure the fertility of the male. It is not definitely known how many of these regions there are in *D. melanogaster*, nor whether they should be regarded as 'genes' in the ordinary meaning of the term; but the absence of any one of them renders the fly infertile (Neuhaus, 1939). In some species of *Drosophila*, at any rate, the *Y* also has more general effects, and may influence the viability of the organism (see Chapter VII).

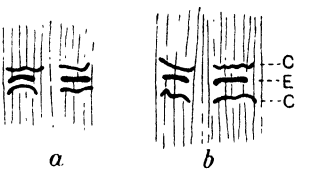
On *a priori* grounds one would expect that any part of the chromosome set that was completely useless would have been lost in the course of phylogeny: the very fact that 'inert' regions and chromosomes have been preserved suggests that they play some role in the life of the cell, even if that role is not a genetical one in the usual sense. In some species of animals and plants so-called super-

numerary chromosomes may be present in some individuals but not in others (see Chapter VI)—they are probably inert or nearly so.

In *D. melanogaster* it is possible to obtain in genetical experiments female flies which contain a *Y* in addition to the normal chromosome set. It has been shown spectroscopically by Caspersson and Schultz (1938) and Schultz (1941*b*) that the oocytes of such females contain larger quantities of nucleotides than the oocytes of normal females. This seems to suggest a possible role for the heterochromatic regions—they may serve as 'factories' of nucleic acid (and possibly of protein molecules as well). If this is so they are to be regarded as portions of the chromosome set which are concerned with a more generalized and less specific part of the biochemical activities of the cell than the genes,



Text-fig. 6. Spermatocyte of the grasshopper, *Mecostethus grossus*, between the first and second meiotic divisions, showing the *X* chromosome and the heteropycnotic VIIth autosome. From White (1937*b*).



Text-fig. 7. Cleavage divisions in the mite, *Pediculopsis graminum*. *a* = early anaphase, *b* = mid-anaphase. *C* = chromosomes, *E* = elimination bodies. From Cooper, redrawn.

each of which is probably concerned with a highly particular and specific reaction or chain of reactions. This conception is in agreement with the results of Caspersson (1941) who reports that the framework of the heterochromatic regions is made of much simpler proteins than that of the euchromatic segments.

In some species of animals a certain amount of material is cast off from each chromosome at anaphase in the form of a definite body which remains in the middle of the spindle as the daughter chromosomes pass to the poles. These 'elimination bodies' degenerate during telophase and ultimately disappear from view. It is probable that this is merely a special case of the denucleination which takes place at the end of every nuclear division; but it is such a striking phenomenon that it seems to deserve a special mention. Perhaps the best example of an organism in which elimination bodies are formed is the mite

Pediculopsis graminum, studied by Cooper (1939). The low number of chromosomes (the diploid number is 6) renders the details unusually clear. The elimination process takes place during both meiotic divisions in the egg as well as during the cleavage mitoses. It has been shown that the elimination bodies are not stainable by the Feulgen technique, although they do stain with all the ordinary nuclear dyes. They are thus probably masses of nucleic acid in which the desoxyribose part of the molecule has been replaced by some other type of sugar. It is not known whether the elimination bodies have any protein framework.

It is interesting to note that in another species of mite closely allied to *Pediculopsis*, namely, *Pediculoides ventricosus*, no elimination bodies appear to be formed (Pätau, 1936).

In many of the Lepidoptera (Seiler, 1914, 1923; Kawaguchi, 1928; Fogg, 1930) and Trichoptera (Klingstedt, 1931) elimination bodies similar to those of *Pediculopsis* are formed during the meiotic divisions in the egg. As in *Pediculopsis* the material which is cast off is Feulgen-negative. Owing to the large number of chromosomes present the details are not so clear, and all the elimination bodies (usually about 30) may appear clumped together as a great plate of 'chromatin' lying midway between the two groups of anaphase chromosomes.

In the earlier text-books of cytology the elimination of masses of nucleic acid from the chromosomes was confused with the casting off of the ends of the chromosomes which occurs in *Ascaris* and with the loss of whole chromosomes that occurs in the embryology of certain cecidomyid flies such as *Miastor* (see p. 208). In reality the three phenomena have little in common with one another —the casting out of material that occurs in *Pediculopsis* and the Lepidoptera does not involve the loss of any segment of the chromosome set and is thus totally different from the *Ascaris* and *Miastor* phenomena.

The spatial arrangement of the chromosomes at metaphase has been the subject of an extensive literature. Where the different chromosomes of a species are all the same size it is, of course, not possible to distinguish them, and any regularity of arrangement which may exist is concealed. Where, on the other hand, there is a considerable range in size the larger chromosomes nearly always occupy the periphery of the metaphase 'plate', the smaller ones lying in the centre (Text-fig. 73). This is particularly the case where the chromosomes are relatively thin at metaphase and of very different lengths, as they are in most vertebrates; where the chromosomes are condensed and highly nucleinated, so that they appear as spheres of different sizes, the tendency for the smaller ones to occupy a central position is usually not so well marked (Text-fig. 74). Where the chromosomes are all long and thin (as they are in most Urodeles) they may all occupy peripheral positions, leaving a gap in the middle. These characteristic arrangements are no doubt due to the mechanical conditions of the developing spindle at prometaphase.

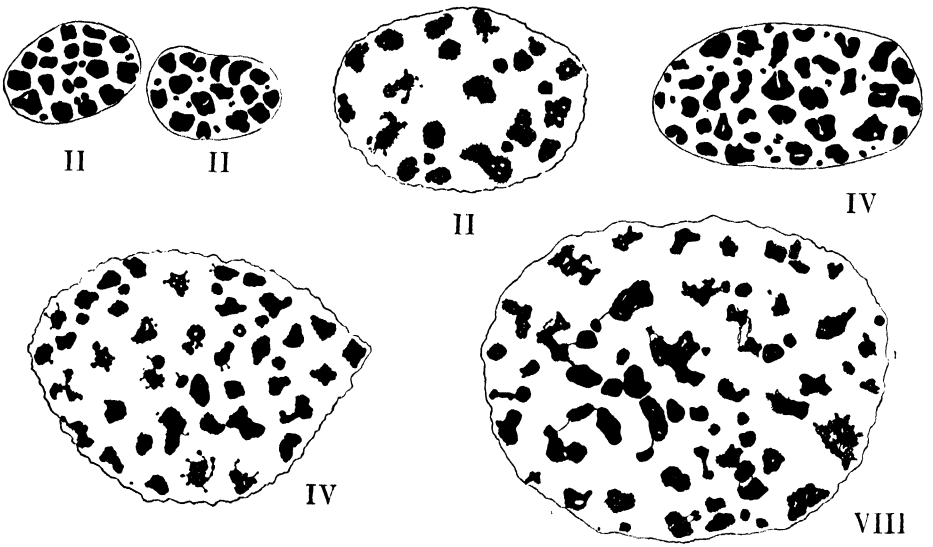
In no organism are the relative positions of the chromosomes at metaphase absolutely fixed—they vary from cell to cell. Nevertheless, Dobzhansky (1936*a*) has shown that in an organism like *Drosophila*, with considerable size differences between the chromosomes and a low chromosome number, the relative positions tend to remain the same from one division to the next—or at any rate that 'sister cells' show the same arrangement more often than can be accounted for by mere chance.

Usually there is no particular tendency for homologous chromosomes to lie near together or far apart, or if such a tendency exists it is not strongly marked. In the dipterous flies, however, the homologous chromosomes nearly always lie roughly parallel to one another throughout the somatic and gonial divisions. This phenomenon, known as *somatic pairing* (although it also exists in the nuclei of the germ-line), is apparently due to a force of mutual attraction between the chromosomes—a force which is identical with (or, at any rate, similar to) the one responsible for meiotic pairing. It is, of course, not certain that the somatic pairing force is completely absent in other groups of organisms—but it is certainly far more marked in the Diptera than in any other group. No suggestions can be made at present as to the reason for this peculiarity of the Diptera. The closeness of association between homologous chromosomes seems to be at a maximum during prophase; at first the threads are almost in contact throughout their length, but by metaphase they have separated somewhat, although they still lie parallel, a short distance away from one another. The declining intensity of the somatic pairing force during prophase may be due to the gradual assumption by the chromosomes of a spiral form, since it is not possible for two compact spirals to approach one another so that all the corresponding loci are in contact.

Speculation as to the nature of pairing forces between chromosomes would be beyond the scope of this book. They are undoubtedly highly specific, that is to say exerted between each pair of homologous chromomeres in the nucleus. It is difficult to conceive of any physical analogy to a system of several thousand different and specific attractions exerted across relatively considerable distances in a fluid medium. Some ingenious speculations as to the possible physical nature of the pairing force have, however, been recently put forward (Muller, 1941; Fabergé, 1942). The somatic pairing force of the Diptera is clearly not confined to pairs of chromosomes, since in triploid and tetraploid cells the chromosomes are 'paired' in threes and fours. In a small percentage of nuclei somatic pairing fails to occur in one or more pairs of chromosomes.

It has frequently been stated that, apart from special cases like *Ascaris* and *Miastor*, the number of chromosomes is the same for all tissues of an organism. In insects, at any rate, this is certainly not so. Most of the cells of an adult insect have lost the power to divide by mitosis, but their nuclei are highly polyploid, different degrees of polyploidy being characteristic of particular tissues. The chromosomes of resting nuclei in insects are frequently irregularly

shaped masses which fix sufficiently well to be counted. A good example of this state of affairs is the investing epithelium of the testis in the Orthoptera. The nuclei of this tissue are flat 'pancake-shaped' bodies, and in fixed preparations contain irregular masses of 'chromatin' which correspond to the diploid, tetraploid and octoploid numbers of the species (Text-fig. 8). Since no mitosis occurs in these cells after an early stage in development it is probable that the

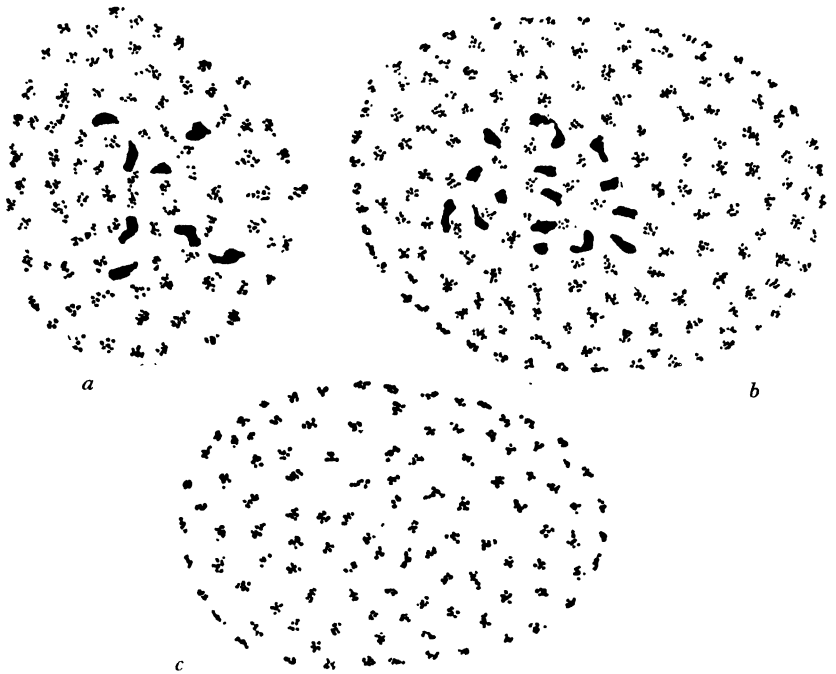


Text-fig. 8. Endopolyploidy in nuclei of the testis sheath in the locust, *Schistocerca gregaria*. The smallest nuclei (II) are diploid and have 23 chromosomes, the medium-sized ones (IV) have 46 and the largest ones (VIII) approximately 92.

tetraploid and octoploid nuclei have arisen by a process of *endomitosis*, in which the chromosomes split and divide within the nucleus without the formation of a spindle or any of the usual apparatus of a cell division. In some other insect tissues this process has been studied in detail. Thus Painter and Reindorp (1939) were able to observe the whole cycle of endomitosis in the nurse cells of the ovary in *Drosophila*. Here the chromosomes pass through a relatively normal prophase, i.e. they become progressively nucleinated. They then split into halves inside the nuclear membrane, without any spindle formation. Finally, a denucleination occurs, similar to that which takes place in the telophase of an ordinary division, the chromosomes gradually staining more and more faintly, until the diffuse 'resting stage' appearance is reached. Every time this process is repeated the nuclear volume increases.

Geitler (1937, 1938*b*, 1939 *a*, *b*) has made a special study of the endomitotic nuclei in the somatic tissues of various Heteroptera, particularly the pond-skaters of the genus *Gerris*. Here the chromosome number is 21 in the males,

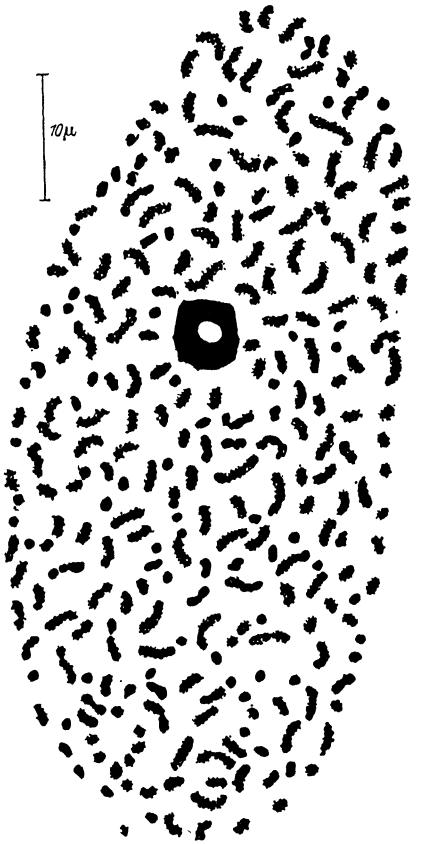
the odd chromosome being an *X* which is conspicuously heteropycnotic in the somatic nuclei of some species such as *Gerris lateralis*, but not in those of others such as *G. lacustris*. The difference between the *X* chromosomes of these two species probably depends on the extent of the heterochromatic regions.



Text-fig. 9. Endopolyploidy in the pond-skaters, *Gerris lateralis* and *G. lacustris*. *a* = octoploid nucleus from testis-septum cell of *G. lateralis*; *b* = 16-ploid nucleus from the same source; *c* = 16-ploid nucleus from testis-septum of *G. lacustris* (*X*'s not distinguishable from autosomes). From Geitler (1937).

Owing to the heteropycnosis of the *X*'s in the somatic nuclei of *lateralis* it is possible to distinguish them from the autosomes and count them. In this way Geitler has shown that the giant nuclei in the salivary glands are very highly polyploid; some of them are 512-ploid, while the largest were estimated from their volume to be 1,024-ploid or even 2,048-ploid (it is not possible to count the *X*'s in these largest cells). The much-branched nuclei in the spinning glands of the Lepidoptera and Trichoptera (Vorhies, 1908) probably have a similar structure. The whole process of histological differentiation in insects seems to be intimately bound up with this phenomenon of endopolyploidy, each organ and tissue having its own characteristic degree of ploidy, some being entirely composed of one type of cell, while others are mosaics of cells with different

multiples of the fundamental diploid number. To what extent endopolyploidy occurs outside the Insecta is not known at present, but there are indications that it may be fairly widespread in many groups of animals. In the vertebrates conditions are not favourable for counting the chromosomes in somatic resting nuclei, but measurements of nuclear volumes (Jacobj, 1925, 1935) suggest that in some mammalian tissues several size classes of nuclei exist, and it is possible that these correspond to different degrees of endopolyploidy.



Text-fig. 10. Endopolyploid nucleus (128- or 256-ploid) from the salivary gland of a male *Lygaeus saxatilis* (Heteroptera). The large black mass is the result of the 'pairing' of many heteropycnotic *Y* chromosomes to form a chromocentral mass. From Geitler (1939*a*).

In the larvae of mosquitoes (*Culex*, *Anopheles* and other genera) it has been known since the work of Holt (1917) that many of the somatic cells are polyploid. Unlike those of most other endopolyploid cells, however, these nuclei periodically pass into a real metaphase stage, in which the chromosomes are arranged in a flat 'plate'. The diploid number in these flies is 6, but cells with 12, 24, 48 and 96 chromosomes are frequent in the gut epithelium of the larvae, and have been studied by Berger (1936, 1937, 1938). This author claims that during the pupal metamorphosis the cells of the iliac epithelium with the higher chromosome numbers undergo a process of 'somatic reduction' whereby the chromosome number is halved. This conclusion is not universally accepted by other workers, and it is possible that the cells with the higher numbers degenerate and are replaced by a new growth of cells which have remained diploid from the beginning.

CHAPTER III

SALIVARY-GLAND CHROMOSOMES

By studying mitotic and meiotic chromosomes in suitable organisms it is possible to obtain a very fair idea of the sequence of euchromatic and heterochromatic segments, the positions of the centromere, secondary constrictions and nucleolar organizers. The genetical results indicated, however, that the structure of a chromosome must be far more complex than could be seen, even in the largest mitotic and meiotic chromosomes. Up till 1934 there was no means of studying the finer details of chromosome structure, but since that time the discovery (or, rather, rediscovery) of the 'salivary-gland chromosomes' has provided the technique of investigation that was so urgently required. These chromosomes are enormously enlarged as compared with ordinary mitotic chromosomes; in life they are probably a hundred times longer and correspondingly thick, but the usual method of preparation involves a good deal of stretching.

Chromosomes of this kind only occur in the dipterous flies: but they are not in actual fact confined to the cells of the salivary glands—the gut epithelia, Malpighian tubules and many other tissues contain nuclei of the same general type (Makino, 1938). Nevertheless, it is usually in the salivary nuclei that these chromosomes attain their maximum size, and the normal technique of investigation consists in removing these glands from full-grown larvae and crushing them on a slide in a solution which fixes and stains at the same time. In other insect orders such as the Heteroptera, Orthoptera, etc., the nuclei of the salivary-gland cells, although probably endomitotic, do not show any special peculiarities, and their chromosomes are not suited for detailed study. In the following account whenever we speak of salivary-gland chromosomes we mean those of the Diptera.

Since the salivary chromosomes are usually longer than the diameter of the nucleus they are tangled up inside the nuclear membrane during life. The crushing ruptures the membrane and spreads out the chromosomes in one plane so that they can conveniently be studied. In a healthy living nucleus the mass of tangled threads probably fills the whole of the nuclear cavity in some species, but even a very slight degree of asphyxiation is sufficient to cause the chromosomes to shrink, expelling a large quantity of fluid at the same time (Buck and Boche, 1938).

Each salivary-gland chromosome is a transversely striated structure, consisting of a sequence of dark-staining bands separated by non-staining internodes. In flies of the same genetic constitution the order of the bands (which can be recognized individually since they differ in detailed structure) is always the same. Structural rearrangements of the chromosome set, such as inversions,

deletions, etc., can thus be actually seen under the microscope instead of being merely inferred from genetical experiments. It has proved extremely fortunate that the organism (*Drosophila*) upon which most genetical work has been carried out should have been one belonging to the only group in which 'salivary' chromosomes occur. Not all the families of the Diptera possess thick salivary chromosomes suitable for cytogenetic analysis: in many genera the salivary-gland nuclei are relatively small and the chromosomes within them thin and weakly staining threads which merely show an indistinct chromomeric structure like that seen in very young salivary nuclei of *Drosophila* or *Chironomus* larvae. In the mosquitoes (Culicidae) E. Sutton (1942) has demonstrated the presence of chromosomes of the salivary-gland type in various somatic tissues, but they are thin and unsuited for detailed cytogenetic study, although their structure might be used for the discrimination of subspecies and races in the medically important Anophelines.

The history of our knowledge of the salivary chromosomes is, in outline, as follows: They were discovered as early as 1881 by Balbiani and were also studied by Carnoy (1884), who published a remarkably accurate figure of their structure in *Chironomus*, but who made the mistake of believing that the same type of nucleus also occurred in other insect orders. It was erroneously believed at this time that the salivary chromosomes formed a continuous 'spireme' (i.e. an endless ring tangled within the nucleus). In 1912 Alverdes gave an account of the development of the salivary-gland chromosomes from the embryo up till the late larval stage. Unfortunately, he interpreted the bands as being gyres of a spiral. Kostoff (1930) correctly regarded the banding as an expression of the linear sequence of genes in the chromosome, but did not carry the analysis any further. In 1933 Heitz and Bauer, working on *Bibio*, showed that the structures in the salivary nuclei really were separate chromosomes and not a continuous thread as the earlier workers had assumed. They further showed that these bodies were present in the haploid number, each of the great worm-like elements being formed by the intimate pairing of two chromosomes. It is probable that this pairing of the salivary chromosomes takes its origin from the somatic pairing force which is so characteristic of dipterous chromosomes (see p. 31). In some instances the homologous threads seem to be actually fused, while in other cases they are in very close contact but still distinguishable as separate strands. A slight spiralization usually seems to exist in the salivaries, the homologues being wound round one another—but they never form compact 'springs' as ordinary mitotic chromosomes do.

Painter (1933, 1934 *a*, *b*, 1935) was the first to study the salivary chromosomes of *Drosophila*, and their use in cytogenetical work really dates from that time. In 1934 Koltzov and Bridges, independently, put forward the view that the salivaries were similar in structure to prophase chromosomes which had uncoiled and divided repeatedly, without any separation of the resulting strands.

Later work has tended to show that this interpretation was, in principle, correct, although it is now clear that the salivaries are longer than can be accounted for by uncoiling alone (i.e. that a real growth in length has also taken place).



Text-fig. 11. The four salivary gland chromosomes of *Chironomus thummi*, showing the banding. Small arrows indicate the approximate positions of the centromeres. The smallest chromosome has its longer arm largely heterochromatic, the other three chromosomes have short heterochromatic regions at the tips. From Bauer (1935).

We can thus say that the salivary-gland chromosomes represent a very special case of the much more general phenomenon of endopolyploidy. Whereas in other groups of insects the growth of the chromosomes within the nucleus is accompanied by periodic splitting, so as to double the chromosome number, in the 'salivary' nuclei of the Diptera no splitting takes place, so that the chromosomes become thicker and thicker, while remaining constant in number.

Naturally it is the largest and thickest chromosomes which are most sought after for detailed cytogenetical work. In many species of Diptera the nuclei at one end of the salivary gland are larger than those at the other. Bauer's pioneer work on the detailed structure of salivaries was largely carried out on *Cryptochironomus defectus*, a species which has three extraordinarily large cells at the anterior end of each salivary gland.

Since the salivary chromosomes are usually paired throughout their length and show a chromomeric structure they are analogous in several respects to pachytene bivalents (see p. 74). By some authors (e.g. Koller, 1935; Cooper, 1938; Melland, 1942) they are referred to as *polytene* chromosomes—a term which is convenient since, as we have already seen, chromosomes of this type are not confined to salivary-gland nuclei.

The dark-staining bands in the salivary chromosomes clearly correspond to the chromomeres of ordinary mitotic and meiotic chromosomes. Each band is in reality a disc, i.e. it goes right through the thickness of the chromosome. In the thinner bands it is often possible to see that each one really consists of granules whose number (32, 64, 128, etc.) has been presumed to correspond to the degree of multiplication of the original thread. The granules of adjacent bands frequently appear to be connected by fine longitudinal threads (Text-fig. 12). If there are the same number of visible chromomeres in the two bands these threads appear to run direct from chromomere to chromomere, but if only half the usual number of chromomeres can be seen in a particular band two threads will converge on each. It has been claimed (Metz, 1935, 1939 *a*, *b*) that these apparent threads are merely 'lines of stress' which are not present in the living chromosomes, but most authorities are agreed that they do exist in life. The distance between the bands varies, i.e. some adjacent bands are situated close together, others have a longer interband space between them.

The thicker bands are considerably more difficult to analyse than those which are represented by separate dots. In the largest bands the chromomeres are closely pressed together so that they form a dense and apparently structureless disc. Where the chromomeres can still be made out they often seem to consist of a dark-staining shell with a paler centre. These 'vesicular' chromomeres are especially characteristic of the bands in the inert regions—they are often referred to as *heterochromomeres*. It is possible that the vesicular appearance is a fixation artefact. It has been shown that the thicker bands are often compound, i.e. composed of several thinner bands with very short interband spaces between them. Only after crushing and stretching the chromosomes can the full number of bands be seen separately. Even then it is doubtful whether all bands situated very close together can be resolved in ordinary 'visual' light; Ellenhorn, Prokofieva and Muller (1935) claimed to have photographed some bands with ultra-violet illumination that were not resolvable with ordinary green light.

In C. B. Bridges's (1938) map of the *X* chromosome in *Drosophila melanogaster* about 1,000 bands were identified. If the other chromosomes of *melanogaster* contain an equal number of bands per unit length the total number in the whole chromosome set would be somewhat over 5,000. The later maps of Bridges and Bridges (1939) and P. N. Bridges (1941 *a*, *b*, 1942) for the IInd and IIIrd chromosomes confirm this estimate (see Table 1). In Patterson, Stone and Griffen's (1940) less detailed maps of the *D. virilis* chromosomes somewhat under 2,000 bands appear to be shown for the whole set. No other salivary chromosome maps published up till now approach these for completeness—most of them merely show the more conspicuous banded regions imperfectly resolved.

TABLE 1. *Number of bands in the chromosome arms of* Drosophila melanogaster

(Data from P. N. Bridges, 1942 and Slizynski, 1944)

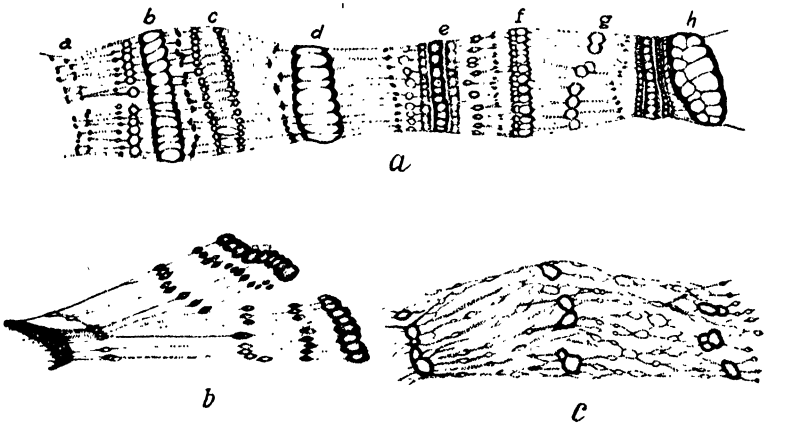
Chromosome arm	Total no. of bands	Number of doublets	No. of loci (counting doublets as single loci)
X	1,011	313	698 (18·1 %)
II *L*	803	196	607 (15·7 %)
II *R*	1,136	282	854 (22·2 %)
III *L*	884	196	688 (17·9 %)
III *R*	1,178	263	915 (23·8 %)
IV	137	49	88 (2·3 %)
Total	5,149	1,299	3,850 (100·0 %)

The appearance of the individual bands is often highly characteristic and distinctive. Some stain intensely, others much more faintly, the intensity of staining not being necessarily correlated with the thickness of the band. It is thus probable that the ratio of nucleic acid to protein varies somewhat—dark-staining bands having a higher nucleic acid content than lighter ones.

It has been calculated by Astbury and Bell (1938*a*) that the long molecules of nucleic acid are probably about 6,000 A. (0·6 μ) long. Since this is about the thickness of a medium-sized band, Demerec (1942) suggests that the width of each band is correlated with the length of the nucleic acid molecules, thicker bands containing longer molecules than thin ones. There is nothing inherently improbable in the idea that the degree of polymerization of nucleic acid varies from one part of the chromosome to another.

Some idea of the detailed appearance of the banding in salivary chromosomes of *Drosophila*, *Simulium* and *Chironomus* can be obtained from Text-figs. 11, 12, 16, 21 and 22. Very often two bands of identical thickness and appearance follow one another with only a very short space between. The interpretation of these *doublets*, as they are called, has given rise to some trouble. It is clear that

they are far too common to be accounted for by chance. In many cases the edges of the two bands forming a doublet are fused together so as to produce a biconvex lens-shaped capsule consisting of an outer shell of staining material with a non-staining space in the centre. When seen in optical section these capsules have the shape of a very narrow letter **O**.



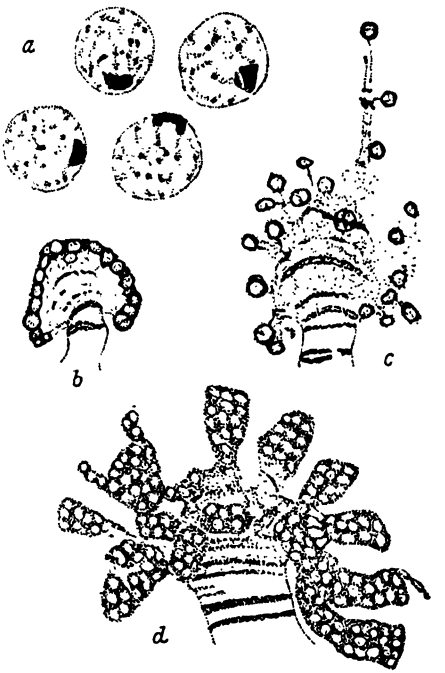
Text-fig. 12. Detailed structure of salivary chromosomes in *Simulium virgatum*. *a* = surface view of a euchromatic region showing the appearance of the bands, some of which are made up of small, distinctly staining chromomeres, while others are composed of large, crowded 'vesicles'; *b* = a small portion of the same, crushed in mounting; *c* = a piece of the heterochromatic, 'spread-out' region, in which the chromomeres are not united to form regular bands. From Painter (1939).

It is now generally believed that doublets and capsules are to be regarded as single genes rather than as pairs of genes. In irradiation experiments the two halves of a doublet have never been separated by breakage: it is thus probable that the protein framework of many genes is symmetrical, consisting of a central region with no affinity for nucleic acid and regions on either side that pick up or synthesise nucleic acid molecules of exactly the same length so that two identical bands are formed with a short region devoid of nucleic acid in between. Owing to the homology of the two bands they frequently 'pair' at the edges, so giving rise to a 'capsule' (Demerec, 1942). If we consider the doublets as single loci the total number of loci in *Drosophila melanogaster* is approximately 3,800 (P. N. Bridges, 1942).

The salivary chromosomes are not of uniform diameter throughout their length: certain 'waist-like' regions are characteristically thinner than others, while some segments are enlarged so that they appear as localized swellings (known as 'puffs' or 'bulbs'). The diameter of the chromosome at a particular level does not seem to bear any relation to the type of band present there: thus enlarged regions may bear either thick or thin bands or both.

The stretching and crushing which the chromosomes undergo during the making of the preparation frequently cause them to break in one or more places, and it has been found that the points of breakage are often constant in position, i.e. there are certain 'weak places' in the protein framework. In one species of *Sciara* (*S. reynoldsi*) there is a chromosome which undergoes fragmentation into two portions during life in the salivary nuclei (Metz, 1939*d*, 1941).

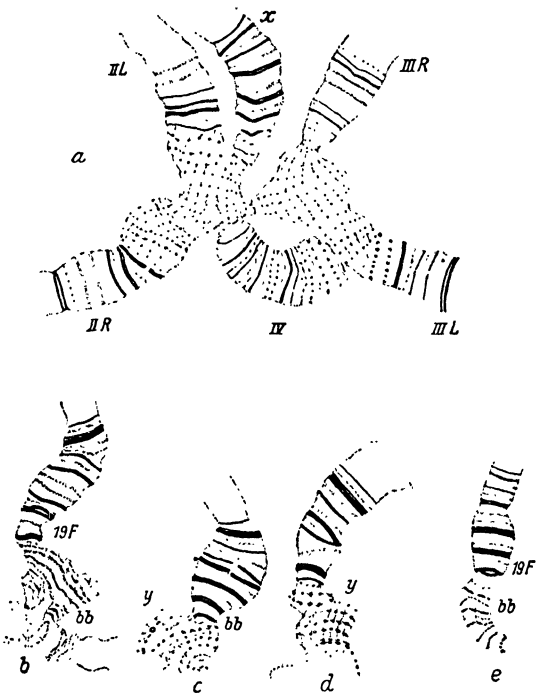
The heterochromatic regions of the salivary chromosomes are much shorter, relative to their length at mitosis, than one would expect them to be. Thus in *Drosophila melanogaster* about one-third of the total length of the *X* chromosome is heteropycnotic at mitosis: but the same region forms considerably less than one-tenth of the length of the chromosome in the salivary nuclei. This inert segment of the salivary *X* chromosome contains only about five or six indistinct bands of peculiar structure made up of 'heterochromomeres' which stain faintly and are not joined together laterally in a regular manner so as to form well-defined bands (Muller and Prokofieva, 1935). The *Y* chromosome has a similar structure in the salivary nuclei, being so short that in the early work on salivary chromosomes it was overlooked. Later Prokofieva-Belgovskaya (1935 *a*, *b*, *c*, 1937*a*) showed that it was represented by a small body containing about eight indistinct bands. The heterochromatic part of chromosome II which lies between the centromere and the secondary constriction forms about one-tenth of the whole chromosome at mitosis, but the same region is represented only by a single band in the salivary chromosome (Hinton, 1942).



Text-fig. 13. Heterochromatin in *Trichotanypus pectinatus*. *a* = small somatic nuclei showing chromocentral masses; *b*–*d* = ends of salivary chromosomes showing the heterochromatic structures; *b* = chromosome III; *c* = chromosome IV; *d* = chromosome V. From Bauer (1936*b*).

All the heterochromatic regions round the centromeres are fused together in the salivary nuclei of *Drosophila* species to form a common mass known as the chromocentre. The heterochromomeres seem to attract one another in a non-specific manner, so that they are all irregularly 'paired' in a rather disorganized way. The *Y* chromosome is completely included in the chromocentre. Thus if we crush a salivary nucleus of *D. melanogaster* the chromosomes consist of six

strands radiating out from a common mass in the centre—something like a six-limbed ophiuroid. One of these limbs is very short and represents the little IVth chromosome,* another represents the *X*. The four remaining strands are the 'right' and 'left' limbs of the two metacentric chromosome pairs II and III.



Text-fig. 14. Structure of the chromocentre in *Drosophila melanogaster*. *a* = chromocentre in a female salivary nucleus; *b–e* = parts of the chromocentre from male nuclei, showing the pairing of the proximal region of the *X* with the *Y*, and the location of the *bobbed* gene (*bb*). From Prokofieva-Belgovskaya (1935 *a*).

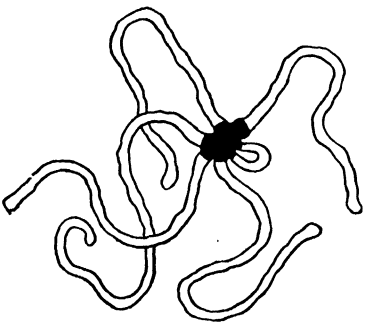
In a structurally homozygous individual the maternal and paternal chromosomes will be completely fused from end to end.

In life it is probable that the distal ends of some or all of the chromosomes are also in contact with one another, owing to some kind of pairing attraction between them. This attraction is apparently a specific one, since the frequencies of association between particular chromosome-ends are constant, and are not

* In some cells both ends of the IVth chromosome are attached to the chromocentre, so that this element forms a loop (Text-fig. 14). Kikkawa (1936 *b*) has shown that in *D. montium* there is a chromosome which normally forms a loop with both ends attached to the chromocentre (Text-fig. 15).

quite the same for different strains of *D. melanogaster* (Hinton and Atwood, 1941).

The actual centromeres are not readily visible in the salivary nuclei. In *Drosophila* they must be contained in the chromocentre, but it is still uncertain whether they have been actually identified. But in some species such as *D. virilis* (Emmens, 1937) there is a dark-staining body in the middle of the chromocentre (the so-called α-heterochromatin of Heitz (1934)) which may represent the 'short arms' of all the chromosomes fused together (*virilis* is a species in which all the chromosomes are acrocentric).



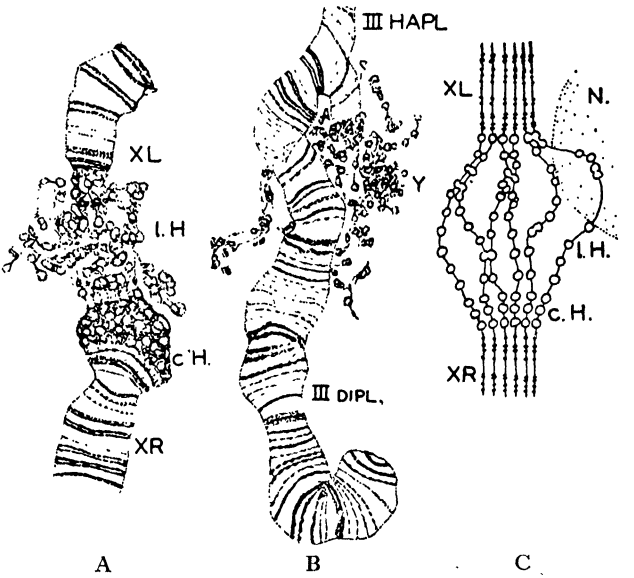
Text-fig. 15. Diagram of the salivary chromosomes of *Drosophila montium*, showing how one of the chromosomes is attached to the chromocentre at both ends. Original, based on the work of Kikkawa (1936*b*).

In a female *melanogaster* the strand which represents the two *X* chromosomes will be as thick as the others, but in a male individual the *X* strand, being haploid, will be thinner and will stain more faintly than the other salivary chromosomes. But according to Schultz (1941*a*) the *X* chromosome of a male salivary nucleus is not so thin and faint as ones which have accidentally failed to pair in a female nucleus. Thus it is probable that the supply of nucleotides available for the building up of the nucleic acid bands in the *X* is only slightly less in the male cell than in the female one, with its two *X*'s. That the supply of nucleotides really does govern the amount of nucleic acid in the bands is suggested by the fact that the bands in an *XXY* female are said to stain more intensely than in a normal *XX* one (Bridges, 1935).

Not all the Diptera possess chromocentres in their salivary nuclei. Thus in the species of *Sciara*, *Bibio* and *Simulium*, as well as in most of the Chironomidae, there is no chromocentre, all the chromosomes being free or only held together very loosely by their ends. In spite of this, many of these forms have extensive heterochromatic regions. Bauer (1936*b*) has described a variety of heterochromatic structures in different species of Chironomidae, some of them intercalary, others terminal. In certain instances single bands of large 'vesicular' chromomeres occur in the middle of a chromosome. These he interprets as heterochromatic segments consisting of only one band: they may also occur at the end of a chromosome. Thus in *Trichotanypus pectinatus* (Text-fig. 13) chromosomes II, III and VI end in trumpet-shaped expansions, each of which bears a single band of large heterochromomeres. In chromosome IV the ends are still more expanded and appear to carry two rows of heterochromomeres. Chromosome V of the same species ends in an enormous frayed-out expansion in which the arrangement of the heterochromomeres is so chaotic that it is

impossible to tell how many bands they have been derived from, although the number is certainly high. These 'spread out' regions are rather common in the salivaries of the Chironomidae; they are also found in *Simulium*, where Painter (1939) has shown that they contain heterochromomeres of many different sizes which do not form definite bands in the fully developed chromosome.

It is possible that there is a real difference between 'compact heterochromatin', in which the chromomeres still form bands, and 'loose heterochromatin', in which the regular arrangement of the chromomeres is entirely lost. In *Drosophila*



Text-fig. 16. Structure of the *X* and *Y* chromosomes in salivary gland nuclei of *Drosophila pseudoobscura*. A = proximal part of the *X*, showing the 'loose heterochromatin', *l.H.*, and the 'compact heterochromatin', *c.H.* B = a translocation between the IIIrd chromosome and the *Y*, showing the loose heterochromatin of the latter. C = diagram of the proximal part of the *X*, showing its relationship to the nucleolus. From Bauer (1936*c*).

pseudoobscura, Bauer (1936*c*) found that it was possible to break up the chromocentre (by pressure on the cover-glass) in such a way that the two arms of the *X* chromosome were left attached to one another by the heterochromatin on either side of the centromere. Part of this heterochromatic segment is composed of compact heterochromatin and seems to represent the proximal portion of the 'right' limb. The remaining part is loose heterochromatin and represents the proximal region of the 'left' limb. The *Y* of this species is entirely composed of loose heterochromatin. While it is probable that the appearance of these heterochromatic regions in fixed preparations is rather different from their

structure in life the differences between the 'compact' and 'loose' types of structure are probably significant.

It is unfortunate that the mitotic chromosomes of the Chironomidae investigated by Bauer have in most instances not been studied, so that it is not known whether the centromeres are median or subterminal. If they are median—as they certainly are in *Chironomus thummi* (Philip, 1942)—then there is an interesting difference between *Chironomus* and *Drosophila*, in that the former does not have extensive heterochromatic regions round the centromeres (although a few bands of heterochromomeres may be associated with each centromere, even in *Chironomus*).

We have already stated that true chromocentres are not found in the Chironomidae. In spite of this some species show a kind of pairing between the heterochromatic ends of the chromosomes. Thus in *Prodiamesa olivacea* three of the chromosomes are attached by their ends to form a triradiate structure, the fourth being free.

In *Drosophila* species it has been shown that the size of the chromocentre depends upon the extent of the heterochromatin. Thus species like *D. virilis*, which have long proximal inert regions in all their chromosomes, possess much larger chromocentres than species such as *D. busckii*, in which the proximal inert regions are relatively short. In *D. ananassae* there is a metacentric chromosome (the 'IVth') which is entirely heterochromatic and which forms a substantial part of the chromocentre.

The pairing of the 'inert' regions to form a chromocentre might be thought to indicate that they were all genetically homologous. This was the conclusion to which Prokofieva-Belgovskaya was led by her studies on the structure of the chromocentre. The proximal regions of the *X* and *Y* are, of course, definitely known to be homologous, since they not only pair at meiosis, but both contain the *bobbed* locus (this locus probably accounts for one of the 5–6 bands in the inert region of the *X*). But as far as the other proximal inert regions are concerned there is no evidence for their genetical homology in *melanogaster*. It seems best, therefore, to say that the pairing of the heterochromatic regions in the salivary nuclei depends on some general similarity of the protein framework in those regions rather than on genetical homology in the strict sense.

The closeness with which the maternal and paternal strands are paired in the salivary nuclei varies considerably throughout the Diptera. In *Drosophila*, *Sciara* and in many species of *Chironomus* the pairing is exceedingly close, so that the homologues usually appear to be completely fused. Occasionally, however, a short region or even a whole chromosome limb may fail to undergo pairing in a particular nucleus. In *Simulium* the homologues are only loosely wound round one another except for a few short segments where a really intimate contact occurs (Geitler, 1934; Painter and Griffen, 1937). In *Chironomus plu-*

mosus the shortest chromosome is frequently unpaired in the salivary nuclei and long regions of the other chromosomes are only very loosely approximated.

It is obvious from the foregoing that it is not homology alone which determines the pairing of the salivary chromosomes. Nor is the cohesion between the homologous strands due merely to a 'force of attraction', since it remains long after the nucleus has been killed in a strong solution of acetic acid and subjected to considerable pressure. During the development of the salivary nuclei it is probable that forces of attraction draw the homologues together—but by the time the larval development has been completed the maternal and paternal strands usually seem to have become physically fused, so that they cannot readily be separated even after fixation. It is therefore probable that the fused homologues are enclosed in a common 'matrix' of some kind.

Kaufmann (1934, 1937, 1938) has made a special study of the nucleoli in the salivary chromosomes of *Drosophila* species. It will be recalled that in the mitotic chromosome set of *melanogaster* there are two main nucleolar organizers, one situated in the heterochromatic region of the *X* and one in the short limb of the *Y*. In the salivary nuclei it can be seen that these two nucleolar organizers are homologous, and that they are fused together and buried in the chromocentre. The nucleolus which they jointly produce appears to be connected to the body of the chromocentre by a chromatic strand or bundle of strands (Frolova, 1936 *a*, *b*). Kaufmann has studied various inversions and translocations in which the nucleolar organizers were broken into two parts. In these cases each portion retained its specific property of forming nucleolar material, and stocks bearing such rearrangements possessed two or more independent nucleoli. It was shown that the nucleolar organizer in the *X* was not coincident with the centromere, but lay some little distance away from it.

In the Chironomidae several different types of nucleoli are formed (Bauer, 1936*b*). Thus in *Chironomus thummi* the IVth (shortest) chromosome in the polytene nuclei bears in addition to the main nucleolus a peculiar nucleolar body of granular appearance, known as *Balbiani's ring*. The remaining chromosomes bear many smaller nucleoli which are formed at fixed loci distributed at intervals along their length. Some other species of Chironomidae are stated to have only one main nucleolus, while yet others have several nucleoli of about the same size. Thus *Glyptotendipes polytomus* has one nucleolus on each of the three longer chromosomes and two on the short IVth one, while *Stictochironomus histrio* has very numerous small nucleoli distributed over all its chromosomes. Clearly the size of each nucleolus is a specific property of its organizer. According to Melland (1942) the IVth chromosome bears the main nucleolus in all the Chironomiinae, while in the subfamily Diamesinae the main nucleolus is borne on the end of one of the longer chromosomes. Philip (1942) has found that in some populations of *Chironomus thummi* an inversion is present in the IVth chromosome which has divided the main nucleolus into two smaller portions.

The fact that nucleolar organizers (unlike genes and most centromeres at any rate) are subdivisible suggests that they extend over a moderate length of the chromosome thread and are not to be regarded as single genes. It also helps to explain the great variation in size and number of nucleoli which is met with in a group like the Chironomidae. Possibly a species like *Stictochironomus histrio* has evolved from forms with fewer but larger nucleoli by repeated fragmentation and redistribution of the nucleolar organizers (as a result of multiple inversions or other structural rearrangements).

In most of the species of *Drosophila* the main nucleolar organizers are located in the proximal parts of the *X* and *Y*. In *D. ananassae*, however, it is clear that part of the basal heterochromatic region of the *X* has been transferred, by translocation, to the IVth chromosome, which instead of being a minute 'dot' as in *melanogaster* is a moderate-sized metacentric element. Thus in the mitotic and salivary-gland nuclei of this species the nucleolus is formed by the co-operation of three separate organizers—one in each of the IVth chromosomes and one in the *Y* (Kaufmann, 1937). The *X* in this species has nothing to do with nucleolus formation.

The importance of the salivary-gland chromosomes for cytogenetical research depends largely on the fact that *all* homologous regions within a nucleus usually pair, even if structural rearrangements are present so that the chromosomes as a whole are only partly homologous to one another. Thus if we consider two chromosomes which are homologous in the sense that they contain the same bands, but in one of which a portion is inverted, pairing will usually take place in the inverted region in such a way as to give a loop, or more exactly the configuration shown in Text-fig. 36*a*. These *inversion loops* occur whenever the inverted segment is sufficiently long to render their formation mechanically possible; if only three or four bands are inverted these will usually form a short unpaired region in the double chromosome instead of an inversion loop.

Where a translocation has occurred so that two chromosomes have interchanged certain regions complete pairing will usually occur unless the translocated regions are relatively short, in which case they may form haploid strands like the single *X* of a male *Drosophila*.

In triploid salivary nuclei it is usual for all three chromosomes of each kind to 'pair' together, although some regions or chromosomes may remain unpaired, as happens occasionally even in diploid nuclei. Where small regions are reduplicated in otherwise diploid nuclei, so that they are present three or even four times in the chromosome set, they may sometimes 'pair' in three's and four's, one of the double polytene chromosomes being attached to another laterally. Where a region is reduplicated within a single chromosome, as in the sequence of letters *abcdefghidefjkl*, the chromosome may loop round so that the two *def* regions are paired with one another.

It was pointed out by Bridges (1935), and has been confirmed by many

workers since, that the normal salivary chromosomes of *Drosophila* contain a number of regions in which the banding pattern is similar or identical. These regions, known as *repeats*, are presumably duplications of small segments which have arisen in the course of evolution and have become established in the normal chromosome set of the species. Some of them must be of considerable antiquity, since the same ones are present in both *D. melanogaster* and *D. simulans* (i.e. they must have arisen prior to the evolutionary separation of these two species). The same situation occurs in *Sciara*, where Metz and Lawrence (1938) and Metz (1938*b*, 1941) have shown that the *X* chromosomes of *S. ocellaris* and *S. reynoldsi* contain the same triple repeat. That repeats do really represent duplications is clear from the fact that such regions are occasionally paired with one another in salivary nuclei.

Repeats may be of several different kinds. In a *tandem repeat* the bands are in the same order in both segments (as in the sequence *abcdefdefgh*). In a *reversed repeat* the order is different (as in the sequence *abcdeffedgh*). Finally, there are cases where the two homologous regions are situated at some distance from one another in the chromosome.

We shall consider in Chapter v the various ways in which repeats can arise. Their existence has a number of important evolutionary implications. In effect it means that part of the gene-complex is present in a tetraploid condition and must be expected to behave genetically in a different way from the genes which are only represented twice in the chromosome set. In a newly arisen repeat two of the four genes will probably be more or less superfluous, physiologically. Thus mutations which would be lethal, or at any rate lower the viability of the organism if they occurred in a non-repeated region, may in many cases have no such disastrous consequences if they occur in a tetraploid segment. It is thus probable that the repeated regions represent an important kind of 'raw material' for future evolution, and that the evolutionary potentialities of an organism depend, in the long run, partly on the extent and kind of repeats in its chromosomes. This is, of course, mere speculation—but it is in accordance with what is known of the genetics of polyploids in plants (Haldane, 1930). We may thus look upon repeats as a source of new genetic possibilities: originally identical with the regions from which they are derived, they must gradually diverge from them in the course of evolution, as a result of independent mutations and structural changes, which will not be the same in the 'model' and the 'copy'.

The relation between the visible segmentation of the salivary-gland chromosomes into bands and internodes and the genetical segmentation into genes has naturally led to both speculation and experimentation. The most direct approach to the problem has been through a study of deficiencies. Most of these are lethal in the homozygous condition, but many of them are viable when heterozygous although the viability is usually reduced as compared with the normal type. Some deficiencies which have a low viability when heterozygous are

actually cell-lethal when homozygous, i.e. single cells are unable to exist if they possess the homozygous deficiency even if surrounded by tissue which is only heterozygous. As an illustration of the kind of results obtained we may take the work of Slizynska (1938). This worker studied fourteen deficiencies which lay in the region of the *X* chromosome containing the genes *white* and *facet*. Two of these deficiencies had arisen spontaneously, the others had been obtained by irradiation with X-rays. The largest of these deficiencies was found to include 37 recognizable bands in the salivary chromosome (the author says 45 bands, but her system of numbering them involved counting the two halves of a 'doublet' as distinct bands in about eight instances). The others included up to 21 bands; five of them were apparently deletions of a single band 3C7. This band is apparently the locus of the *facet* gene, and all flies which lack this band in one of their *X* chromosomes also show the Notch character (small notches in the edge of the wing). By a careful comparison of the effects of these fourteen deletions and of their extent in the salivary chromosome it proved possible to localize the *white*, *roughest* and *facet* loci in individual bands. Later work by Demerec, Kaufmann, Fano, Sutton and Sansome (1942) has considerably extended these results and located a number of genes in single bands; in some instances it is known that a gene lies in a small group of adjacent bands, although it is not certain which band represents the gene.

The viability of flies heterozygous for deficiencies is in general correlated with the length of the missing region—in other words 1-band deficiencies are more likely to be viable than 2-band ones and so on. But there are many exceptions to this rule; evidently some genes can be dispensed with more readily than others. The longest deficiencies known to be viable in the heterozygote include about 50 bands. In very rare instances flies homozygous for a small deficiency may be viable (Bridges, 1938; Panshin, 1938).

Demerec (1940) suggests that 'it would be difficult to foresee a situation' in which a deficiency had a higher survival-value than the original chromosome, and hence that deficiencies do not play 'any significant role' in evolution. But since duplications certainly become established from time to time deficiencies must also do so, or there would be a continual accumulation of genetic material.

These results, and many others of the same general type, are entirely compatible with the view that each band corresponds to a gene, doublets being counted as single bands. On the other hand, the internodes may also possess genetic properties and it has been suggested that a gene may be represented by a band together with an internode (or, more probably, by a band and two half-internodes, one on each side of it). We shall return to this question again in Chapter v, when we come to consider the mechanism of breaks and structural changes in chromosomes.

The system of numbering the bands originally introduced by Bridges (1935) has been adopted, with minor modifications, by subsequent workers. The

chromosome set of *D. melanogaster* was first of all divided into 102 segments of approximately equal length (1–20 in the *X* chromosome, 21–60 in II, 61–100 in III and 101–102 in IV). Each numbered section was then divided into subsections indicated by capital letters. Thus 1 A is the tip of the *X* chromosome, 42 C lies near the middle of chromosome II and 102 B is in chromosome IV. Within each subsection the bands are indicated by numbers. Originally the two halves of each doublet were numbered separately, so that now 3 C 2.3 indicates the doublet between 3 C 1 and 3 C 4. For *D. virilis*, Patterson, Stone and Griffen (1940) have devised a different system, in which each chromosome, whatever its length, is divided into eight sections, A–H, the H section including only the heterochromatin next to the centromere.

The density of staining of the salivary chromosome bands varies considerably in the genus *Drosophila*. Thus *D. robusta* has very dark-staining bands while some other species have bands which stain, on the whole, more faintly. Fujii (1940) has claimed that in hybrids between two strains of *D. virilis* one of the paired VIth chromosomes has darker bands than the other. Cole and Sutton (1941) have shown, however, that this may happen for some bands even in homozygous stocks. Sometimes, indeed, a band in a single homologue may appear thicker or darker across one half of its diameter than on the other side. The reasons for these individual variations in the appearance of the bands are not understood, and until they have been explained it would be inadvisable to attach too much significance to observations such as those of Fujii.

CHAPTER IV

THE MECHANISM OF STRUCTURAL REARRANGEMENTS

The method whereby segments of chromosomes change their location within the chromosome set depends on two kinds of biological events: transverse breakage of the chromosomes and the reunion of the broken ends in a way which is different from the original one.

We may classify chromosome breakages into those which have arisen 'spontaneously', those which have resulted from mechanical tension at mitosis or meiosis, and those which have been produced by experimental treatments such as irradiation, chemical agencies or exposure to temperature shocks. Fortunately, the breakages produced in all these ways seem to be of the same type, so that the results of experiments in which the chromosomes have been artificially broken can be utilized in the analysis of changes in gene-sequence which have occurred in the course of evolution.

Spontaneous rearrangements occur so rarely that they have hardly ever been studied. It is in fact possible that all 'spontaneous' breakages are really due to temperature shocks and other external accidents. Among the clearest cases of 'spontaneous' rearrangements in *Drosophila* are the *pale* translocation (Bridges, 1923) and a translocation between chromosomes II and III described by Sturtevant and Dobzhansky (1930). In both these cases the breakages must have taken place in the germ-line. L. V. Morgan (1939) has described a translocation which occurred in the salivary gland of a *Drosophila* larva: only two of the nuclei of the gland were affected, so that the aberration must have arisen just before the last mitosis in the development of the gland.

The laws and principles which govern the rearrangement of chromosome parts have been discovered mainly as a result of work on *Drosophila*, maize and (to a lesser extent) the plants *Tradescantia* and *Datura*. In the parasitic wasp *Habrobracon* and in the fowl, mouse and rat (all of which have been extensively studied from a genetical point of view), few or no chromosomal rearrangements are known, and those that have been detected have not been studied in detail. To a considerable extent the principles of chromosomal rearrangement seem to be the same in animals and plants, but there are some differences in detail: it is thus clear that the laws governing structural change are not precisely the same in all groups of organisms, and they may vary much more than has been suspected hitherto).

It is of course possible to study in genetical experiments a large variety of chromosomal rearrangements which diminish viability or fertility so seriously that they would stand little or no chance of surviving in the wild state. Thus in most organisms dicentric chromosomes produced by translocation cannot pass

through more than a few mitoses without becoming stretched on the spindle and breaking under the strain. Rearrangements of this and similar types may be cell-lethal, i.e. they may lead to the death of the cells containing them. Nevertheless, most of the main types of rearrangement which have been studied in the laboratory (translocations, inversions, deficiencies, duplications, etc.) have either been found in natural populations or can be inferred to have occurred in the phylogeny of one group or another. Nor is there any clear evidence of chromosomal changes other than mutation and structural rearrangement having taken place in evolution. There is thus a solid foundation for the attempt which has been made in the past twenty years to analyse evolution by reference to laboratory experiments on mutation and structural rearrangement.

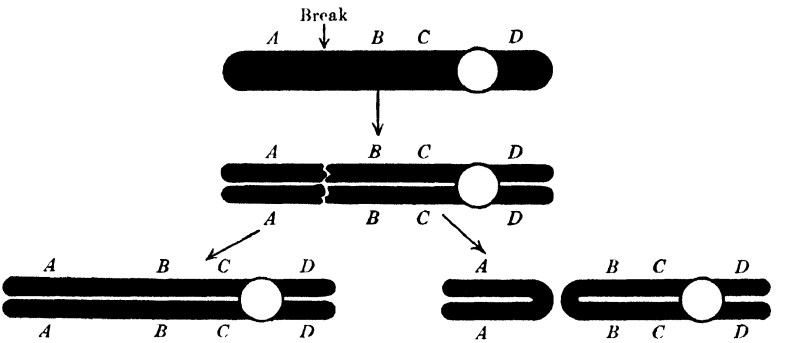
The first law governing the occurrence of chromosomal rearrangements has been formulated by Muller (1938, 1940*a*, *b*). In its most general form it states that before any rearrangement can take place at least two breaks must occur in the same nucleus (either in the same chromosome or in different ones). Muller believes that the surfaces produced by breakage differ from 'natural' ends of chromosomes in two ways: (1) the freshly broken surfaces tend to rejoin with other broken surfaces, whereas natural ends show no tendency to fuse either with broken surfaces or with other natural ends; (2) chromosomes with natural ends are capable of indefinite survival, whereas those with broken ends soon degenerate or lead to the death of the cell, unless the broken end manages to fuse with another broken end.

Muller's standpoint implies that the natural chromosome ends (which he calls *telomeres*) are self-perpetuating structures which are incapable of occupying an interstitial position in the chromosome or of being replaced by any non-terminal part of the protein framework of the chromosome. The telomere-concept is one that has grown up as a result of experimental work; the 'telomeres' have not been identified with any structural entities in the way that the centromeres have. The telomere-concept obviously breaks down in *Ascaris* spp., where the ends of the chromosomes become broken off during the cleavage divisions; and more especially in *A. megalocephala*, where the central regions of the chromosomes also undergo fragmentation.

According to Muller a single fracture in a nucleus can lead to (1) a refusion of the broken ends in the same manner as before, i.e. a *restitution*, or (2) a fusion of two identical sister strands if the breakage takes place before chromosome splitting and the reunion after splitting (see Text-fig. 17). Restitution cannot be detected genetically, since it merely restores the original sequence, while *sister strand reunion* produces acentric and dicentric chromatids which are incapable of indefinite survival.

The idea that only monocentric chromosomes can perpetuate themselves through a large number of mitoses and that acentric and polycentric ones always come to grief in the course of a few cell divisions was first clearly enunciated by

Navashin (1932), who emphasized the essential difference between the centromere and other parts of the chromosome body and maintained that centromeres do not arise *de novo* nor lose their properties in the course of evolution. Subsequent work has confirmed the general validity of Navashin's law, although it now



Text-fig. 17. Diagram showing how a single chromosome-break may give rise either to 'restitution' or to 'sister strand reunion'.

appears that in some organisms (such as *Ascaris megalocephala*) chromosomes containing several centromeres may exist without breaking during cell division. The appearance of Navashin's paper was quickly followed by the work of Mather and Stone (1933), who studied acentric and dicentric plant chromosomes which had been produced by irradiation and confirmed Navashin's ideas. The theory that centromeres only arise from pre-existing centromeres has proved to be one of the foundation stones of the general theory of chromosomal evolution (it had previously been supposed that chromosomes could undergo simple 'fusion' or 'fragmentation' in the course of evolution without gain or loss of parts).

Since even single breaks are extremely rare in unirradiated nuclei, the occurrence of two chromosome breaks within one nucleus must be regarded as an extremely unlikely event under natural conditions. If, however, chromosome breakage is largely due to temperature shocks or abnormal metabolic conditions in the cell, it is possible that the occurrence of two or more breaks within a single nucleus is more frequent than it would be if breakages were entirely spontaneous, i.e. independent in causation.

The two or more breaks necessary to produce a viable rearrangement need not occur simultaneously. In *Drosophila* sperms the breakages accumulate during the whole life of the sperm and no refusion of the broken ends (whether restitutional or not) takes place until fertilization (Sidky, 1940; Muller, 1941*b*). In plant material, however (and perhaps in all ordinary resting nuclei), the breaks must both (or all) occur within a certain critical time interval (usually

a few minutes or hours), since otherwise the first break is ineffective owing to restitution or 'healing' of the broken ends taking place before the second break occurs. In maize it has been shown by McClintock (1941*a*) that broken ends retain their capacity for fusing with other broken ends for an indefinite length of time in the gametophyte and the endosperm: in the sporophyte nuclei the broken ends undergo a 'healing' process, after which they resemble natural ends and will not join up. This 'healing' is entirely unknown in *Drosophila* chromosomes.

There is a certain amount of statistical evidence which tends to show that if there are several freshly broken ends within a nucleus those lying closer together (i.e. in the same chromosome or chromosome arm) are more likely to fuse together than broken ends lying farther apart. Muller (1941) has suggested that this 'propinquity effect' is less strong in sperms than in ordinary resting nuclei, but that even in sperms most breaks only lead to restitutions (owing to the two broken ends produced by a single break being on the average closer together when the chromosomes are set free from the sperm-head at fertilization than broken ends produced by different breaks).

Muller's view that 'natural' ends of chromosomes cannot join up with broken ends has been challenged by Kaufmann (1936), Sutton (1940) and Demerec, Kaufmann, Sutton and Fano (1941), all of whom claim to have observed terminal deficiencies or terminal inversions (i.e. single-break rearrangements). Muller (1940*a*) is of the opinion that these structural changes were in all cases two-break rearrangements with one break so near the chromosome end that the region beyond it was too small to be seen in salivary preparations. But Dobzhansky and Dreyfus (1943) agree with Kaufmann in regarding the II*L* rearrangement which occurs in some wild populations of *D. ananassae* as a true terminal inversion.

The exact manner in which chromosome breakage occurs is not fully understood. It seems certain that there is no difference in quality between the two broken surfaces produced by a break; any broken surface will rejoin with any other one, and there is no question of 'positive' and 'negative' ends, such as might be expected to result from breakage of peptide linkages (Muller, 1940*b*, 1941*b*). Rejoins between euchromatic and heterochromatic ends are quite common in irradiated *Drosophila* material, thus suggesting that the protein framework possesses the same *general* type of structure in both eu- and heterochromatin (although the *detailed* structure is undoubtedly different).

It has generally been assumed that chromosome breakage takes place in non-genic parts of the protein framework, i.e. in internodes between the genes. Unfortunately, the existence of these internodes has never been conclusively proved, and it is possible that the genetic activity of the chromosome is continuous, each 'gene' being contiguous with its neighbours on either side.

There are several ways of classifying structural rearrangements. We may

distinguish first of all between two-break changes, three-break ones and so on. The vast majority of 'spontaneous' rearrangements will of course involve only two breaks, but in irradiated material it is possible to obtain very complex rearrangements in which as many as eight breaks have occurred (Dubinin and Khvostova, 1935).*

Rearrangements where all the breaks are in a single chromosome Muller has called *homosomal*, rearrangements where the breaks are in two or more chromosomes being termed *heterosomal*. Paracentric (*homobrachial*) rearrangements are those where all the breaks are in the same chromosome arm, *pericentric* (heterobrachial) rearrangements being ones in which the breakage points occur on either side of the centromere.

From every point of view there is a great difference between rearrangements that merely alter the sequence of the parts, leaving the total number of genes (or bands) the same, and the deletions and duplications which lead to an increase or decrease in the total number of genes in the chromosome set.

Inversions are simply pieces of chromosome which have been turned through 180°, so that their position in the sequence is reversed. Single inversions are two-break rearrangements; they may be either peri- or paracentric. Two successive inversions (resulting from three breaks in the same chromosome) may be either 'in tandem' or reversed with respect to one another, i.e. the sequence *a*bcd*e*f may give rise to *a*cbed*f* or to *a*edcb*f* (the inversions being in ordinary type).

Translocations are of several kinds. The simplest type is where two breaks occur in non-homologous chromosomes, and the four fragments join up in such a way as to give two new monocentric chromosomes. This type of translocation is called a *mutual* or *reciprocal* one (also known as an *interchange*).

If three breaks occur in a single chromosome the portion between two of them may be inserted into the gap left by the third break. This is known as a *shift*. Shifts may, of course, be either homobrachial or heterobrachial, and may be either inverted or not. Where two breaks occur in one chromosome and a third in another member of the set the portion between the two breaks may be transferred to the break in the other chromosome; this is known as an *insertional* translocation.

Translocations in which the chromosomes are broken very close to the centromere represent rather a special category of rearrangement, since they involve transpositions of entire or virtually entire chromosome arms. Several kinds of these translocations can occur, according to whether the chromosomes concerned are acrocentric or metacentric.

If we consider two acrocentrics, each consisting of a long limb 'distal' to the centromere and a minute second limb 'proximal' to it, then a break may occur

* Kaufmann (1943) has more recently described a very complex rearrangement in which at least thirty-two breaks had occurred.

just proximal to the centromere in one chromosome and just distal to it in the other. If a mutual translocation takes place we shall be left with a large metacentric chromosome and a minute body which contains a centromere and a very small region on either side. The former may survive as a permanent member of the chromosome set; the latter will probably be almost completely inert and may be lost in subsequent generations.

There is evidence that translocations of this type (in which two acrocentrics give rise to a metacentric) have occurred rather frequently in the phylogeny of some genera and families (Robertson, 1916; Painter and Stone, 1935). They will be referred to in subsequent chapters as *centric fusions* (or $A+A \rightarrow M$ changes). Muller (1940*a*) has used the more general term 'whole-arm transfers' for all translocations in which both breakage points are very near the centromeres. Where an acrocentric and a metacentric are involved (instead of two acrocentrics) we may have a change of the following type:

$$abc.def+g.hij \rightarrow abc.hij+g.def$$

(the dot indicating the position of the centromere). Lastly where two metacentrics exchange arms we have a change of the following type:

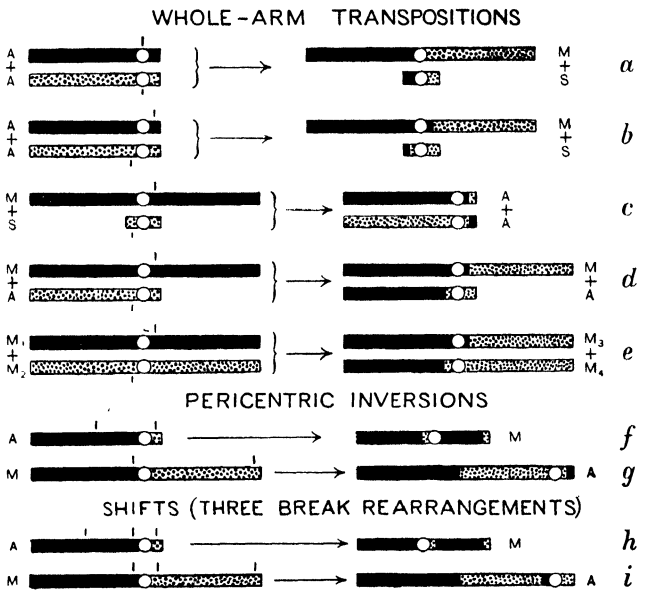
$$abc.def+ghi.jkl \rightarrow abc.ghi+def.jkl.$$

These types of whole-arm transfers we shall refer to as $M_1+A_1 \rightarrow M_2+A_2$ and $M_1+M_2 \rightarrow M_3+M_4$ changes.

It should be obvious from what we have said above that although $A+A \rightarrow M$ changes can occur as a result of a single translocation there is no simple mechanism whereby the reverse process $M \rightarrow A+A$ can occur, since an ordinary metacentric contains only a single centromere. Where a small supernumerary chromosome is present, however, an apparent $M \rightarrow A+A$ (really $M+S \rightarrow A+A$) change can occur, the metacentric and the supernumerary being both broken very near their centromeres, and an interchange of arms taking place. But centric fusions, being one-stage processes, will tend to be commoner in evolution than $M+S \rightarrow A+A$ processes, since the latter require the presence of a small supernumerary before the translocation can take place.

Various authors have claimed in the past that centric fusions do not result from mutual translocation, but are produced by direct adhesion between chromosome ends. This point of view has been recently championed by Helwig (1941) who claims that the V-shaped metacentrics found in some grasshoppers possess two centromeres situated very close together. It is, of course, conceivable that two acrocentrics might undergo an apparent 'fusion' if each of them broke in the minute 'second arm'—in that case we should be left with a very small acentric fragment and a large metacentric chromosome with two centromeres in the middle separated by a region $0{\cdot}25\,\mu$ or less in length. Whether such a metacentric could pass through an indefinite number of mitoses without being

frequently disrupted is open to doubt. In *Drosophila* all metacentrics seem to be strictly monocentric—but the example of *Ascaris megalocephala* shows us that in some other organisms polycentric chromosomes can exist in nature. It is thus not impossible (although rather unlikely) that some metacentrics which



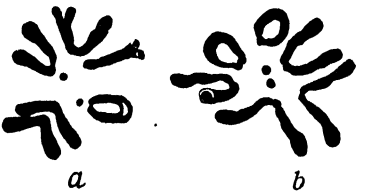
Text-fig. 18. Diagram of various whole-arm transpositions and rearrangements which alter the position of the centromere within the chromosome. Position of breaks indicated by short vertical lines. It is uncertain whether the type of rearrangement indicated in *a* can actually occur. *b* is the type of rearrangement referred to as a centric fusion.

have arisen by centric fusion possess two independent centromeres situated very close together.

Although the majority of centric fusions that have been studied are between non-homologous chromosomes, there is no theoretical reason why two homologous acrocentrics should not fuse together so as to produce a metacentric with two identical limbs. Such a structure would be most unlikely to establish itself in evolution except in a polyploid or clonal species, but it is known in the case of the *X* chromosome in laboratory stocks of *Drosophila melanogaster*. This so-called *attached-X* condition, in which the two *X*'s of the female are united at the centromere, has arisen spontaneously on no less than seven different occasions (L. V. Morgan, 1938). In several of these cases it is probable that the attached-*X*'s have arisen in two steps, each step consisting in the replacement of one arm of the *Y* by an *X* chromosome. Thus some at least of the attached-*X*'s have a centromere derived from the *Y* (others have probably arisen

by straightforward centric fusions between two X's). The meiotic behaviour of attached-X's will be dealt with in the next chapter.

The 'closed-X' stocks of *Drosophila melanogaster* (in which the normally acrocentric X is replaced by an endless ring-shaped chromosome in which the proximal and the distal ends have been fused together) have arisen from flies carrying attached-X's (L. V. Morgan, 1933; Schultz and Catcheside, 1937). Some of these closed-X's have occurred as a result of a translocation in an attached-X, the two breakage points being situated one in one arm very close to the centromere, one in the other arm very close to the distal end. Such a translocation will produce a ring-X containing a centromere and an acentric rod-shaped X; both chromosomes will contain a small deficiency and a corresponding duplication, but if these are sufficiently small they may not affect the viability of flies carrying the closed-X chromosome.



Text-fig. 19. Somatic metaphases of *Drosophila melanogaster* females carrying closed-X chromosomes. a = a fly heterozygous for the closed-X condition; v = a homozygous closed-X fly. From L. V. Morgan (1933).

Other closed-X's have arisen not by translocation, but by crossing-over between two limbs of an attached-X in which one limb contained a large inversion—their mode of origin will be discussed more fully in the next chapter when we consider the meiosis of abnormal chromosomes such as attached-X's.

In maize ring chromosomes have been studied in considerable detail by McClintock (1932, 1941*b*). It was found that when they split at mitosis they frequently do so in such a manner as to give a double-sized ring with two centromeres instead of two rings with a single centromere each. Exactly how the double-sized rings are produced is not quite clear, but the effect would be produced if the 'plane' of splitting was actually spiral, so that it made a complete turn per ring.

The fate of these double-sized rings in somatic mitoses is as follows: they become stretched upon the spindle owing to one centromere going to each pole and they then break in two places under the tension at anaphase. Thus each daughter cell receives a metacentric chromosome with two freshly broken ends which quickly unite, thus producing a new ring chromosome. These rings will not necessarily be the same size as the original one, and most of them will contain duplications and deficiencies. Thus plants containing a ring chromosome will always show a considerable amount of mosaicism.

It was formerly believed that the closed-X chromosomes in *Drosophila* did not form double-sized dicentric rings at mitosis, since closed-X stocks do not show mosaicism. It has recently been shown, however, that some ring chromosomes in *Drosophila* do show the same type of abnormality as the maize ones, and give rise to somatic variegation in early developmental stages. Thus the

fact that ring chromosomes have never been formed in any wild populations is easily explained if they always suffer from disabilities of this type at mitosis.

A special type of chromosome breakage occurs sometimes at meiosis, when the centromere, probably as a result of a mechanical accident (e.g. irregular stretching of the spindle), splits transversely instead of longitudinally. This 'misdivision' of the centromere, as Darlington (1939*a*) calls it, has been observed in a number of species of plants, but not so far in any animal. It obviously leads to the production of strictly telocentric (as opposed to acrocentric) chromosomes. These will usually be inviable, but in some instances Darlington (1940*b*) has observed that at the next division a telocentric chromosome may be converted into what he calls an *iso-chromosome*, namely, a metacentric with two identical limbs united in a median centromere. It is doubtful whether these processes have played any part in normal chromosomal evolution, in animals at any rate, but they are interesting as showing that the centromere is a divisible body.

It has been pointed out by Muller (1940*a*) that whereas the same gene-mutation (i.e. from allelomorph x to x') will occur again and again, the chance of exactly the same rearrangement occurring spontaneously (i.e. in unirradiated material) more than once will be so small that it can probably be neglected. This is because a rearrangement depends, not on a single rare event, but on two independent events occurring by chance in the same cell (each event being so rare that it probably only happens once in several million individuals).

Writers on the mathematical theory of natural selection frequently speak of 'mutation pressure', a metaphor used to describe the continual recurrence of particular mutations in a population or species. It is clear from what we have said above that the 'pressure' in the case of structural rearrangements is very weak. Thus a mutation which fails to establish itself on its first appearance may do so upon a subsequent occasion under different environmental circumstances and in another genetical situation. But a particular gene-sequence which has become extinct is hardly likely to occur again.*

The importance of this from an evolutionary standpoint is that wherever we find exactly the same gene-sequence in two groups of individuals (populations, subspecies or species) we are justified in concluding that they have had a common origin subsequent to the establishment of that particular gene-sequence. In the case of rearrangements where one or both breaks are in an inert region it is technically very difficult to determine the exact locus of breakage in the salivary chromosome. Thus what appears to be the same whole-arm transfer may have occurred a number of times. In general, the thesis that a particular rearrangement will not happen more than once should not be applied unless the exact breakage points have been very precisely located.

* If a chromosome has n loci it can form $\frac{1}{2}(n-1)(n-2)$ different inversions (all breaks between two loci being regarded as identical). This number is 242,556 for the *X*-chromosome of *D. melanogaster* and 3741 for the IVth chromosome, according to the data in Table 1.

In the early days of *Drosophila* genetics it was supposed that the genes were entirely discrete and independent entities separated by intergenic connexions devoid of genetic properties. This view was in harmony with the known facts of crossing-over, since it is clear that cross-overs take place between the genes rather than within their limits.

As soon as chromosomal rearrangements began to be studied in detail, however, suspicions were aroused that the original conception of the chromosome as a linear assemblage of completely independent units was somewhat too simple. Had it been entirely true structural rearrangements which merely altered the sequence of parts in the chromosome (without producing any deficiency or duplication) should not have been accompanied by any phenotypic effects. This was soon found not to be the case: the majority of inversions and translocations known in *Drosophila* affect either the viability, fertility or appearance of the flies carrying them. Some idea of the effects of translocations on viability can be obtained from Table 2. These phenotypic effects associated with rearrangements resemble gene-mutations in many respects—they may be either dominant or recessive, and they comprise many different types of changes, both lethal and visible.

Three main types of explanation have been put forward to account for these phenomena (Muller and Altenburg, 1930). The first suggestion was that structural changes tend (for some unknown reason) to be accompanied by gene-mutations in the same chromosome (the 'group-effect' hypothesis). The second was that chromosome breakage often involved the loss of, or damage to, the genes adjacent to the point of breakage. Lastly, it was suggested that the functioning of a gene might depend to some extent on its position in the sequence, so that its properties would be somewhat altered when it was transferred to a new situation ('position-effect' hypothesis).

It has not been easy to decide between these alternative explanations. If the position effect has eventually come to be generally accepted it is because there are a few cases which can only be otherwise interpreted by making further unproved and improbable assumptions (Dobzhansky, 1936*c*, *d*). Some of these crucial cases will be discussed later (see p. 66).

No certain position effects are known outside *Drosophila*. In maize the translocations which have now been studied seem to be entirely devoid of any phenotypic effects. It is thus quite uncertain how far the position effect should be regarded as a phenomenon of general occurrence. On *a priori* grounds we may expect to find position effects in other animals, but until we know how widespread they are it is difficult to decide how important they should be regarded in cytogenetical evolution. It has been suggested by Muller (1941*a*) that the position effect might conceivably depend on a disturbance of somatic pairing following on structural rearrangement. If this were the explanation the effect would be confined to the Diptera. But there is no real evidence for this

hypothesis, and no really satisfactory interpretation of the mechanism of position effect has yet been put forward.

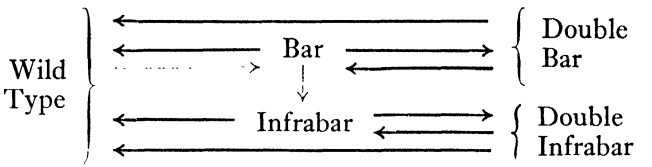
The first instance of a position effect to be properly investigated was the *Bar* condition in *Drosophila melanogaster*. *Bar* is a sex-linked dominant character affecting the development of the compound eyes. *Bar* individuals have narrower eyes with fewer ommatidia than the wild type, the heterozygous females being

TABLE 2. *Viability and fertility of homozygous translocations*

(From Dobzhansky (1936*d*) after Patterson, Stone, Bedichek and Suche (1934))

Chromosomes involved	No. tested for viability	% viable	No. tested for fertility	% fertile
I and II	57	52·6	23	91·3
I and III	71	42·2	30	90·0
I and IV	14	100·0	13	100·0
II and III	120	15·8	19	100·0
II and IV	33	69·6	17	88·2
III and IV	37	48·6	18	88·8

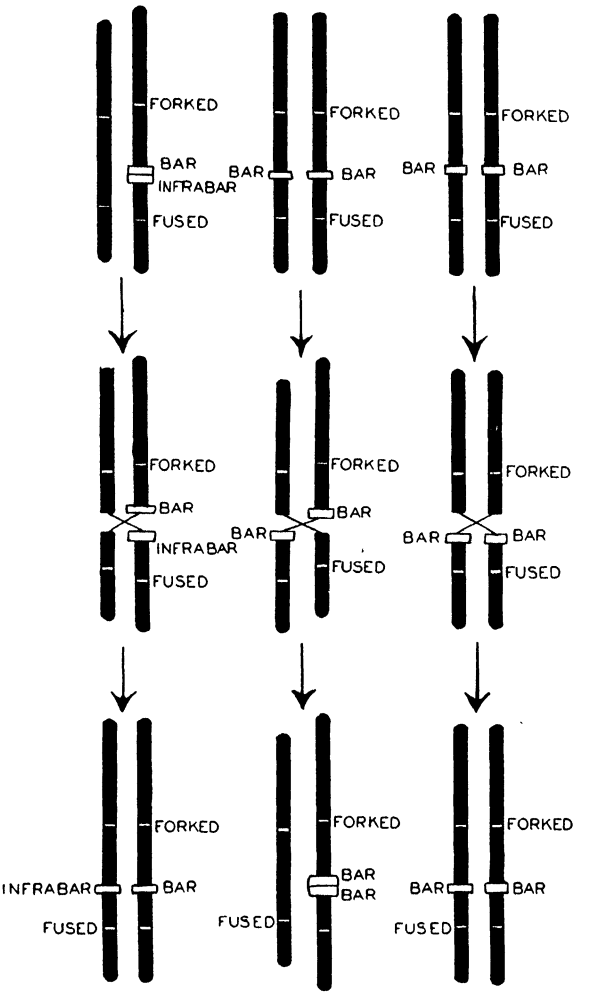
intermediate between the homozygotes and the wild-type flies. The original *Bar* 'mutation' arose spontaneously in the early days of *Drosophila* genetics (Tice, 1914); it was soon found to possess very remarkable properties (Zeleny, 1921). Thus it frequently changed back to the wild type or to an even more extreme condition known as *Double Bar* (or *Ultrabar*). The latter was also unstable, reverting back both to *Bar* and to the wild type. These changes took place about once in every 1,600–10,000 flies (i.e. far more often than most gene-mutations). But they only occurred in the female sex; in males the *Bar* condition seems to be absolutely stable. On one occasion *Bar* gave rise to a less extreme allelomorph known as *Infrabar*, which was likewise unstable, producing wild-type flies and *Double Infrabars* in the female sex. We may represent these relationships in the following diagram, in which the dotted lines represent changes that have only taken place once, while 'full' lines indicate frequently occurring changes:



Since the changes from *Bar* into wild type and *Double Bar* only occurred in females it was suggested by Sturtevant and Morgan (1923) that they were not true gene-mutations but were due to a special type of crossing-over. This suggestion was proved to be correct by a genetical study of *Bar* chromosomes carrying the genes *forked* and *fused*, which lie on either side of the locus of

Bar. It was found that each apparent mutation of *Bar* was accompanied by a cross-over between *forked* and *fused* (Text-fig. 20).

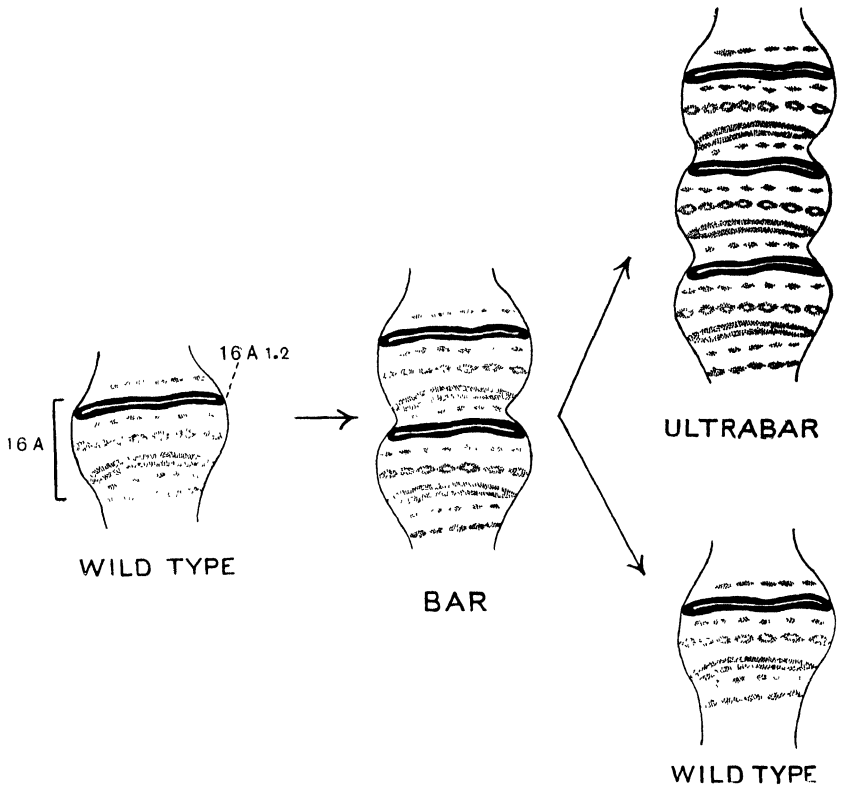
It is now known that the original *Bar* is a duplication of a short region (16A) which is normally present in the *X* chromosome, the *Bar* condition in the



Text-fig. 20. Equal (right-hand column) and unequal (middle and left-hand columns) crossing-over at the Bar locus in the *X* chromosome of *Drosophila melanogaster*. From Dobzhansky (1936*d*).

female being due to this region being present three times in the nucleus (twice in one *X*, once in the other). In the *Double Bar* chromosome 16A is present three times (i.e. flies homozygous for *Double Bar* have six *Bar* regions per

nucleus). Cytological studies of the salivary chromosomes (Bridges, 1936; Muller, Prokofieva-Belgovskaya and Kossikov, 1936; Hager, 1941) have confirmed these views, which had previously been based solely on the genetical evidence: it was found that a single *Bar* region includes five bands (including two doublets) and forms a characteristic 'puff' in the *X* chromosome; the duplication is of the 'tandem' or non-reversed type (1234512345 and not



Text-fig. 21. The 16A region in the salivary *X* chromosomes of wild type, Bar and Ultrabar flies. Bar is the 16A1.2 band. Based on the work of Bridges (1936) and Sutton (1943).

1234554321). The changes from *Bar* to wild type and *Double Bar* are due to unequal cross-overs which result in a transference of *Bar* regions from one chromosome to the other (Text-fig. 20). Theoretically it should be possible to increase the number of *Bar* regions in the chromosome indefinitely by means of unequal crossing-over, and Rapoport (1940) has, in fact, succeeded in building up the number of *Bar* regions to as many as eight by taking advantage of this fact.

TABLE 3. *Numbers of ommatidia in compound eyes of females of* Drosophila melanogaster

(From Sturtevant, 1925)

Wild type	779·4 ±4·1
Heterozygous Bar	358·4 ±7·9
Homozygous Bar	68·12±7·9
Heterozygous Double Bar	45·42±0·24
Homozygous Double Bar	24·96±0·3

Infrabar probably arose from *Bar* as a true gene-mutation, since *Infrabar* salivary chromosomes are not visibly different from *Bar* chromosomes.

So far we have not dealt with the connexion between these changes and the position-effect hypothesis. Since flies heterozygous for *Double Bar* and those which are homozygous for *Bar* both contain four *Bar* regions per nucleus, one might imagine that they would be phenotypically indistinguishable. But it will be seen from Table 3 that the number of facets is very significantly lower in the heterozygous *Double Bars*. Thus 'extra' *Bar* regions seem to be more potent when present in the same chromosome than when lying in different ones. It was to this type of phenomenon that the term position effect was originally applied by Sturtevant. Since the early work on the original *Bar* stock it has been found that a number of inversions in which the *X* is broken in the 16A region give rise to a *Bar* effect, even without any duplication. The later work of Sutton (1943) has shown that the *Bar* locus is probably situated in the doublet 16A1.2. The *Bar* effect apparently occurs whenever this band is brought into contact with certain other loci as a result of rearrangement. *Bar* is thus not in any way different from other position effects, although the fact that the first rearrangement giving rise to a *Bar* effect happened to be a duplication made it appear for some years as if *Bar* were a special case, essentially different from other position effects.

A condition very similar to *Bar* but less extreme and entirely recessive was discovered by Dobzhansky (1932) in the descendants of an irradiated wild-type male. It was found that in these flies a translocation was present, the breakage points being in the *X* (next to 16A1.2) and in the IInd chromosome (between the genes *cinnabar* and *vestigial*). The translocation was named *baroid*; since no bands are duplicated the phenotypic expression must be due to the new gene sequences.

According to Demerec and Hoover (1939) the dominant character *Hairy wing* is due to a tandem duplication similar to *Bar*; in this case also two *Hw* regions are more potent when present in the same chromosome than when situated in different ones, but the analysis is less complete, because crossing-over hardly takes place at all in the neighbourhood of *Hw*, and unequal crossing-over has never been observed at this locus.

A rather different type of position effect is where a gene has its degree of dominance altered (usually weakened) by a rearrangement in which one break is near the gene in question. Thus Dobzhansky and Sturtevant (1932) showed that when small portions of the *X* chromosome containing wild-type allelomorphs of the genes *yellow*, *kurz*, *rudimentary* and *forked* were present as duplicated fragments the wild-type allelomorphs were no longer capable of completely dominating over the corresponding mutant genes in an entire chromosome. Sivertzev-Dobzhansky and Dobzhansky later (1933) showed that this was also true for the *bobbed* locus in the inert region of the *X*. Fragments of the inert region derived from wild-type *X* chromosomes behaved as if they contained a weak allelomorph of *bobbed*. This effect is not confined to the *X*—many autosomal genes behave in the same way when a break has occurred near them. Thus the wild-type allelomorph of *cubitus interruptus* (a IVth chromosome character) is normally entirely dominant over the mutant gene. Various authors (Dubinin and Sidorov, 1934*a*, *b*; Dubinin, 1935) have found, however, that in flies heterozygous both for IVth chromosome translocations and for *cubitus interruptus* the dominance of the wild-type gene is weakened, so that such flies show the *cubitus interruptus* phenotype (an incomplete cubital vein in the wing).

It was found by Dubinin, Sokolov and Tiniakov (1935) and also by Khvostova and Gavrilova (1935) that, in order to obtain a weakening of the wild-type allele of *cubitus interruptus*, it was necessary that the IVth chromosome should be broken within a certain minimum distance of the gene; breaks situated farther away did not lead to a weakening. But this was not the only factor involved, since the position of the other break also plays a part in determining whether or not a weakening takes place; thus if the second break is in the heterochromatin of chromosome II or III no weakening occurs, but if it is in the *Y* or in the autosomal euchromatin a weakening effect is produced.

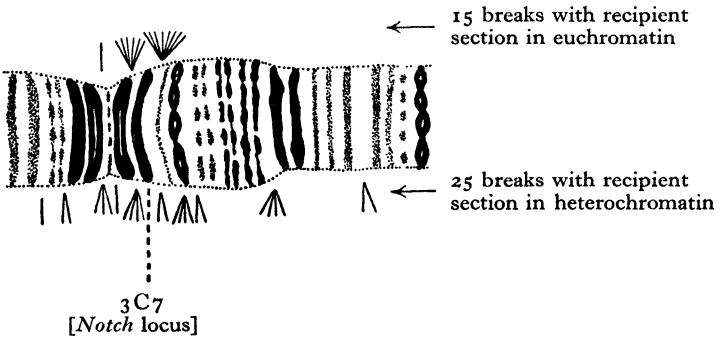
This experiment introduces us to a most important characteristic of the position effect, namely, that a break may affect not only the loci situated on either side of it, but also genes situated some little distance away. In some cases the effect may extend over about a dozen salivary bands.

It is obvious that if the position-effect hypothesis is true the effect should be reversible, i.e. a gene whose function has been altered by a change in position should reacquire its original properties when returned to its old position in the chromosome. Grüneberg (1937) obtained a spontaneous reinversion in which a reversal of a position effect occurred; but since this case is unique and cannot be repeated at will it is less satisfactory as a proof of the reversibility of the position effect than experiments in which the restoration of the original sequence is accomplished by means of crossing-over. Such an experiment was carried out by Dubinin and Sidorov (1935), using a translocation between chromosomes III and IV in which the former was broken near the *hairy* gene and the latter in the neighbourhood of *cubitus interruptus*. The wild-type alleles of both genes

were weakened so that they were no longer able to suppress the effects of the corresponding recessive genes. By crossing a stock containing this translocation with flies containing the recessives *hairy* and *eyeless* it was possible to introduce the *hairy* gene into the translocation chromosome. It was found that this led to a weakening of the hairy gene: on subsequently removing the gene to an unbroken chromosome (by crossing-over) it reacquired its original potency.

This seems to be as good a proof of the reality of the position effect as any that could be desired. An essentially similar experiment was carried out by Panshin (1935), using another III–IV translocation in which the IIIrd chromosome was broken near the *curled* gene. The wild-type allele of *curled* had its dominance considerably weakened by the translocation; when the weakened gene was transferred back into a normal chromosome by crossing-over it regained its original degree of dominance.

A special study of cytogenetical changes at the *Notch-facet* locus has been made by Demerec and his collaborators (Slizynska, 1938; Demerec, 1941, 1942). *Notch* is a dominant allele, *facet* a recessive one; the locus is near the distal end of the *X* chromosome.



Text-fig. 22. Diagram of a portion of the salivary *X* chromosome in *D. melanogaster*, showing the 3C7 band (Notch locus) and the positions of 40 breaks involved in rearrangements giving a Notch phenotype. After Demerec (1942), re-drawn.

Flies showing the *Notch* phenotype have a characteristic nicking of the edge of the wings, and the wing veins are also thickened in a peculiar manner. When homozygous or hemizygous, *Notch* acts as a lethal, i.e. it can only be transmitted in the female line, since males carrying it always die.

A great many *Notch* stocks exist; some of them have arisen spontaneously, but the majority have been obtained from irradiated material. Out of 101 studied by Demerec and his co-workers, forty-six proved to have detectable deficiencies covering the 3C7 band. Forty *Notch* stocks possessed large cytological rearrangements such as inversions or translocations, while in fifteen stocks the *X* chromosomes were cytologically normal, i.e. indistinguishable from the wild type in salivary preparations.

It would thus appear that the *Notch* phenotype can be produced in a number of different ways. Where the salivary *X* is entirely normal in gene-sequence it is probable that a true gene-mutation has occurred. The normal allelomorph of *Notch* somehow prevents the formation of notches in the wing margin, and loss of this locus or its inactivation by mutation or by a position effect leads to the production of the *Notch* phenotype.

The notches associated with rearrangements are particularly interesting. They may be divided into those where the 'recipient' region was heterochromatic and those where it was euchromatic. In the latter case the break was always very close to the *Notch* locus (at most two bands away from 3C7), while in those cases where the recipient region was heterochromatic the 'first' break might be situated some distance away from the locus of *Notch* (Fig. 22). Thus if we regard these *Notches* as position effects the heterochromatin must be capable of exerting an influence over a much longer distance than any euchromatic region.

A number of structural rearrangements are known which give rise to a characteristic type of mosaicism or variegation in the tissues. Flies carrying these rearrangements are flecked or mottled in an irregular manner, as if they carried a gene undergoing frequent somatic mutation. Thus in a fly showing variegation for the *white* locus in the *X* chromosome the ground colour of the eye will be that of the wild type, with single facets or groups of ommatidia differently coloured. The size of the flecks varies from single cells to large masses of tissue, and all parts of the fly, including internal organs such as the Malpighian tubules and gonads, may be affected in the same way. It is thus fairly clear that the variegation depends on events which, whatever their precise nature, occur during the organogeny of the fly. Demerec (1941) suggests that since the smallest flecks are single cells, these events probably occur at mitosis, and that only one of the daughter cells may be affected.

Rearrangements causing mottling have been studied especially by Muller (1930), Noujdin (1935, 1936, 1938), Schultz (1936, 1941*a*, *b*), Demerec (1941) and Demerec and Slizynska (1937). It has been shown that they always involve one break in euchromatin and one in heterochromatin. (Griffen and Stone (1940*a*) claim, however, to have obtained 'mottleds' in which both breaks were in euchromatin, so it is possible that some exceptions occur.) The genes which show variegation lie in the euchromatin, near the point of breakage, so that in terms of the position-effect hypothesis we may say that their abnormal behaviour is due to their being brought within the range of influence of a heterochromatic region.

As an example of a rearrangement causing mottling we may take an *X*–IV translocation studied by Schultz (1941*a*). In this case the *X* was broken between the genes *diminutive* and *echinus*, the IVth in the heterochromatin, not far from *cubitus interruptus*. Female flies heterozygous for this translocation show variegation for the genes *split*, *diminutive* and *white* (all of which lie in the *X*,

near the point of breakage). The degree of variegation is greatest for the genes nearest to the break, least for *white* which is farthest away.

Schultz has put forward the following general explanation to account for the 'mottling' effect: he believes that the regular reproduction of the protein framework of a chromosome during mitosis depends on the supply of, and demand for, nucleotides and the juxtaposition of euchromatic and heterochromatic regions frequently upsets the nucleic acid metabolism of the bands nearest to the point of breakage. He has claimed that euchromatic bands brought into the proximity of 'inert' material sometimes undergo a 'heterochromatization' and thus appear darker under the microscope than the same bands when present in their normal position. The significance of this observation is open to some doubt since, as we have seen (p. 50), the amount of darkening of the bands is rather highly variable, even in chromosomes without rearrangements. Other workers (e.g. Cole and Sutton, 1941) have failed to confirm the darkening of the bands claimed by Schultz, or have found it too inconstant to be significant. Schultz believes not merely that a 'heterochromatization' of the bands near the rearrangement takes place, but that this leads to the production of minute rearrangements at mitosis since the protein framework fails to reproduce or split in a proper manner at the appropriate time. The 'mottled' patches of tissue are assumed to be so because they contain small deficiencies, duplications, etc. Whether or not Schultz's observations on 'heterochromatization' are finally confirmed, there is a good deal to be said for his view that 'mottling' is in some way associated with the nucleic acid metabolism of the chromosome. Thus it has been shown that the addition of an extra *Y* to the chromosome set suppresses the variegation effect (Gowen and Gay, 1933; Dubinin and Heptner, 1935; Schultz, 1941*a*), and the highly viable 'mottled white 258–18' stock studied by Demerec and Slizynska is completely inviable in males lacking a *Y* (Schultz, 1941*a*).

Closely connected with the interpretation of the position effect is the question: Can the chromosomes be broken at any point along their length or only at certain places? The answer would appear to be that they can only be broken *between bands* (doublets and capsules being regarded as single bands). This would seem to indicate the existence of certain primary units or segments (which we may provisionally consider as genes). These primary units are probably unbreakable or cannot reproduce if broken, but whether there is only one possible breakage point between two successive units is unknown. Muller (1940*b*) has adduced several reasons for believing that chromosome breakage does not involve a rupture of chemical bonds such as those in a polypeptide chain. If he is right in this, we should not regard the chromosome as a single molecule, but as a series of molecules (each probably corresponding to a gene) with joints in between. In the fully developed chromosome each gene-molecule would probably have undergone lateral reduplication ('copying') many times.

The discovery of the position effect and the existence of cases like *Bar* and

Hairy necessarily gave rise to the suspicion that all mutations might possibly be structural rearrangements such as minute inversions, translocations and the like. It was soon shown that the vast majority of gene-mutations did not involve any visible alteration in the appearance of the salivary chromosome, but the possibility still remained that gene-mutations might be rearrangements on a subvisible scale but not otherwise different from transpositions of large regions. It has been shown by a number of authors that in irradiation experiments the relation between X-ray dosage and the number of mutations produced is a linear one. On the other hand, the frequency of gross rearrangements is proportional to about the $1\frac{1}{2}$ power of the dosage. These relationships seem to indicate that mutations are single events, whereas viable structural rearrangements (since they always involve two or more breaks) are dependent on two or more independent events (strictly speaking, the exponent should be two or over, rather than 1·5, but the more complex rearrangements—involving more than two breaks—are usually inviable). It has recently been shown, however, that very minute rearrangements are (1) far more frequent than they should be if the two breaks were distributed at random along the chromosomes, and (2) directly proportional to X-ray dosage and not to an exponential power of the dosage as the 'gross' rearrangements are. These results would seem to indicate that there is a real difference, other than size, between the gross and the minute rearrangements and that the latter should be regarded as due to 'single' events.

We are thus faced with the fact that it is extremely difficult to distinguish between gene mutations and 'minute' rearrangements. Some preliminary experiments (Muller and Mackenzie, 1939) seemed to indicate that ultra-violet irradiation produced gene-mutations but hardly any rearrangements, either gross or minute. The evidence is, however, conflicting, since Slizynski has later obtained rearrangements after ultra-violet irradiation. Various other types of indirect evidence which suggest that there is a real difference between gene-mutations and minute rearrangements have been considered by Muller (1941 *b*).

From the point of view of chromosomal evolution it is still uncertain how far minute rearrangements occur spontaneously. In wild populations of *Drosophila* species large inversions are usually quite common, but minute ones are almost unknown, although they must sometimes establish themselves in evolution, since closely related species of *Drosophila* frequently differ in respect of minute inversions (see Chapter VII). In the small midges of the genus *Sciara*, however, the situation is reversed, i.e. minute rearrangements are quite common whereas large ones have hardly ever been observed except in *Sciara impatiens* (see p. 105). Nevertheless, Metz and Boche (1939) have obtained a considerable number of 'large' inversions and translocations in *Sciara* by irradiation, so that their apparent absence in natural populations is more likely to be due to their being eliminated by natural selection than to their not being formed from time to time.

CHAPTER V

MEIOSIS

An understanding of the mechanism of meiosis is essential for the interpretation of the mechanism of chromosomal evolution. Historically, it was not until the cytological basis of crossing-over had been worked out (mainly by Janssens (1909, 1924) and Darlington (1930, 1931, 1932*a*, *b*, 1936, 1937*a*, *b*)) that the laws and principles governing the inheritance of inversions, translocations and other structural changes of the chromosome set could be put on a rational basis. Many types of structural rearrangements are unable to establish themselves in natural populations of animals, not because they are in any way directly harmful to the individuals carrying them, but because they interfere with the orderly sequence of processes involved in meiosis, and hence lead to partial or complete sterility. Moreover, since the details of the meiotic process vary to some extent from one group to another, certain kinds of structural rearrangement which would lead to a high degree of sterility in one group may hardly lower the fertility of the organism at all in another. Thus, when interpreting the chromosomal evolution of a population, species or group it is first of all necessary to know the details of its meiosis.

The various types of meiosis which exist in animals and plants may be classified into two main groups: (1) the 'normal' type which is characteristic of the vast majority of the Metazoa and higher plants, and (2) the various anomalous types which have been developed in particular groups, often in association with parthenogenesis or male haploidy, but also in some groups with a bisexual method of reproduction and diploidy in both sexes. In the present chapter we shall consider only the 'normal' type of meiosis, reserving the various anomalous types for separate treatment in Chapters IX, XII and XIII.

'Normal' meiosis may be regarded as consisting of two successive nuclear divisions which have been considerably modified, so that the details are no longer the same as in somatic mitosis. These two divisions usually follow rapidly on one another, with a very short resting stage ('interkinesis') in between. In some organisms, however, interkinesis can hardly be said to exist, the transition from the first to the second division being direct. In general the phenomena of meiosis are similar in the two sexes, except for the fact that in the female each meiosis leads to the production of a single egg and three non-functional polar bodies, while in the male the four sperms produced are all potentially functional.

For purely technical reasons spermatogenesis is much easier to study than oogenesis, so that most of our knowledge of meiosis is based upon information derived from the former. Enough observations have been made upon meiosis

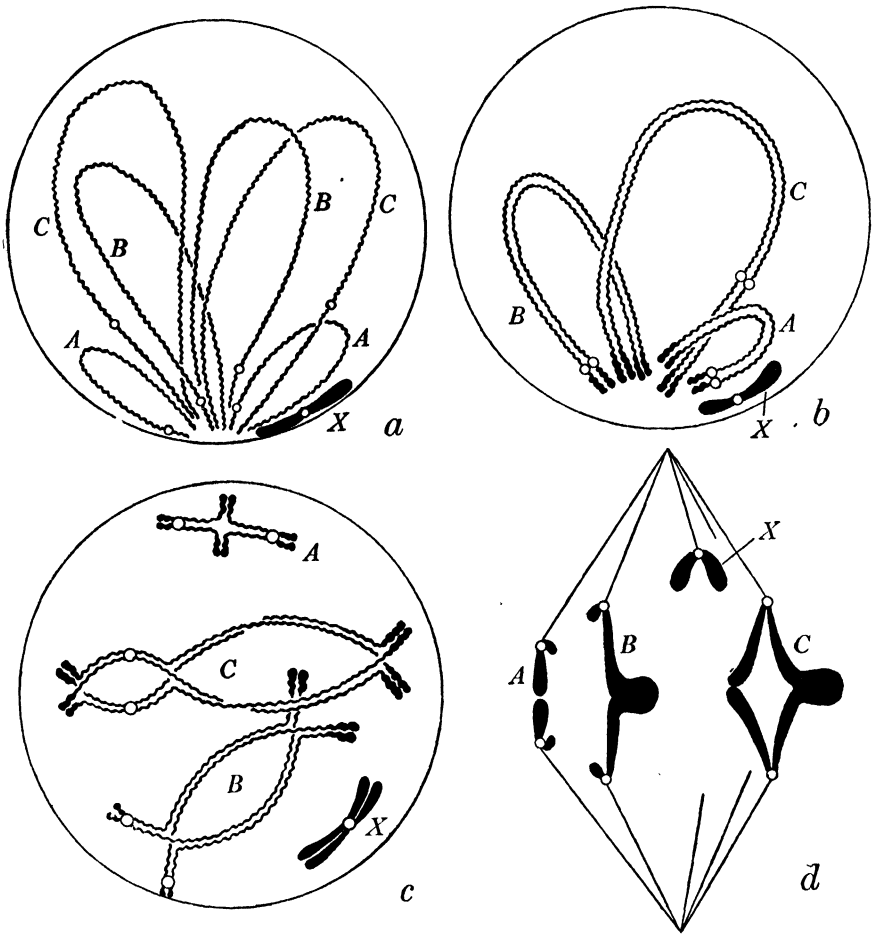
in the egg, however, to make it clear that the general course of events is in most species the same in the female as in the male. In Chapter IX, however, we shall meet with some instances where spermatogenesis is of a highly anomalous type, although oogenesis is quite 'normal'. This is the case in the species of *Drosophila*, where it has long been known that crossing-over occurs in the female, but not in the male.

The prophase of the first meiotic division is usually a long stage, and it involves a complicated sequence of processes that do not occur in the prophase of an ordinary mitosis. For this reason a special terminology has been developed in order to describe the various substages into which it may be divided. These substages, in the order in which they occur, are called *leptotene*, *zygotene*, *pachytene*, *diplotene* and *diakinesis* (various other terminologies were adopted by some of the earlier authors, but this is the one which is now generally accepted).

The leptotene stage follows on the last premeiotic (spermatogonial or oogonial) division; it corresponds to the earliest part of a mitotic prophase. The chromosomes at this stage are very long slender threads with numerous chromomeres of different sizes distributed at intervals along their length. Leptotene is a particularly difficult stage to study for technical reasons. Darlington believes that the chromosomes are unsplit at this time and that this constitutes a distinction of primary importance between leptotene and the corresponding stage of a somatic mitosis. Many other workers (e.g. Huskins) claim to have seen split leptotene chromosomes. Since the observational difficulties are very great, owing to the extreme slenderness of the threads, the matter cannot be regarded as finally settled. It is fairly clear, however, that leptotene chromosomes are both longer and thinner than those at a comparable stage of mitosis, and that the chromomeres are much more obvious as discrete entities. If there is any spiralization at all in leptotene chromosomes it is at a minimum.

During the next stage (zygotene) the homologous chromosomes come together, side by side, throughout their entire length. This process, known as *pairing*, seems to result from a force of attraction which is exerted between homologous genes or parts of the protein framework of the chromosomes. The 'pairing force' is still hypothetical, since it has not yet been studied experimentally; but there seems to be no other way of interpreting the fact of pairing. From a physical point of view this force must possess two very remarkable properties: it must be *specific* (i.e. exerted only between regions having an identical structure), and it must be operative over relatively considerable distances (up to several μ). There can be little doubt that the zygotene pairing force is similar in kind to the 'somatic pairing force' of the Diptera, which is responsible for the pairing of the salivary-gland chromosomes. Some speculations as to the physical nature of the pairing force have recently been put forward by Muller (1941) and Fabergé (1942). It is clear that zygotene pairing is not an instantaneous process, but takes some time to be completed—thus a cell which is killed in the

middle of the zygotene stage will have some parts of its chromosomes paired and others still unpaired. The pairing starts at one or more points and spreads slowly along the length of the chromosome in a 'zipper-like' manner. If the



Text-fig. 23. General diagram of meiosis in an imaginary organism with three pairs of autosomes and an *XO* sex chromosome mechanism. *a* = leptotene; *b* = pachytene; *c* = diplotene; *d* = first metaphase.

organism is structurally homozygous—that is to say, if the two haploid sets of chromosomes have the same gene sequences—zygotene pairing will lead to a condition in which every chromosome is lying alongside its homologue with almost no space between (see the figures of Gelei, 1921, 1922). The apparent number of threads is thus half what it was before, the visible bodies in the nucleus being henceforth *bivalents* and not single chromosomes. If any chromo-

some (such as a sex chromosome) lacks a homologue, it will be unable to undergo pairing, but the fact that it is a *univalent* will not prevent it from going through the processes of nucleination, etc., which lead up to metaphase. In cells that are heterozygous for structural rearrangements, such as translocations, the pairing of homologous parts is usually complete, irrespective of the fact that one chromosome may have to pair in different regions with parts of two others. Thus where an inversion is present a 'reversed loop' will be formed exactly as happens under similar circumstances in salivary-gland nuclei (Text-fig. 36*a*, *b*). If the inverted region is very short, however, it may remain unpaired.

The arrangement of the threads within the leptotene and zygotene nuclei is rarely, if ever, random. In all probability the disposition of the chromosomes at leptotene facilitates the 'finding' by each chromosome of its homologue. Unfortunately it is not possible, save in very rare instances, to distinguish individual chromosomes at leptotene.

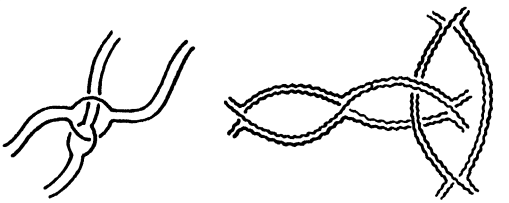
Two kinds of arrangement have been distinguished in leptotene nuclei of different groups of organisms. In the first type the chromosomes are tangled up to one side of the nucleus, leaving the rest of the nuclear cavity almost empty. In the second type of arrangement the chromosomes are distributed throughout the nucleus but all their ends are gathered together in a small area somewhere on the surface of the nucleus, so that the threads all radiate out from this area, running more or less parallel and looping back when they come to the other side of the nucleus. The first type of arrangement is probably a fixation-artefact, but the 'polarized' orientation is undoubtedly a genuine phenomenon. How it arises is somewhat obscure. In some cases it may be due to a persistence of the telophase orientation of the previous division: but this can hardly be so where chromosome-ends, and not centromeres, are brought together on one side of the nucleus. More probably there is some kind of unspecific attraction between chromosome-ends that draws them together in the pre-leptotene nucleus, as they are often drawn together in salivary nuclei. On the other hand, in some organisms pairing is probably initiated in the telophase of the last premeiotic division (S. G. Smith, 1942).

Usually the chromosomes do not become interlocked as they undergo pairing, but occasionally two pairs of chromosomes may come together in the manner shown in Text-fig. 24. Such an event must be regarded as an extremely rare accident, probably due to a disturbance of the normal orientation of the chromosomes at the time when they are undergoing pairing.

When the pairing process has come to an end the nucleus may be said to have entered upon the pachytene stage. The chromosomes are now considerably shorter and thicker than at leptotene; each bivalent consists of two threads which appear to be slightly separated in fixed preparations but may be in contact in life. As a result of the shortening and thickening which have gone on, the 'ultimate' chromomeres are no longer visible and the outline of the chromosome threads

is irregular and 'woolly' just as it is in a mid-prophase chromosome at mitosis.

Darlington (1935*a*, 1940*c*) considers that nucleoli may delay or prevent pairing in their immediate neighbourhood, thus suppressing crossing-over for a short distance on either side; but this view is not supported by the observations of S. G. Smith (1942).



Text-fig. 24. Diagram showing how interlocked bivalents occasionally arise through accidental interlocking during pairing.

It will be recalled that the leptotene chromosomes are regarded by Darlington as unsplit. This author believes that the division of the chromosomes into chromatids takes place during pachytene. On this view the pachytene bivalents consist of two strands at first and of four strands later on. Certain other workers believe that the division of the chromosomes has taken place at a much earlier stage, before leptotene. Whichever view is correct, it is certain that by the end of the pachytene stage each bivalent consists of four chromatids, all lying parallel and separated by two 'splits' at right angles to one another. One of these splits corresponds to the space between the maternal and paternal chromosomes, the other to the division of the chromosomes into chromatids. The pachytene bivalents may be spirally twisted so that each homologue is wound once or twice round the other, but this is not always the case, especially in short chromosomes. Usually the 'polarized' orientation of the chromosomes is retained during pachytene, although it may have disappeared by the end of this stage.

The beginning of the diplotene stage is characterized by a remarkable change which takes place in the structure of the bivalents. The attraction between the homologues seems to come to an end, and the two chromosomes of each bivalent separate from one another, so that they are only held together at a few points where two of the chromatids cross-over from one chromosome to the other, forming an *X*. These chromatid exchanges are called *chiasmata*, and it is known that they correspond to the genetical cross-overs. At each chiasma two out of the four chromatids (one of maternal, the other of paternal origin) have broken transversely and then rejoined in the opposite way to the original one.

The number of chiasmata per bivalent varies from 1 to about 10. A general relationship exists between the length of the chromosome and the number of chiasmata. Very short chromosomes show only a single chiasma, and never 0 or 2.

Medium-sized chromosomes may show 1–4, the number varying even in the same bivalent in different cells. In some organisms all the bivalents show about the same number of chiasmata, while in others there may be an approximate proportionality between the length of the chromosome and the number of chiasmata. Direct proportionality is not always found, however, and in some instances short chromosomes have more chiasmata, on the average, than longer ones, even in the same organism (White, 1936*a*). The literature on chiasma frequencies is now quite extensive and will be discussed later (pp. 82–86).

The appearance of the bivalents at diplotene naturally depends upon the number of chiasmata they contain. Thus corresponding bivalents which are genetically identical may look quite different in different cells because the number of chiasmata is not the same. A bivalent with a single chiasma has the form of a cross, each of the four limbs being composed of two chromatids lying side by side. A bivalent with several chiasmata appears as a series of loops (Text-fig. 23), with an incomplete 'half-loop' at each end.

A number of different theories have been put forward as to the cause of crossing-over. It seems clear that the actual breakage of the chromatids must be due to some kind of mechanical strain which is relieved when they break: but it is not known why the two chromatids should always undergo fragmentation at exactly the same level; possibly the breakage of one suddenly increases the mechanical strain on the other so that it breaks immediately afterwards. Darlington (1935*b*) has suggested that crossing-over occurs simultaneously with the splitting of the chromosomes; he believes that it results from a torsional stress due to the spiralization of the chromosomes, which are wound round one another at pachytene. This winding of one homologue round the other does not seem, however, to be universal, and is probably always absent in very short chromosomes, where crossing-over nevertheless occurs. Moreover, in endless 'ring chromosomes', which could hardly become relationally coiled round one another, crossing-over is almost normal.

An alternative hypothesis as to the cause of crossing-over has recently been put forward (White, 1942*a*). It is based on the idea that the splitting of the chromosome thread is probably not simultaneous along its whole length. If we imagine that the unsplit parts are still held together while the split ones are separating, it follows that a localized strain will develop at the meeting-point of the split and unsplit regions (Text-fig. 25). The idea that splitting does not take place quite at the same time all along the length of the chromosome is supported by observations on salivary chromosomes in which multiplication of the protein framework seems to proceed at different rates in different regions of the chromosome (see p. 40). Moreover, Schultz (1941*b*) has recently produced some evidence that the *Y* of *Drosophila melanogaster* splits less often than the euchromatic regions in endopolyploid nuclei. There are thus grounds for believing that the regions which split tardily may (in many instances at any rate) be the hetero-

chromatic segments. When we turn to the data on chiasma localization we find that the regions where cross-overs occur most frequently often lie near the boundaries between heterochromatic and euchromatic regions. Thus in the grasshopper *Mecostethus grossus* ten of the eleven bivalents have a single large heterochromatic 'block' adjacent to the centromere (Janssens, 1924; White, 1936*a*); these chromosomes almost invariably form a single chiasma in the euchromatic region, but very close to the 'frontier' (Text-fig. 26). In the eleventh bivalent there are two large heterochromatic blocks, one proximal, the

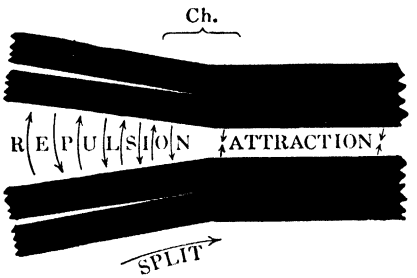
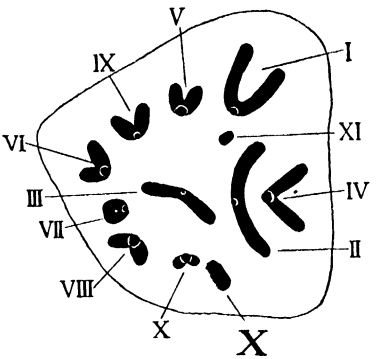


Fig. 25. Diagram illustrating the theory of chiasma formation explained in the text. Ch. = region where the chiasma will be formed.



Text-fig. 26. First metaphase in the grasshopper *Mecostethus grossus*. Each bivalent except VII shows a single chiasma near the centromere. VII has two chiasmata, and consequently forms a small ring bivalent. From White (1937*b*).

other distal, and this is the only chromosome which regularly forms two chiasmata (some of the others do so occasionally). In *Schistocerca gregaria*, where all the larger chromosomes have both proximal and distal heterochromatic regions, a chiasma is usually found in the neighbourhood of both 'frontiers'. It must not be supposed, however, that each frontier always produces a single chiasma: if this were so the number of chiasmata in a particular bivalent would be absolutely fixed instead of varying within certain limits. Moreover, in the 'megameric' bivalent of some grasshoppers there may be as many as 26 'frontiers' (Carlson, 1936)—but only one or two chiasmata are formed in this bivalent.* It is even unlikely that there is a strict correspondence between heterochromatic regions and those which split at a different time (i.e. some segments which split tardily may be euchromatic). But it now appears virtually certain that crossing-over results from an alternation of different types of protein framework in the chromosome and that certain regions *always* produce a chiasma while others do

* It is also necessary to point out that in *Drosophila* the cross-overs are mostly situated some distance away from the frontiers between eu- and hetero-chromatin.

so in some bivalents but not in others, thus leading to the observed variation in number of chiasmata (some chromosomes are invariable, always forming a single chiasma, but where the chiasma frequency is above 1·0 there is probably always some variance). The only naturally occurring chromosomes with a chiasma frequency of less than 1·0 are the 'supernumerary chromosomes' found in some organisms (see p. 119). These have probably been derived from fragments of chromosomes present elsewhere in the set; they are usually heterochromatic and probably lack a 'frontier' which will produce a cross-over on every occasion. Metacentric chromosomes always seem to have one limb with a chiasma frequency equal to or greater than 1·0, though the chiasma frequency of the other arm may be less than unity.

If the 'theory of frontiers' has any validity it furnishes an additional explanation for the existence of the heterochromatic regions and especially for the very orderly way in which they are distributed throughout the chromosome set. It may at first sight appear as if the 'theory of frontiers' required that chromosome splitting should occur at pachytene and not at leptotene or earlier. Actually, however, there may be several 'degrees of splitting', only the last of which is effective in determining crossing-over. Thus if chromosomes consist of a 'chromonema' and 'matrix' the former may undergo splitting before the latter.

There is always a certain minimum distance between successive chiasmata. Thus the occurrence of a cross-over at a particular locus altogether prevents the formation of another within a certain region, beyond which the probability of a second cross-over being formed gradually increases. This phenomenon, which was first discovered genetically, is known as *interference*. Some chromosomes may be shorter than their own interference distance, so that they never have a chance to form a second chiasma. Mechanically, interference probably means that crossing-over immediately releases a localized tension in that part of the bivalent, so that there is no further tendency to form a second chiasma. Haldane (1931) has calculated the amount of interference in various species of plants by comparing the frequencies of bivalents with 1, 2, 3, ... chiasmata with the Poisson distribution that would be expected if there were no interference. The amount of interference varies considerably, even in different parts of the same chromosome. In *Drosophila* and maize, at any rate (Rhoades, 1941), there is no genetical interference across the centromere region. It has been suggested that this indicates that two chiasmata may be separated by less than the 'prohibited' distance provided that there is a centromere between them, but since most centromeres have a genetically inert region on either side it is doubtful if this conclusion is really valid.

It is not clear just why the pairing attraction between homologous chromosomes lapses at the end of pachytene; one suggestion that has been put forward is that the force of attraction is sufficient to keep two threads together, but inadequate to maintain all four in the 'paired' condition. On this view the

separation of the homologues is a direct consequence of the splitting of the threads—as soon as they have divided, the attraction between the maternal and paternal chromosomes is replaced by an attraction between the 'sister' chromatids of each chromosome. An alternative view is that the lapsing of the pairing force is somehow bound up with the progressive nucleination and spiralization of the protein framework (it will be recalled that the 'somatic pairing' of dipterous chromosomes becomes less close towards the end of the prophase stage).

The fact that each chiasma does really represent a single genetical cross-over has now been established in a number of different ways (Darlington, 1930; Mather, 1933). It had earlier been assumed that the breakage of the chromatids took place at a later stage (i.e. metaphase or anaphase), and that the loops between the chiasmata were alternately 'reductional' and 'equational'. It is now known, however, that the loops are always 'reductional', i.e. two paternal chromatids are paired on one side of the loop and two maternal ones on the other (Text-fig. 28). Thus crossing-over has already occurred *before* the appearance of a visible chiasma, and the 'opening out' of the bivalent is always in the 'reductional' plane, i.e. along the split between the two original chromosomes and not along that at right angles to it. Since each chiasma represents a crossing-over between two out of the four chromatids it follows that a chromosome with a chiasma frequency of 1·0 will show 50% crossing-over, i.e. it will have a genetic length of 50 units. It is thus possible to predict the total map-lengths from chiasma frequencies and vice versa.*

After diplotene the nucleination of the bivalents proceeds and the loops between the successive chiasmata open out widely. At the same time there is in some organisms a tendency for the chiasmata to 'slip along' the bivalents towards the ends, so that the position of the chiasma no longer coincides with that of the original cross-over. In some instances the process of terminalization is so complete that some or all of the chiasmata are forced along to the very ends of the chromosome. When this happens, however, the ends of the homologues always remain attached to one another in an end-to-end fashion, so that the two halves of the bivalent are still held together at one or both ends. In some instances several chiasmata may be 'terminalized' to the same chromosome-end, so that it is no longer possible to tell from an inspection of the bivalents how many chiasmata were present at an earlier stage. Many authors have spoken

* Map-lengths calculated in this manner may be longer than the genetically known region of the chromosome. Since the known genetic length of the small IVth chromosome in *Drosophila melanogaster* is only about 0·2, many geneticists seem to have assumed that this chromosome only rarely forms a chiasma. It would seem more probable that it always forms a single chiasma, but that this chiasma usually occurs in the inert region or at any rate beyond the genetically known region between the genes *bent* and *eyeless*. The statement made by Griffen and Stone (1940*b*) that the IVth chromosome contains no heterochromatin is almost certainly incorrect (see Slizynski, 1941).

of bivalents in which chiasmata are formed near the ends (or terminalized at a later stage) as *rod-* or *ring*-bivalents, according to whether the homologues are held together at one or both extremities.*

These processes (nucleination and terminalization) lead to the stage known as diakinesis, which corresponds to the late prophase of an ordinary mitosis. By this time the alternate loops in a bivalent with several chiasmata have usually come to lie in planes at right angles to one another, so that the general appearance is similar to that of a chain stretched out tightly.

Usually the bivalents are entirely free from one another from pachytene onwards, but in some species where the chromosomes have extensive heterochromatic regions at both ends several bivalents are often attached to each other in an end-to-end manner. These terminal associations may persist until diakinesis in some forms such as the Corixidae *Sigara carinata*, *Corixa punctata* and *Cymatia bonsdorffi* (Slack, 1938*b*) and the pentatomid *Edessa irrorata* (Schrader, 1941*a*), but the bivalents always seem to break free before metaphase. These terminal associations of heterochromatic segments are probably analogous to the associations between the distal ends of the chromosomes in many salivary nuclei (see p. 42).

In some grasshopper species where there is a 'megameric' bivalent (i.e. one with very extensive heterochromatic segments) a close association exists between it and the heteropycnotic *X*-chromosome at diplotene and diakinesis. Thus the megameric chromosome of *Mecostethus grossus* was referred to by Janssens (1924) as the 'dyade compagnon de l'*X*', since it lies alongside the *X* and may even appear to be stuck on to the side of it. But since the heteropycnosis of the *X* is of the reversible type, while that of the 'megameric' is not reversed (see p. 27), it would seem that no real genetical homology is involved and that this association, like that between the ends of the bivalents in *Edessa irrorata* and the Corixidae mentioned above, results from a non-specific attraction between all types of heterochromatin.

In some species the nucleic acid content of the chromosomes is at a low level during diplotene, so that they are difficult to observe. Some authors speak of a 'confused' or 'diffuse' stage in these species. The 'confused stage' is, however, merely a superficial modification of the normal diplotene condition and does not occur in most groups.

In oogenesis the diplotene nuclei are always very large and the stage may last a very long while (up to months or years in the case of yolky eggs such as those

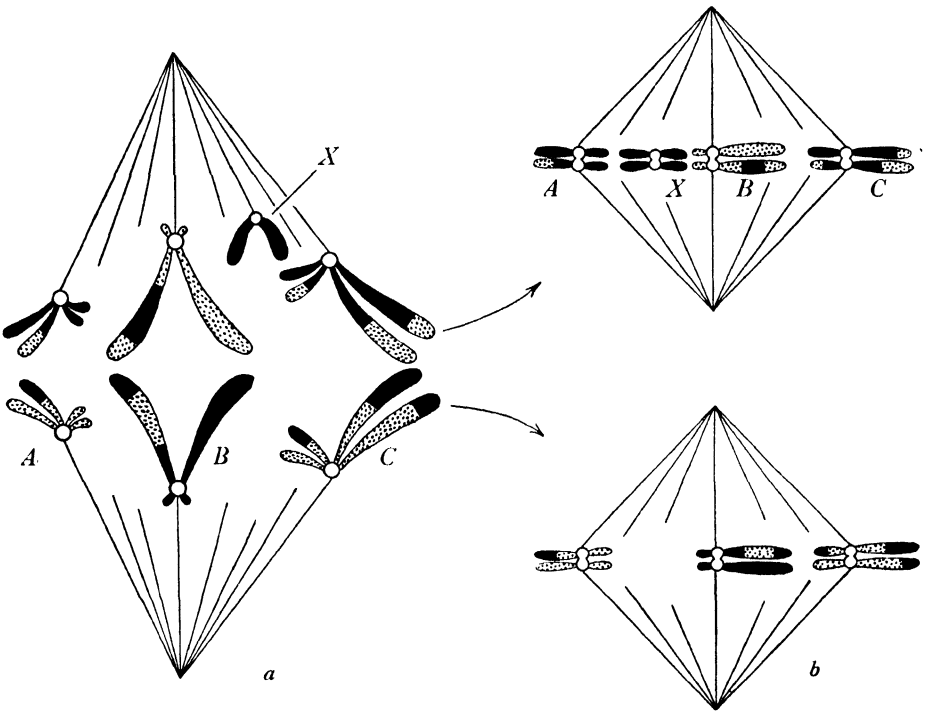
* The old controversy between the adherents of the theory of *telosynapsis* and those who believed in the alternative viewpoint (*parasynapsis*) is only of historical interest, since 'parasynapsis' (i.e. side-by-side pairing of homologous chromosomes at zygotene) is now known to be universal. The believers in telosynapsis observed diplotene or diakinesis bivalents in which the chromosomes were only held together by their ends (by 'terminalized' chiasmata, as we now know), and concluded that an end-to-end pairing, rather than a side-by-side one, had occurred at an earlier stage. Since the controversy is now settled, the cumbrous terminology associated with it can be discarded.

of birds). The chromosomes are correspondingly large and have a curious irrégular outline rather like a lamp brush (or its more familiar laboratory equivalent, a test-tube brush). 'Lamp-brush' chromosomes may be seen in the oocytes of all groups of Vertebrata with yolky eggs (elasmobranchs, Amphibia, reptiles and birds). They were studied by Rückert (1892) in the shark *Pristiurus*, and more recently by Duryee (1941) in Amphibia and Koltzov (1938) in birds. The largest chromosome in the domestic chicken may be 70–80 μ long in the diplotene oocyte, so that these 'lamp-brush' chromosomes approach the dimensions of salivaries, although they do not show any distinct banding. They gradually decrease in size as they approach metaphase, their nucleic acid content increasing at the same time.

Following upon diakinesis the nuclear membrane disappears and the spindle of the first meiotic division begins to form between the chromosomes, just as in an ordinary mitosis. The essential difference from a somatic division lies in the way the chromosomes are attached to the spindle. At the first meiotic division each bivalent possesses two independent centromeres, and these arrange themselves not on the equator of the spindle, but an equal distance above and below it.

At the anaphase of the first division the centromeres do not split: each one travels towards the nearest pole, dragging the attached chromatids after it. Thus in the course of this anaphase each bivalent is torn in half, the chiasmata slipping along to the ends if they have not already done so during the process of 'terminalization'. There is in general no special tendency for maternal and paternal chromatids to go to the same or to opposite poles at anaphase; thus as a general rule the various pairs of autosomes segregate independently of one another and of the sex chromosomes, so that in *Drosophila melanogaster* with four bivalents all the paternal centromeres will go to the same pole (and all the maternal ones to the other) once in 16 times, while in the moth *Phigalia pedaria* with 112 bivalents this event will happen only once in 2^{112} divisions. In a few special cases non-random segregation of independent chromosomes takes place at meiosis. Thus it has been shown by Sturtevant (1936) that in triplo-IV individuals of *Drosophila melanogaster* (flies with three IVth chromosomes) each IVth chromosome shows a slight but significant deviation from randomness in relation to the segregation of the other two. At the second meiotic division the chromosomes are univalent in structure, i.e. they consist of a centromere and two limbs each of which is made up of two chromatids. The split between the chromatids is often very wide, but no further split becomes evident between the first and second divisions. Thus meiosis has sometimes been shortly defined as two successive cell divisions in the course of which the chromosomes only split once (at pachytene or earlier). There are some indications, however, that the split corresponding to the second division is not always completely suppressed, although it cannot normally be seen. Thus in certain interspecific

hybrids in the lepidopteran genus *Pygaera* (see p. 220) the chromosomes of the parent species fail to pair at meiosis and remain univalent. They then split in both the meiotic divisions, so that the spermatids eventually contain the somatic number of chromosomes. Another instance where chromosomes split in both meiotic divisions is in the so-called sex-ratio condition in *Drosophila pseudoobscura* where the *X* chromosome divides twice during meiosis, so that



Text-fig. 27. Diagram showing the genetical consequences of meiosis. Maternal portions of chromosomes black, paternal parts stippled. *a* = first anaphase; *b* = second metaphases.

all four sperms come to contain an *X*. These and other facts suggest that the second split may exist at any rate potentially, and that it is capable of manifesting itself under special circumstances.

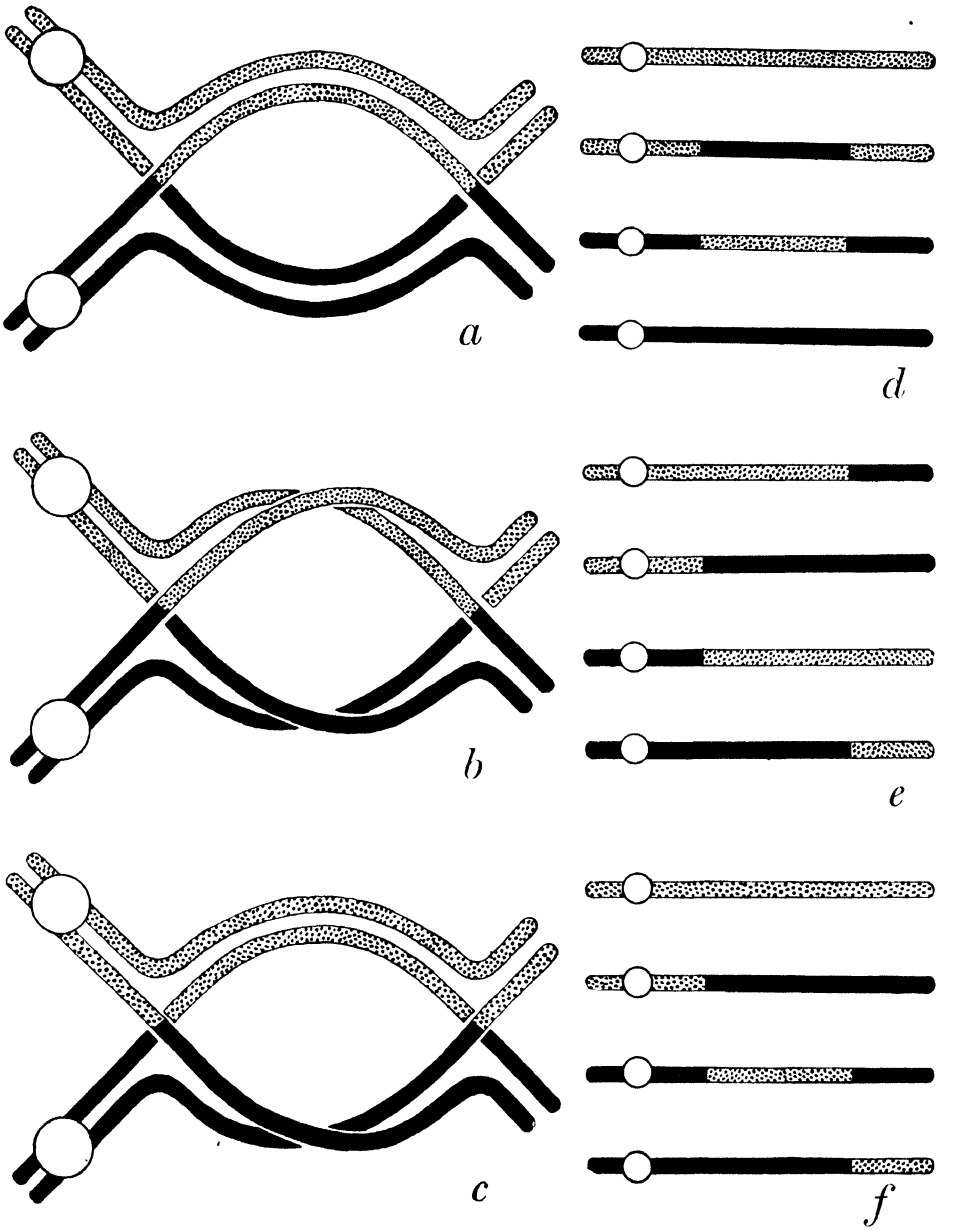
The second meiotic division looks like an ordinary mitosis except that the chromatids frequently diverge widely from one another, so that an acrocentric chromosome looks like a V and a metacentric one like a cross with the centromere in the middle. This divergence of the chromatids at the second division is probably due to the way the chiasmata have been dragged along the chromosome at the anaphase of the first division. At the second anaphase the centromeres divide and the half-chromosomes pass to the poles.

Such, in outline, is the process of meiosis. It will be obvious that the two divisions must be considered together. Before the significance of crossing-over was generally understood much discussion took place as to whether the first or the second meiotic division was the *reductional* one (the other being conceived of as an *equational* division, similar to an ordinary mitosis). It will be realized that the disagreement is meaningless if one thinks in terms of whole chromosomes. It is now certain that the first division is always reductional for the centromeres and for parts of the chromosome proximal to the first chiasma, but equational for the region between the first and second chiasmata (Text-fig. 27). The second division is naturally equational at the centromere and reductional between the positions of the first and second cross-overs.

Four different relationships may exist between two successive chiasmata in the same bivalent. If we call the chromatids A, A', B, B', then if A and B cross-over in the first chiasma the chromatids that cross-over in the second one may be A and B, A and B', A' and B, or A' and B'. These different relationships and the nomenclature used to describe them are shown in Text-fig. 28. Unfortunately it is only rarely possible to distinguish reciprocal, complementary and diagonal pairs of chiasmata under the microscope owing to the difficulty of following the course of the chromatids between the chiasmata.

From a genetical standpoint two reciprocal chiasmata give rise to two double cross-over chromatids and two non-cross-overs, a pair of complementary chiasmata produce four single cross-over strands, while diagonal chiasmata give rise to one double cross-over, two single cross-over and one non-cross-over strand.

The significance of chiasmata seems to be twofold. In the first place they permit recombination of genes situated in different homologous chromosomes and separation of those in the same chromosome. If there were no crossing-over the linkage groups would be permanent and unchangeable apart from mutation, and would constitute the only units of heredity. It is easy to see how disastrous this would be in the course of evolution—many 'advantageous' genes would be permanently linked with 'disadvantageous' ones and natural selection would not result in the building up of 'desirable' genic combinations. Chiasmata, by permitting a 'shuffling' of the genes, are thus a positive factor in the evolutionary process. On the other hand, an unlimited amount of crossing-over would prevent the formation of any stable combinations of genes altogether. There is thus probably an optimum amount of crossing-over for each type of genetic system. Darlington (1937*a*, 1939*b*) has used the term *recombination index* to indicate the sum of the haploid number and the chiasma frequency of an organism. This index represents the average number of chromosome regions which segregate independently at meiosis; it is consequently a measure of the total amount of linkage in an organism. In *Drosophila melanogaster* with four chromosome pairs and no crossing-over in the male the recombination index is



Text-fig. 28. Reciprocal (*a*, *d*), complementary (*b*, *e*) and diagonal (*c*, *f*) pairs of chiasmata. The reciprocal and complementary types of relationship are sometimes described as *compensating*, diagonal pairs of chiasmata being *non-compensating*.

about 10·6 in the female,* and 4·0 in the male. Most species of grasshoppers have recombination indices of about 27–32 in both sexes, while organisms with very high chromosome numbers may have indices of 200 or more. Whether any sexually reproducing metazoan or higher plant exists in which crossing-over has been abolished in both sexes is unknown; none has been discovered so far, but in view of the very small amount of work that has been carried out on the cytology of oogenesis, that is to be expected in any case.

Darlington (1939*b*) has considered the frequency of crossing-over as a quantity likely to be affected by selection, provided that one considers periods of time sufficient for the evolution of species and genera; but if crossing-over depends on the sequence of different types of protein framework in the chromosome it is probable that the selectional control is of a more indirect kind.

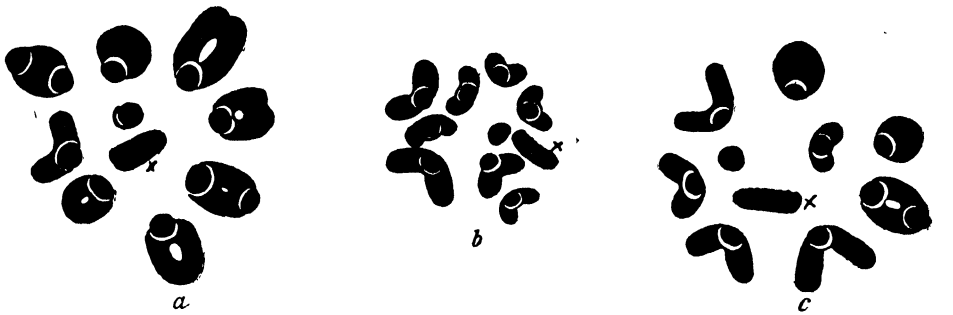
The second 'function' of the chiasmata seems to be a purely mechanical one. By holding together the chromosomes of which the bivalents are composed they ensure that the two centromeres of each bivalent travel to opposite poles of the spindle at the anaphase of the first meiotic division. There are, of course, organisms (the male *Drosophila* being the best-known example) in which the association of the chromosomes in the paired condition is maintained between pachytene and metaphase without chiasmata being present. But these cases are exceptional, and in any 'ordinary' animal or plant if a bivalent fails for any reason to form at least one chiasma at pachytene it then falls asunder and the two univalents behave henceforth independently, and may travel to the same pole at the first meiotic division. It is no doubt due to this reason that all normal chromosomes form at least one chiasma at meiosis (chromosomes with a chiasma frequency of less than 1·0 would be inherited too irregularly to form part of the normal chromosome set of a species). Only in a few groups have alternative meiotic mechanisms been evolved which circumvent the necessity for crossing-over.

Localization of crossing-over is probably universal; that is to say, the chiasmata are always found more frequently in some chromosome regions than in others. In many instances, however, localization is so slight that it is only detectable with difficulty by cytological methods (it is not easy to measure accurately the distances of chiasmata from one another or from some fixed point such as the centromere or chromosome-end). In the genetical maps of *Drosophila* species the genes appear crowded on either side of the centromeres and to a lesser extent at the ends of the chromosomes. It is now known that this apparent crowding is merely due to the rarity of crossing-over in those sections—it does not indicate that the genes are really closer together in the centric regions.

* We have made the following assumptions in calculating this figure:

Haploid chromosome number	=4·0
Chiasma frequency of chromosome IV (mostly in heterochromatin)	=1·0
Chiasma frequency of I + II + III (based on a combined genetic length of about 280 units)	=5·6
	10·6

The commonest kinds of localization are (1) the proximal type, where the chiasmata are confined to the regions next to the centromeres (seen in its most extreme form in the grasshoppers of the genera *Mecostethus* (McClung, 1914, 1927, 1928; Janssens, 1924; White, 1936*a*, 1937*b*) and *Osmilia* (White, unpublished)), and (2) the distal type, where the chiasmata are confined to the ends of the chromosomes (seen in some other grasshoppers such as *Philocleon* (Helwig, 1941)). Not infrequently the two types are combined, as they are in the larger chromosomes of the grasshoppers *Arphia* and *Tropinotus*, where there is usually a single chiasma at each end of the bivalent with an intermediate region in which little or no crossing-over takes place. The chromosomes of a particular species do not all necessarily show the same type of localization, although they often



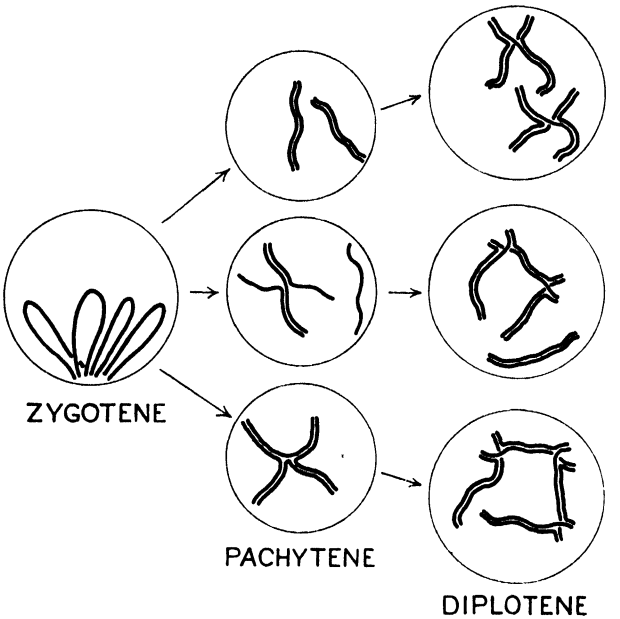
Text-fig. 29. First metaphases in three species of Pyrgomorphine grasshoppers (10-chromosome group). *a* = *Aularches milaris* (7 ring-bivalents with two chiasmata each); *b* = *Pyrgomorpha bispinosa* (no ring bivalents, i.e. each bivalent with only one chiasma); *c* = *Chrotogonus* sp., showing three ring bivalents. From Rao (1937).

show the same kind in different degrees. Thus in many Acrididae and Tettigoniidae localization is of the proximal-distal type in the larger bivalents, proximal only in the shorter ones. The statement that the chiasma frequency is proportional to chromosome length is only approximately true—usually small chromosomes have more chiasmata relative to their length than larger ones in the same species, and there are even cases of small chromosomes which have an absolutely higher number of chiasmata (not merely relative to their length). The evolution of localization is a subject which has been very little studied. In most genera of grasshoppers all the species seem to have the same general type and degree of localization; thus *Mecostethus gracilis* and *M. lineatus* have the same extreme proximal localization as *M. grossus* (McClung, 1928), and Ch'en (1942) has shown that a species of the closely related genus *Arcyptera* also has the same type of localization. On the other hand, in the genus *Trimerotropis* there are two groups of species in one of which localization is proximal-distal in the longer chromosomes, while in the other it is exclusively distal (see p. 115).

Very few direct comparisons have been made between chiasma frequencies and chiasma localization in the two sexes of the same organism. In the fowl the

genetical evidence suggests that the amount of crossing-over is about the same in the cock and hen (Warren, 1940), while in the mouse Crew and Koller (1932) showed cytologically that the female had slightly more chiasmata than the male. In the neuropteran *Macronemurus appendiculatus* (Text-fig. 101) there seems to be a higher chiasma frequency in the male (Naville and de Beaumont, 1933).

In acrocentric chromosomes no chiasma is formed, as a rule, in the short arm beyond the centromere. Occasionally, however, acrocentric bivalents have been

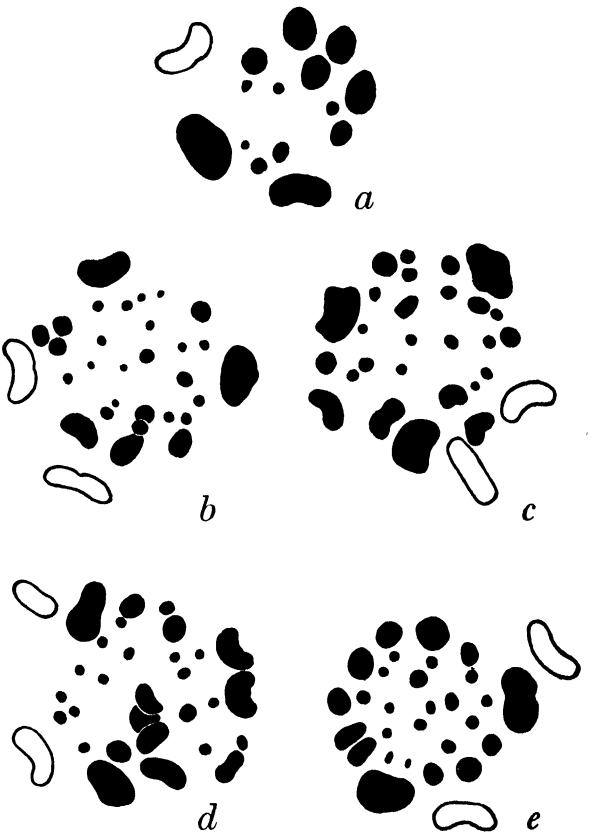


Text-fig. 30. Diagram showing how four homologous chromosomes in a tetraploid may behave in several different ways at meiosis, forming bivalents, trivalents or quadrivalents.

described in which a chiasma exists in the short arm but not in the long one. Such bivalents have been called *ditactic* by McClung and Helwig, who have figured them in *Mecostethus* and other genera of grasshoppers.

A great deal has been learnt about the physiology of meiosis by studying the process in polyploids. In animals polyploid species are so few in number that there is not much opportunity for investigations of this kind. On the other hand, nearly all animal species show occasional tetraploid spermatocytes which have arisen in the testis through failure of one or more spermatogonia to divide completely. Sometimes a single tetraploid spermatocyte is found, surrounded by diploid ones; more usually they occur in groups of 2, 4, 8, 16 or 32. In the long-horned grasshopper *Tettigonia viridissima* a cyst of 256 tetraploid spermatocytes was found in one individual (White, unpublished).

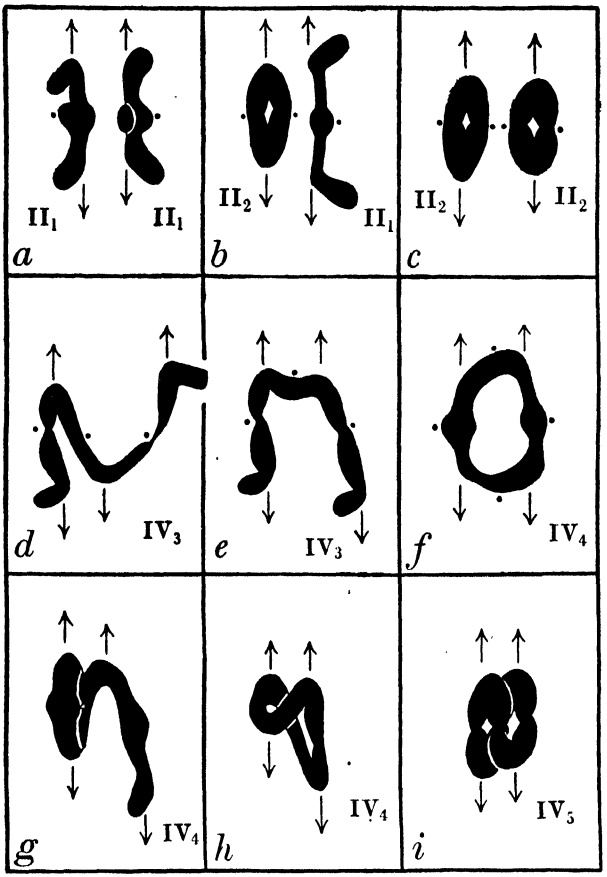
In cells of this type every autosome will be represented four times, while the *X*'s and *Y*'s will be represented twice (Wilson, 1932; White, 1933; Klingstedt, 1937*a*; Moffett, 1936; Makino, 1939*a*). Each set of four homologous autosomes can behave in three different ways at meiosis. It may form (1) a single quadrivalent, (2) a trivalent and a univalent, (3) two bivalents (other theoretical



Text-fig. 31. A diploid and four tetraploid first metaphases in *Tettigonia viridissima*. Not counting the *X* chromosomes (shown in outline) which are always unpaired at metaphase, *b* and *d* show 27 bivalents and 2 univalents, *c* one quadrivalent and 26 bivalents and *e* 28 bivalents.

possibilities such as four univalents or a bivalent and two univalents hardly ever occur). Which of these events happens in any particular case seems to depend on a number of factors. Where the region of complete interference is longer than the chromosome no multivalents can, of course, occur, since only one chiasma can be formed. Thus very short chromosomes will always form two bivalents in a tetraploid spermatocyte. But length is not the only factor which controls the formation of multivalents. It is now generally agreed that in a polyploid cell

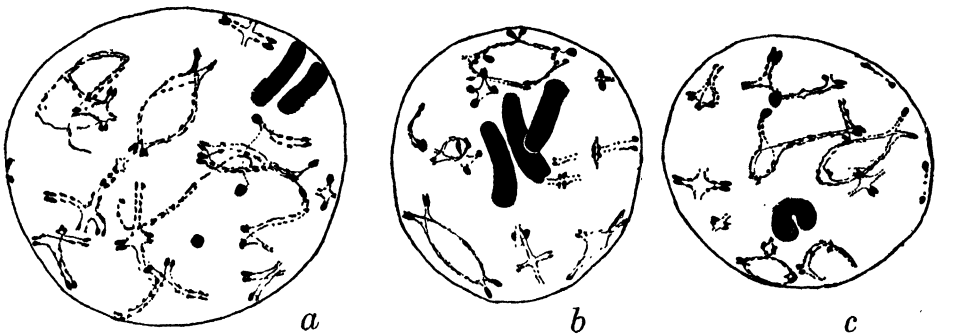
chromosome A may be paired with portions of A' and A'' at different levels, but that more than two chromosomes are never associated at the same level in meiosis. Thus the speed at which the pairing spreads along the length of the



Text-fig. 32. Behaviour of the largest chromosome in nine tetraploid spermatocytes of *Tettigonia viridissima*. In *a*, *b* and *c* the four chromosomes have formed two separate bivalents (II_1 is a bivalent with one chiasma, II_2 a bivalent with two chiasmata). In *d–i* the four chromosomes have formed a quadrivalent (IV_3, IV_4 and IV_5 being quadrivalents with 3, 4 and 5 chiasmata respectively). The arrows indicate the positions of the centromeres and the dots (in *a–f*) the positions of the chiasmata. *d* and *e* are 'chain quadrivalents', *f* is a 'ring quadrivalent'.

chromosomes must play some part in determining the frequency of multivalent formation in a polyploid cell (if pairing were instantaneous no multivalents would be formed, while if it were very slow every chromosome would be part of a multivalent at pachytene, although some might fall asunder in diplotene, owing to failure of chiasma formation).

In the coreid bug *Archimerus* all the ordinary autosomes form bivalents in tetraploid spermatocytes (Wilson, 1932). The situation seems to be essentially similar in tetraploid cells of those Orthoptera which have few chiasmata even in the longer chromosomes (e.g. *Podisma*, studied by Makino, 1939*a*). On the other hand, in grasshoppers such as *Schistocerca gregaria* (White, 1933) and *Chrysochraon* (Klingstedt, 1937*a*) the longer chromosomes form 2–4 chiasmata in the diploid cells, so that there is a fair chance that these longer members of the chromosome set will form trivalents or quadrivalents in a tetraploid cell. *Tettigonia viridissima* occupies an intermediate position: the only chromosome



Text-fig. 33. Tetraploid spermatocytes of the grasshopper *Schistocerca gregaria* in early diplotene. *a* = a cell with the full tetraploid number of chromosomes (four sets of autosomes and two *X*'s); *b* and *c* are a pair of cells of which the first contains three *X*'s, the second only one (the result of non-disjunction at the last pre-meiotic division). Not all the autosomes are drawn—note that most of them end in heteropycnotic 'blobs'.

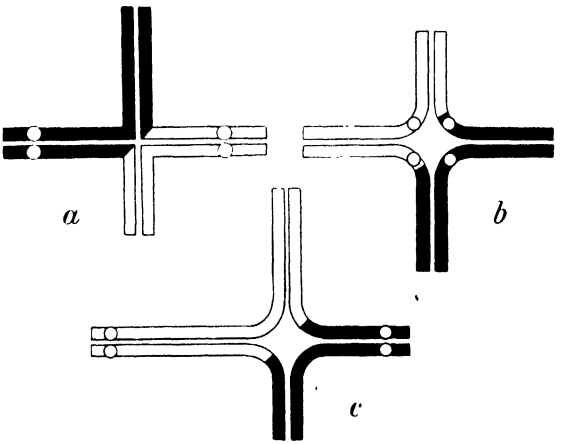
that regularly forms a quadrivalent in a proportion of the tetraploid cells is a big metacentric one which has a chiasma frequency of about 2·0 in ordinary diploid spermatocytes (Text-figs. 31 and 32).

The behaviour of the sex chromosomes in these tetraploid nuclei is instructive. In the Orthoptera the *X* chromosome is strongly positively heteropycnotic during spermatogenesis, and this heteropycnosis is equally strongly manifested in tetraploid spermatocytes as well as in hypo- and hyper-tetraploid ones, with 1 and 3 *X*'s respectively (Text-fig. 33). But the *X*'s never form chiasmata in these cells, so that although they are closely paired at pachytene they fall apart later and are univalents at the first metaphase (Text-fig. 31). This behaviour is in striking contrast to what happens in normal diploid oocytes, where the two *X*'s are not nearly so strongly heteropycnotic and form a true bivalent in which they are held together by chiasmata (McNabb, 1928). The only conclusion that can be drawn is that intense positive heteropycnosis in some way prevents chiasma formation. Tetraploid spermatocytes presumably give rise to diploid sperms, but it is not known whether these are ever functional in insects.

If so they should give rise to occasional triploid individuals, which would probably be sterile.

So far we have been considering meiosis in organisms which are 'structurally homozygous', i.e. in which the sequence of chromosome parts is the same in the two haploid sets. In individuals which are heterozygous for structural rearrangements pairing may be either complete or incomplete, some regions (but usually only short ones) being left in the unpaired condition.

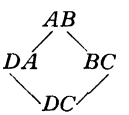
In an individual which is heterozygous for a reciprocal translocation the four chromosomes will usually pair in such a manner as to form a cross at pachytene



Text-fig. 34. Pachytene pairing in translocation heterozygotes. Pairing is always interrupted in the middle of the cross as in *b* and *c* (not as in *a*, which represents a condition that is never actually found). The breakage points may be near the centromeres (*b*) or far away from them (*c*). Chiasmata may be formed later in any or all of the four arms of the cross.

(Text-fig. 34). For purely mechanical reasons a short region on either side of the point of translocation will usually be left unpaired, i.e. the pachytene cross will be of the type shown in Text-fig. 34*b* rather than *a*.

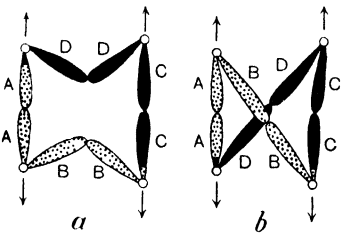
The subsequent history of the four chromosomes will depend on the positions where the chiasmata are formed. If a chiasma occurs in each of the four arms of the cross a ring of four chromosomes will result:



This ring will have the same kind of appearance as a true quadrivalent in a polyploid, but will be essentially different in that none of the four chromosomes is completely homologous to any other. If chiasmata are formed only in three of

the limbs of the cross we shall get an open chain (*AB–BC–CD–DA*) instead of a ring, while if only two chiasmata occur we shall be left with two bivalents (*AB–BC* and *CD–DA*).

The genetical results of a reciprocal translocation will naturally depend on the frequency with which these events occur. If two bivalents are formed there will be no mechanism for ensuring that each gamete receives the regions *A*, *B*, *C* and *D*, and a certain percentage will receive *A*, *B*, *D* and *A* or *B*, *C*, *C* and *D*. Similarly, in the case of rings or chains of four chromosomes the gametes will only contain a complete haploid set of genes if the centromeres arrange themselves in a zigzag fashion on the first meiotic spindle—if they arrange themselves in a square (see Text-fig. 35) the gametes will have one region in duplicate and another lacking altogether. Thus most reciprocal translocations will seriously lower the fertility of individuals which are heterozygous for them (assuming that zygotes carrying a deficiency for one region and a duplication for another are inviable, as will nearly always be the case).



Text-fig. 35. Diagrams showing how a ring of four chromosomes in a translocation heterozygote may orientate itself in a 'square' or a 'zigzag' at first metaphase. The former leads to the formation of gametes lacking some regions and possessing others in duplicate; the zigzag arrangement gives rise to gametes having a complete haploid set of genes.

The extent to which the fertility of the organism is affected by a translocation will depend largely upon the length of the segments which are interchanged. Where both of these have chiasma frequencies of 1·0 or over pairing in the heterozygote will usually be complete and a ring of four chromosomes will be formed in almost every cell. Such a heterozygote may be moderately fertile if the zigzag arrangement of the centromeres occurs more or less regularly. Whether it does so or not will depend largely on the dimensions of the chromosomes relative to those of the spindle. A chain of four chromosomes, especially if they are metacentric, is so much larger than an ordinary bivalent that it will usually have considerable difficulty in arranging itself upon the developing spindle at prometaphase, and all kinds of irregular orientations may result.

Where very small regions are interchanged the four chromosomes in the heterozygote will normally form two separate bivalents instead of a ring or chain. The effect of this will be that approximately 50% of the gametes will contain a duplication and a deficiency. The viability of the zygotes arising from such gametes is likely to be very low, although in very exceptional cases (where the regions are minute or inert) it may approach the normal level.

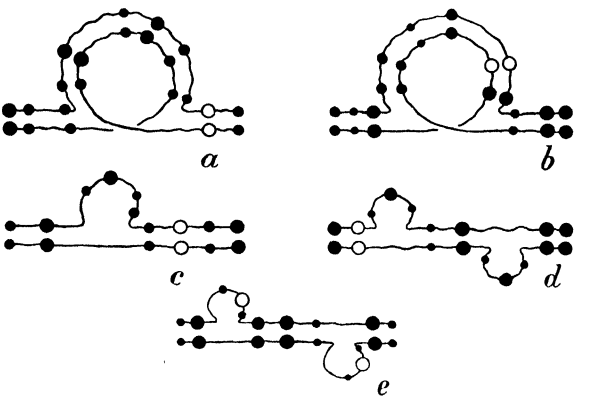
The translocations which would seem to stand the best chance of establishing themselves in evolution are the whole-arm transfers of the $A+A \rightarrow M$ and $M+S \rightarrow A+A$ types (see p. 56). Here the heterozygotes will show a chain of 3 chromosomes (which will not have so much difficulty in orientating itself as a

chain or ring of 4). Other types of whole-arm transfers (such as $M+A \rightarrow A+M$ and $M+M \rightarrow M+M$) will probably not fare any better than translocations involving smaller portions of chromosome limbs. But it is impossible to predict how a translocation will behave at meiosis simply from a consideration of the lengths and chiasma frequencies of the portions exchanged—much will depend upon the properties of the spindle and upon the mechanical relationships of the chromosomes to it. The probability of a mutual translocation establishing itself in a population has been worked out mathematically by Wright (1941) and shown to be exceedingly low except in very small populations.

Reciprocal translocations differ from most other kinds of structural rearrangements in not producing new gene sequences by crossing-over. Other types of translocations (i.e. insertional translocations and shifts) will give rise to deficiencies and duplications in individuals which are heterozygous for the rearrangement. The frequency with which gametes bearing these deficiencies and duplications are produced will depend on the frequency of pairing between the translocated portion and its homologue, and the chiasma frequency of this region. Thus if we consider an individual which is heterozygous for a small insertional translocation so that its chromosomes may be represented in the following way:

abcdefghi *abcdfghi* *pqrsetuvwxyz* *pqrstuvwxyz*

the overwhelming majority of spermatocytes and oocytes will contain two bivalents. If these segregate at random one-quarter of the gametes will lack the



Text-fig. 36. Diagrams of pachytene or salivary pairing in a bivalent heterozygous for (*a*) a paracentric inversion, (*b*) a pericentric inversion, (*c*) a deletion, (*d*) a paracentric shift, (*e*) a pericentric shift. Centromeres indicated by circles.

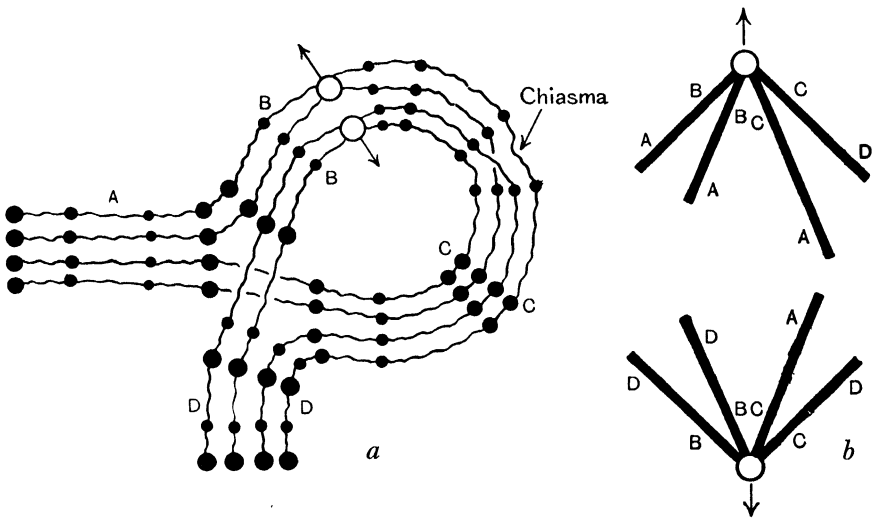
e region, one-quarter will have it in duplicate, while the remaining half will have all regions present once and once only. Assuming that haploidy or triploidy for the *e* region is lethal to the zygote such an individual will have a very low

fertility. In a few cells, however, the two *e* regions may pair together and a chiasma may be formed between them. In this case entirely new chromosomes:

abcdetuvwxyz and *pqrsefghi*

will be produced. These will nearly always be lethal in the heterozygous condition.

In the case of inversions the pachytene configuration in a heterozygote will be a loop with two straight arms projecting from it (Text-fig. 36). If the inversion is paracentric the centromeres will be in one of the arms, if it is pericentric they will be situated within the loop.



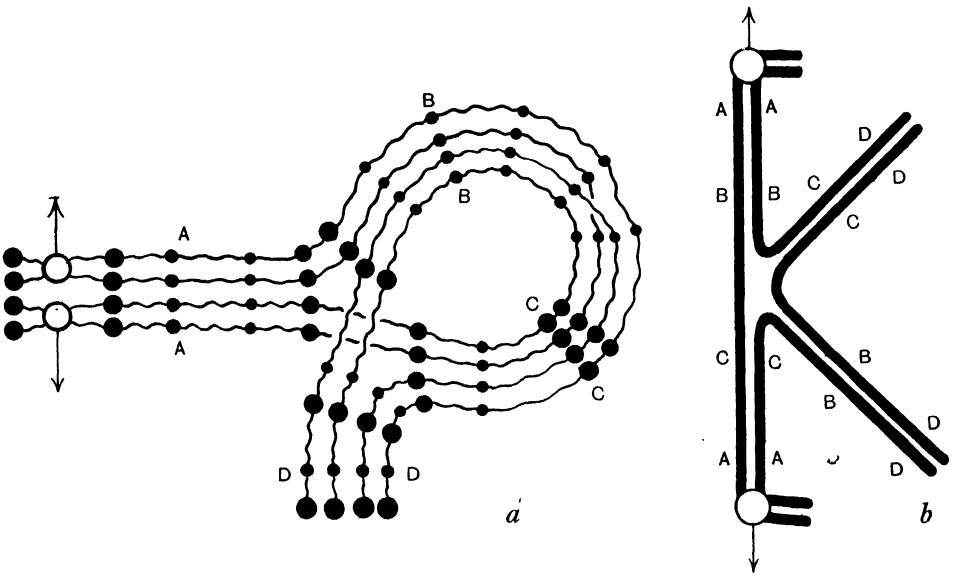
Text-fig. 37. Diagrams showing how a single chiasma within a pericentric inversion leads to the production of gametes with deficiencies and duplications. *a*=end of pachytene; *b*=first anaphase.

In such a bivalent chiasmata may be formed either in the loop or in the arms. The consequences of chiasma formation will be quite different according to whether the inversion is paracentric or pericentric. In a pericentric inversion all cross-overs within the loop will lead to the formation of chromatids with a deficiency and a duplication (see Text-fig. 37). Thus individuals heterozygous for a pericentric inversion will produce a large number of lethal gametes unless (1) the inversion is so small that crossing-over hardly ever takes place in it, or (2) it is so large that the duplication and the deficiency are very minute and hence not lethal.

In a bivalent which is heterozygous for a paracentric inversion the consequences will be quite different. A single chiasma within the inverted segment will give rise to a dicentric chromatid and an acentric one. At the first anaphase the former will be stretched between the two centromeres and will either prevent

the separation of the two daughter nuclei or will break under the strain. The acentric chromatid will usually remain in the equatorial part of the spindle without passing to either pole.

If two chiasmata are formed within the limits of the inversion the result will depend on their relationship to one another. If they are reciprocal it will be as if no cross-over had occurred, i.e. no acentric or dicentric chromatids will be



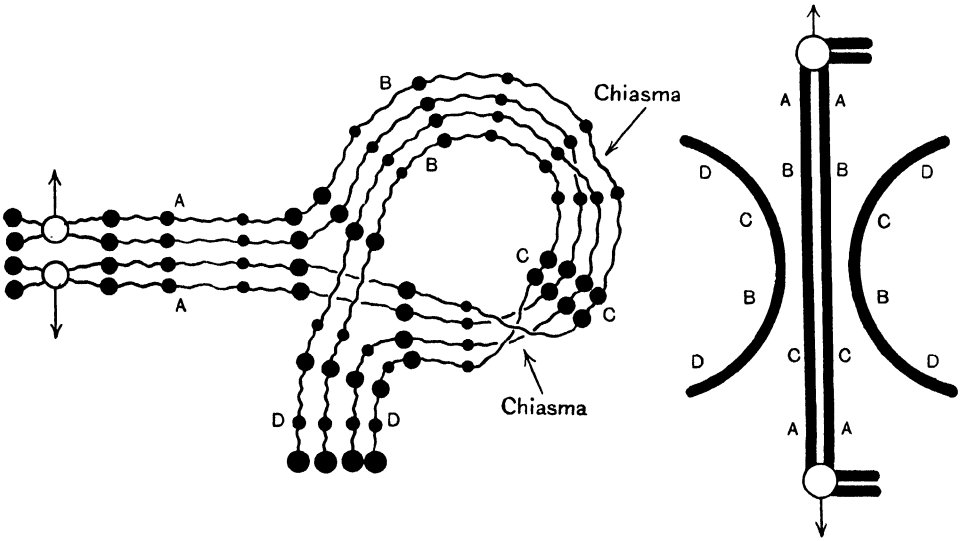
Text-fig. 38. Diagram of the consequences of crossing-over in a paracentric inversion. *a*=end of pachytene; *b*=first anaphase. A single crossover gives rise to a dicentric 'bridge' and an acentric chromatid.

produced. On the other hand, a pair of complementary chiasmata within the loop will give rise to two dicentric chromatids and two acentrics. The dicentrics will later form a 'double bridge' at the first anaphase. A pair of diagonal chiasmata will produce a dicentric and an acentric chromatid in the same way as a single chiasma does.

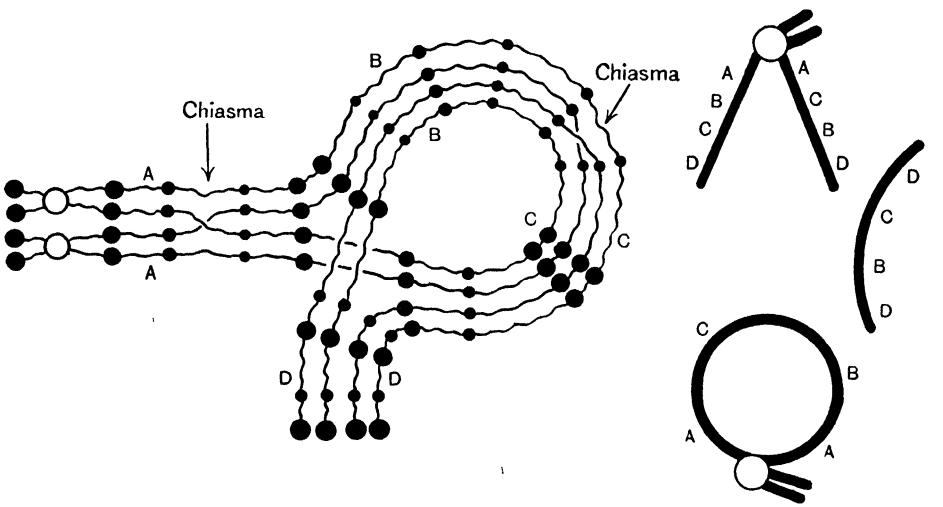
More complicated situations arise when chiasmata occur between the inverted region and the centromere as well as within the inversion (Text-fig. 40). It will be seen that in some instances loop chromatids (i.e. ones in which both ends are attached to the two halves of one centromere*) are produced. These pass to the poles normally at the first anaphase, but give rise to dicentric 'bridges' at the second meiotic division.

Naturally all these various types of acentric, dicentric and looped chromatids

* The distinction between a loop chromatid and a ring chromosome (such as the closed-*X*) is illustrated in Text-fig. 41.

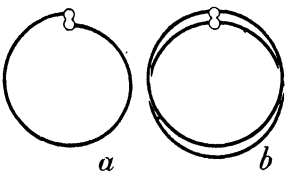


Text-fig. 39. Diagram showing how two complementary chiasmata within an inversion loop give rise to a double 'bridge' and two acentric chromatids.

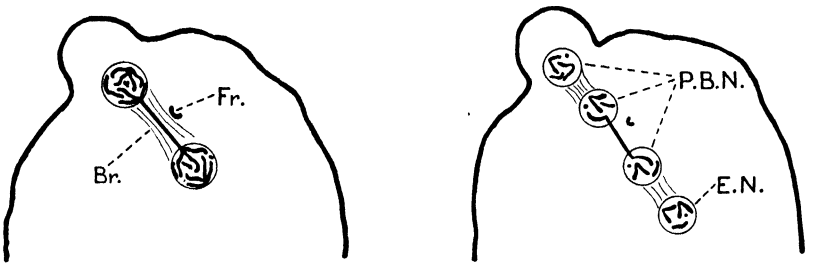


Text-fig. 40. Diagram showing how one chiasma within an inversion loop and another between the inversion and the centromere may give rise to a loop-chromatid and an acentric fragment.

cannot survive. It has been known for a long time, however, that in *Drosophila* paracentric inversions do not lead to a serious loss of fertility. The reason for this lies in a rather special combination of circumstances. In the first place there is no crossing-over in the male, so that there is no possibility of acentric or dicentric chromatids being formed during spermatogenesis. In inversion-bearing females they are of course produced; but it has been shown by Sturtevant and Beadle (1936) that they nearly always pass into the polar bodies, the egg nucleus receiving a normal monocentric chromatid. The mechanical reason for this is as follows: if a dicentric chromatid is present at the first meiotic division it will form a 'bridge' between the interkinetic nuclei; at the second meiotic division the two spindles are arranged in line with one another and at right angles to the surface of the egg (Text-fig. 42). Any dicentric bridges from the first division will be stretched between the two middle nuclei of the row of four, so that the innermost nucleus which always remains in the egg will receive a normal chromatid while the dicentric,



Text-fig. 41. Diagram showing the difference between a ring-chromatid (*a*) which will form a 'bridge' at the next division and a ring chromosome (*b*) such as the closed-*X* in *Drosophila*.



Text-fig. 42. Diagram showing the orientation of the four nuclei in a *Drosophila* egg at the second division. A single cross-over has taken place in an inversion loop. *Br.* = bridge; *Fr.* = fragment; *P.B.N.* = polar body nuclei; *E.N.* = egg nucleus.

broken or acentric chromatids will be passed out and lost in the polar bodies. Thus from a genetical point of view the cross-overs which take place within the inversion loop are not passed on to the progeny. It is for this reason that in the early days of *Drosophila* genetics, before the nature of inversions was properly understood, they were referred to as 'cross-over suppressors'. In many cases the suppression is a true one; presumably because the inverted region remains unpaired in the meiotic chromosomes.

The characteristic orientation of the four nuclei in the egg does not, of course, ensure that 'second division bridges' will be cast out in the polar bodies. Thus, even in *Drosophila*, the simultaneous occurrence of chiasmata in the inverted region and between it and the centromere may lead to the production of an

inviable egg. But this will be a relatively rare event since the genetical data indicate that none of the chromosome limbs in *D. melanogaster* has a chiasma frequency of over 1·5.

In the vast majority of animals chiasmata are formed in the male as well as in the female, so that heterozygosity for a paracentric inversion will lead to the production of a certain number of 'lethal sperms' (i.e. ones which will give rise to inviable zygotes if they succeed in fertilizing an egg). If the inversion is situated in a region of the chromosome where chiasmata are not ordinarily found the consequence will probably not be serious; but an inversion of a segment with a high chiasma frequency must necessarily lead to the death of a large number of potential offspring. Very small inversions having a negligible chiasma frequency will probably not affect the fertility of the individual appreciably.

To what extent the mechanism which ensures the elimination of first division dicentrics and acentrics in the maturation of the egg of *Drosophila* occurs in other groups of animals is unknown; possibly it is rather widespread.

It has been pointed out by Sturtevant (1938) that although single paracentric inversions do not lead to a noticeable loss of fertility in *Drosophila*, two overlapping inversions in the same chromosome arm may do so. This is because a chiasma may be formed in the region of overlap, thus giving rise to duplicational and deficient chromosomes. The result will be exactly the same irrespective of whether both inversions are in the same homologue or not.

The behaviour of attached-X and ring-X chromosomes at meiosis is interesting, although it does not seem to have much direct bearing on problems of chromosomal evolution, since these types of chromosome are not known to occur outside the laboratory.

Attached-X females of *D. melanogaster* possess a Y in addition to the metacentric $\widehat{XX}$ chromosome. At the first meiotic division the Y passes to one pole, the $\widehat{XX}$ to the other. Thus such a female produces two kinds of eggs, $\widehat{XX}$ and Y. Four kinds of zygotes result from fertilization by a normal male: $\widehat{XX}Y$ (like their mother), XY (like their father), $\widehat{XX}X$ and YY (both inviable). The fact that the $\widehat{XX}$ and Y chromosomes pass to opposite poles at the first division suggests that they form a bivalent.

Two kinds of crossing-over seem to occur in $\widehat{XX}$ chromosomes: (1) between the two arms of the $\widehat{XX}$, (2) between the Y and the $\widehat{XX}$ in the neighbourhood of the centromere (Kaufmann, 1933). The first type of crossing-over can only be detected in $\widehat{XX}$ chromosomes which are heterozygous for some mutant gene or structural rearrangement: it is theoretically important as proving that chiasmata can occur between two parts of the same chromosome. The second kind of crossing-over leads to 'detachment' of the $\widehat{XX}$, one arm being replaced by the long or the short limb of the Y.

Ring-*X*'s may be present in either the heterozygous or homozygous condition. A rod-*X* may pair with a ring and undergo crossing-over with it—in this case a single chiasma gives rise to a bridge at the first anaphase, just as in the case of a single inversion. This bridge is cast out in the polar bodies, so that eggs of females heterozygous for a closed-*X* carry either a non-cross-over rod-*X* or a non-cross-over ring.

In a female with two ring-*X*'s pairing between them is usually complete, and a single chiasma between the two rings leads to the formation of a double bridge between the two centromeres.

CHAPTER VI

CHROMOSOMAL EVOLUTION IN WILD POPULATIONS

In view of the manifold types of inviability and sterility which they produce, it is perhaps at first surprising that chromosomal rearrangements should ever manage to establish themselves in wild populations. A number of investigations have, however, shown beyond all possibility of doubt that they occasionally do so. Thus in *Drosophila melanogaster*, Dubinin, Sokolov and Tiniakov (1936, 1937) examined 34,515 chromosomes of wild individuals by the salivary-gland method. In addition to the normal or 'standard' gene-sequences they found seven different paracentric inversions, some of which were relatively common, so that altogether 525 (1·5%) of the chromosomes examined bore inversions.

This very extensive survey gives some idea of the extent to which rearrangements occur in free-living populations and suggests that they may play a part in evolution. It is clear, however, that most kinds of rearrangement cannot cause speciation at a single step, since they are capable of existing in the heterozygous state. They may furnish the basis upon which isolation mechanisms are subsequently built up, but they cannot in most cases serve as isolation mechanisms in themselves.

Free-living populations of *Chironomus* species present essentially the same picture (Bauer, 1936*b*; Philip, 1942), but in some species of this genus inversions have not been found in spite of an extensive search. Thus whereas most populations of *C. riparius* and *C. dorsalis* contain one or more inversions, material of *C. thummi* from six different localities in England and Germany did not show a single inversion. *Chironomus* differs from *Drosophila* in forming chiasmata in the male; thus these inversions in *riparius* and *dorsalis* will lead to the production of 'lethal' sperms unless (as is probably the case) they are confined to regions of the chromosomes where crossing-over seldom or never occurs. Philip's data suggest (1) that the various inversions found in *Chironomus* spp. are neutral as far as selection is concerned, and (2) that mating between the various cytological types is at random.

It is probable that real differences exist between the species of a genus in regard to the number and type of rearrangements present in natural populations. Thus in some species of *Drosophila* relatively few inverted sequences have been found although extensive cytological studies have been made.

Very little information exists as to the frequency of inversions in animals which lack salivary chromosomes. The only means of detecting their presence in such groups is by observing the presence of 'bridges' at either the first or the second meiotic division. But since *a priori* the inversions are likely to occur

in regions with very low chiasma frequencies the method is not really satisfactory. Nevertheless, Darlington (1936) was able to show that several species of grasshoppers (*Chorthippus parallelus*, *Stauroderus bicolor*) carried inversions in free-living populations. Unfortunately it is not possible to determine the exact limits of inversions by this method: if bridges are frequently observed in a particular chromosome arm we may have one large inversion or several shorter ones.

By far the most extensive surveys of inversions in natural populations have been carried out by Dobzhansky and his colleagues in the *Drosophila* species of North America, particularly *D. pseudoobscura*, *D. azteca*, *D. algonquin*, *D. athabasca* and *D. miranda* (Dobzhansky, 1937*d*, 1939*a*, *b* and *c*, 1941*a*; Dobzhansky and Queal, 1938; Dobzhansky and Sturtevant, 1938; and Dobzhansky and Socolov, 1939).

D. pseudoobscura includes two subspecies or 'races', 'A' and 'B', which do not seem to hybridize in nature and which produce almost completely sterile hybrids when crossed in the laboratory (see p. 221). Tan (1935) and Koller (1936*e*) have shown that the two races differ in at least four inversions, one in each limb of the *X*, one in the IInd and one in the IIIrd chromosome. Within each race, however, the gene-sequences are not constant, since a number of different inversions are present.

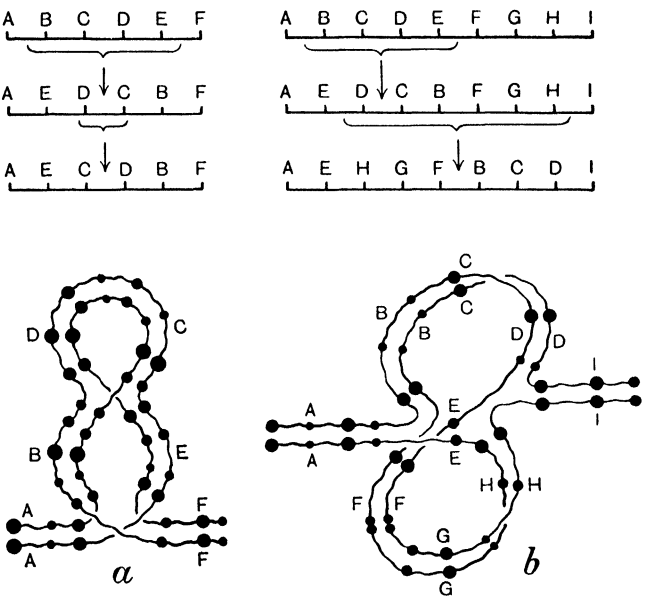
The IIIrd chromosome of *pseudoobscura* seems to be especially variable: a total of 21 different inversions is now known in this chromosome. Seven of these are only found in race B, 13 only in race A, while one (known as 'Standard') occurs in both. As far as the other chromosomes are concerned, five sequences are known in the IInd chromosome, two in the IVth, while in the *X* three are known in the 'right' limb and two in the 'left' one. The unusual variability of the IIIrd chromosome is quite unexplained, but Helfer (1941) has shown that all the chromosomes are equally fragmented by X-rays, in proportion to their total length.

The geographical distribution of the various inversions in the IIIrd chromosome of *pseudoobscura* has been studied in great detail by Dobzhansky. Some of them have so far been found only in one locality, while others occur throughout a considerable part of the total area occupied by the species. *Pseudoobscura* occurs in pine and oak woods on mountain slopes. Its distribution on the west coast of North America from Alaska to Guatemala is thus highly discontinuous, since it does not occur in the valleys and deserts between the mountain ranges.

Each gene-sequence has received the name of the locality at which it was first found. No single sequence extends throughout the entire range of the species, nor is there any locality where they all occur together. Some of the sequences have irregular and discontinuous ranges: thus 'Tree Line' occurs in California, Texas, Mexico and Guatemala, while 'Olympic' occurs in the states of Washington, California, Texas and in Central Mexico. Most populations contain several

different sequences, but there is a fairly large area including parts of Arizona, New Mexico, Utah and Colorado where the only sequence is Arrowhead.

The frequencies of homozygous and heterozygous individuals in these *Drosophila* populations indicate that mating between the different chromosomal types is at random. Koller (1939) has found significant differences in the chromosomal constitution of particular populations between one year and the next, suggesting that the number of individuals in the population undergoes periodic fluctuations, and is probably reduced to a very low figure in the winter

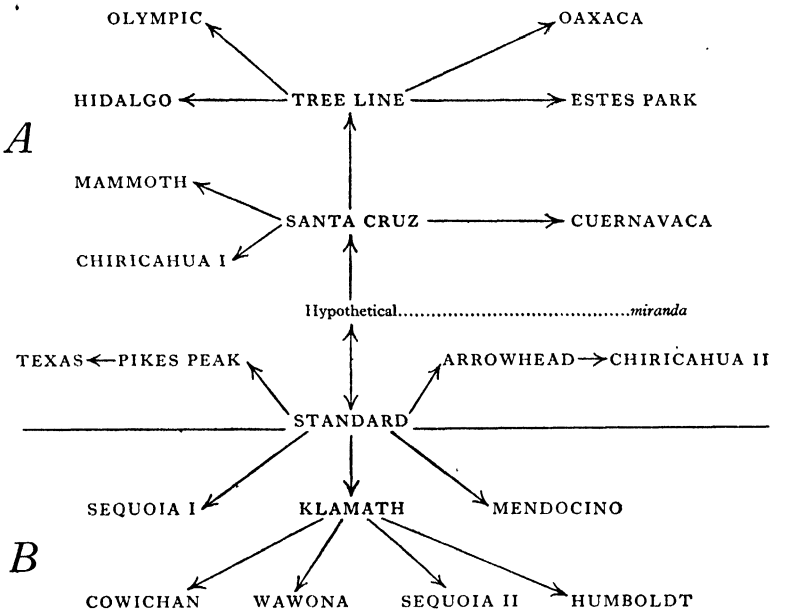


Text-fig. 43. Diagrams of pachytene or salivary pairing in a bivalent heterozygous for (*a*) included inversions, (*b*) overlapping inversions. Based on the work of Dobzhansky (1937*d*).

months. Dobzhansky (1943) has also found that the relative frequencies of the different sequences change from month to month throughout the year, the changes being regular and cyclic.

Where two inversions are present in the same chromosome (as a result of four breaks, two on one occasion, two on another) they may be either 'independent', 'included' (i.e. one inside the other) or 'overlapping'. The latter are particularly interesting, since it has been shown by Sturtevant and Dobzhansky (1936*c*) that it is often possible to trace the past history of a chromosome by an analysis of the overlapping inversions present in wild individuals collected from different localities. The method is, in principle, as follows: if three arrangements are known in a particular chromosome, (1) *ABCDEFGHI*, (2) *ABFEDCGHI*, and (3) *ABFEHGCDI* (the inverted segments being underlined for the sake of

clarity), then an individual carrying (1) and (2) or (2) and (3) will show a single 'inversion loop' in its salivary nuclei, while one carrying (1) and (3) will show a double loop (Text-fig. 43*b*). If we consider these sequences from an evolutionary standpoint it will be seen that there are three ways in which they can have arisen. Either (1) gave rise to (2) and that to (3), or (3) gave rise to (2) and that to (1), or else (2) gave rise to both (1) and (3). We may represent these three modes of origin in the following way: 1→2→3, 3→2→1 and 1←2→3. (1) cannot have



Text-fig. 44. Phylogenetic chart showing how the various gene sequences in the third chromosome of *Drosophila pseudoobscura* are related to one another. Each sequence is a single inversion in respect to those connected with it by one arrow. The hypothetical sequence seems to have become extinct. The sequences above the horizontal line are only found in race A, those below it only in race B (*Standard* is found in both). From Dobzhansky (1941*a*).

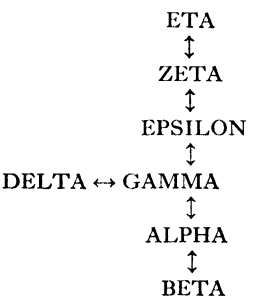
arisen from (3) or vice versa unless all four breaks took place in the same cell at the same time and the pieces rejoined in such a way as to simulate a pair of overlapping inversions (an event so improbable that it can safely be disregarded).

This method enables one to construct phylogenetic diagrams of the various sequences in a chromosome (Text-figs. 44, 45). In the case of the IIIrd chromosome of *D. pseudoobscura* the diagram is a fairly complex branching tree. One gap occurs in it (between 'Standard' and 'Santa Cruz'); this probably represents a sequence that has become extinct (though it may of course still exist in some locality where *Drosophila* populations have not been collected as yet). Confirmation that this hypothetical sequence did really exist at one time is provided

by the fact that an essentially identical sequence occurs in the very closely related species *D. miranda*.

The fact that 'Standard' is the only arrangement found in both races suggests that it or the extinct one should be regarded as the most archaic sequence from which all the others have been derived in the course of evolution. The very sporadic and irregular distribution of the various inversions throughout the range of the species suggests that their spread from one locality to another has taken place by accidental and unpredictable means over a very long period of time.

A somewhat simpler series of gene-sequences has been studied in *D. azteca* by Dobzhansky and Socolov (1939). In the long arm of chromosome '*A*' of this species seven different sequences are now known (described by the Greek letters *alpha* to *eta*). These may be arranged in a linear diagram except for



Text-fig. 45. Phylogenetic chart of the gene-sequences in the *A* chromosome of *Drosophila azteca*.

sequence *delta*, which forms a side-branch. It is interesting to note that the sequence *zeta* was at first hypothetical, but was found in the wild at a later date (Dobzhansky, 1941*b*), thereby providing a striking justification of the method of building up phylogenetic trees of gene-sequences. The geographical distribution of the seven sequences is not known in detail, but *alpha* and *beta* only occur in Guatemala and Mexico, while *eta* is only known from the U.S.A. (Arizona and California). *Gamma* and *delta* are only known in central Mexico, where they occur together with *alpha*.

In this case we have no means of telling which of the seven sequences was the original one. If it was *alpha* or *beta* then the species has probably spread northwards from Central America to California. If, on the other hand, the ancestral sequence was *eta*, then *D. azteca* probably originated in the U.S.A. and spread southwards until it reached Guatemala. If the most ancient sequence was *gamma* or *delta* then the species probably arose in central or northern Mexico and spread both northwards and southwards from there. *Pseudoobscura* and *azteca* are examples of *Drosophila* species whose geographical distribution does not seem to have been seriously affected by man. Some other species have a more or less cosmopolitan distribution, having been carried round the world on ships.

In one of these species, *ananassae*, it has been shown by Kikkawa (1938), Kaufmann (1936, 1937) and Dobzhansky and Dreyfus (1943) that the same inversions are present in populations from eastern Asia, south-eastern U.S.A. and Brazil, thus suggesting that the spread of this species has probably taken place fairly recently.

The fact that all the inversions found in these species of *Drosophila* are paracentric and not pericentric is not unexpected, since we have already seen that crossing-over within pericentric inversions leads to the production of many chromosomes possessing duplications and deficiencies. Unlike dicentrics these chromosomes are not necessarily lost in the polar bodies, and they will hence lead to the death of a considerable number of offspring.

One case is known, however, in which a pericentric inversion occurs in wild populations of a *Drosophila* species. In *D. algonquin*, Miller (1939) has shown that in one of the autosomes two sequences exist which may be represented by the following diagram (the dot represents the centromere):

	Name of sequence
A B C D E . F G H I J	Standard
A B C D H G F . E I J	Hypothetical
A B G H D C F . E I J	b_3

Thus the two sequences actually found differ by a pair of overlapping inversions, one pericentric, the other paracentric. The hypothetical sequence connecting them has not been found. It is possible that the paracentric inversion suppresses most of the crossing-over which would otherwise lead to the production of inviable eggs. If so we may regard the survival of the b_3 sequence as due to the protection of the second inversion, the extinction of the hypothetical sequence having been caused by the fact that it gave rise to a high degree of sterility when heterozygous.

It is still far from clear why all these inversions should have spread through the distribution areas of species such as *pseudoobscura* and *azteca*, since they do not seem to be associated with any position effects that might confer a selectional advantage on the individuals bearing them. A possible reason for the spread of inversions has, however, been suggested by Sturtevant and Mather (1938). It is known that recessive lethal mutations are relatively common in natural populations of *pseudoobscura*. Since little or no effective crossing-over takes place between two relatively inverted chromosome segments which are present in the same population, the lethals will usually be different in the two segments. Thus an individual which is heterozygous for one or more inversions is less likely to be homozygous for a lethal mutation. There may thus be a certain amount of selection in favour of heterozygotes, which would lead to the spread

of inversions within the populations. If, however, the inverted segment is sufficiently long for two compensating chiasmata to be formed within it the effect should tend to disappear, since there will be a chance for effective crossing-over to take place between the two relatively inverted regions. It is therefore of interest to note that most of the inversions known in the IIIrd chromosome of *pseudoobscura* are too short for double crossing-over to take place within them. Sturtevant and Mather's mechanism should theoretically give newly arisen sequences an initial advantage, but it should also tend to prevent established sequences from becoming extinct. It has been pointed out by Darlington (1937*a*, *b*) that an inversion which contains several advantageous genes will, by suppressing crossing-over, prevent the combination from being broken up. Thus some inversions may have a 'positive selective value' because they contain two or more genes which, acting together, produce an increase in fertility or viability. By selection of 'modifying genes' such combinations within inversions can gradually become more effective without any risk of being disintegrated by crossing-over.*

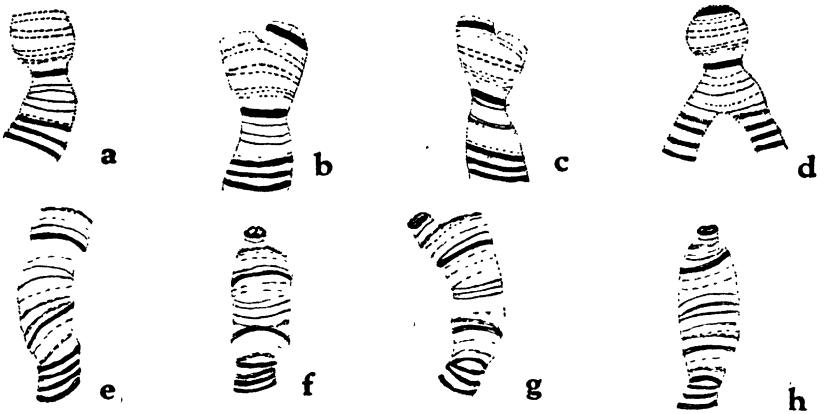
Natural populations of *Sciara* spp. (Diptera, suborder Nematocera) seem to differ from those of *Drosophila* and *Chironomus* in two important respects (Metz, 1938*b*, 1939*c*, 1941). In the first place no inversions have been found in any of the chromosomes.† On the other hand, minute duplications and deficiencies involving about 1–3 bands are relatively common in the chromosomes of wild flies, at least seventeen different ones being known in the one species *Sciara ocellaris*. It is unfortunately difficult to decide how many of these small aberrations in the salivary chromosomes are to be regarded as duplications and how many as deficiencies. In some instances a band was seen in one homologue which was not present at all in the other, while in other cases a thick band in one chromosome was replaced by one about half as thick in the other. It is possible that the first kind were true deficiencies, the second category duplications, the thick band being really compound. No phenotypic differences appear to be associated with these minute structural changes, and the part that they play in the dynamics of *Sciara* populations is not known.

In *Drosophila* deficiencies and duplications are hardly known at all in natural populations, but in some species such as *ananassae* races or strains may differ in respect of small duplications and deficiencies at or very close to the ends of the chromosomes (Kikkawa, 1938; Dobzhansky and Dreyfus, 1943). It appears that in the formation of races and species in *Sciara* a process which has hardly

* In *Drosophila subobscura* Philip, Rendel, Spurway and Haldane (1944) have been unable to obtain cytologically honozygous stocks, even after 19 generations of brother-sister mating. There is thus definite evidence suggesting that in this species cytologically homozygous individuals are either less viable or less fertile (under laboratory conditions, at any rate) than heterozygotes for inversions.

† Since the above was written Carson (1943, 1944) has reported finding numerous inversions, as well as minute rearrangements, in wild populations of *Sciara impatiens*.

occurred at all in *Drosophila* has taken place on a grand scale.* Chromosomal differences between *Sciara* species seem to be similar to the intraspecific variations. Thus in the hybrids between *ocellaris* and *reynoldsi* no inversions were detected, but there were a number of small duplications and deficiencies.



Text-fig. 46. *Drosophila ananassae*: minute terminal deficiencies or duplications which are present in stocks from certain localities. *a* and *e*=the homozygous deficient types; *b*, *c*, *f*, *g*=the heterozygous types; *d* and *h*=the types homozygous for the presence of the terminal band. From Kikkawa (1937).

In chironomids, as we have already seen, large inversions occur in some species, but there are some indications that 'minute' changes of the type met with in *Sciara* also occur. E. Goldschmidt (1942) succeeded in crossing two Palestinian chironomids which she regarded as strains of a single species, but which were more probably distinct species. Although pairing was very incomplete in the salivary nuclei of the hybrids, the latter were quite fertile, and F_2 and F_3 generations were reared. In the longer chromosomes certain subterminal regions were always paired in the hybrid salivary nuclei, and appeared to be completely homologous, but there were long regions in the middle of the chromosomes and shorter ones at the ends where pairing seldom or never occurred. Numerous 'minute' differences were found in these unpaired regions. One strain had a large 'puff' in the middle of one of the chromosomes, the corresponding region in the other form being of normal diameter. It is suggested that the homologous subterminal regions are the ones where crossing-over occurs at meiosis, and that minute changes have occurred very freely in those regions where chiasmata are seldom or never found. The fact that the hybrids between the two forms are fully fertile in spite of the numerous cytological differences is very remarkable, and suggests that many of them may be small shifts rather than duplications or deficiencies.

* Some *Drosophila* populations contain large numbers of lethals (Dobzhansky, 1939*a*, 1941*a*). It has usually been assumed that these are due to gene mutations, but some wild lethals may be minute deficiencies which have not been detected cytologically.

It is difficult to conceive how net losses or gains of genetic material could become established in evolution unless they were very small or else in respect of inert regions, but they evidently do so from time to time in most species. Obviously, if a repeat has once established itself it is likely to be less essential to the species than a non-repeated segment of the chromosome, and portions of it may probably be lost without seriously lowering viability. There is little direct evidence for this, however, since, although a certain number of small repeats have been observed in the salivary chromosomes of *Sciara* species, the duplications and deficiencies found in wild populations are not known to occur in these regions. One of the clearest examples of a repeated sequence of bands occurs in the *X* chromosome of *S. ocellaris* and *S. reynoldsi*. In both species the *X* often forms a figure of eight in the salivary nuclei, a short region near each end being paired with one in the middle. Metz (1941) has suggested that this configuration is due to a triple repeat, a short region of 3–4 bands being present three times in the chromosome. It is interesting that the arrangement is the same in the two species, thus suggesting that it is one of considerable antiquity.

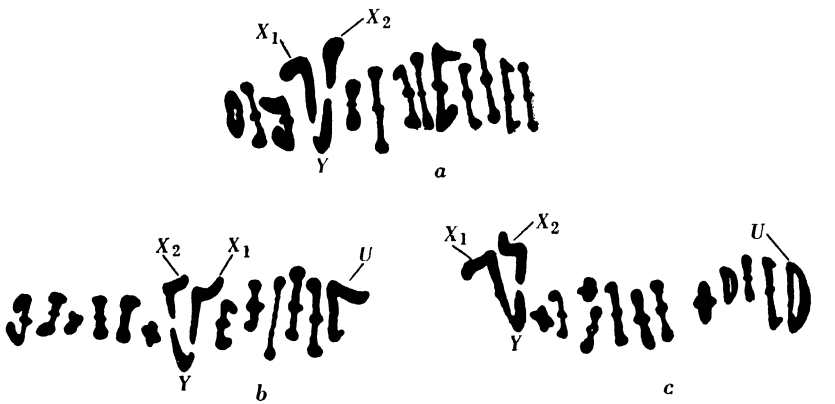
In a number of species of animals asymmetrical or unequal bivalents have been described. Most of these were probably heterozygous for deletions, duplications, pericentric inversions, or shifts—or for various combinations of these changes. We shall use the term *asymmetrical* bivalent for one which is heterozygous for a displacement of the centromere, so that the two chromosomes are of different *shapes*, *unequal* bivalent for one which is heterozygous for a deficiency or duplication, so that the two chromosomes are of different *sizes*. In a few instances asymmetrical or unequal autosomal bivalents have probably been mistaken for a pair of *X* and *Y* sex chromosomes.

As an example of an insect with asymmetrical bivalents we may take the neuropteran *Hemerobius stigma*, of which four individuals from a Finnish population were studied by Klingstedt (1934). In one the smallest bivalent was asymmetrical, in two individuals two bivalents were both asymmetrical, while in the fourth three bivalents were asymmetrical. In this case the two chromosomes in each of the asymmetrical bivalents appear to have been equal in total length (although it is difficult to be certain of this from the figures); so that in all probability no deficiencies or duplications were present.

Some asymmetrical bivalents which were probably similar to those of *Hemerobius* were found in the mantids *Paratenodera* (= *Tenodera*) *sinensis* and *T. aridifolia* (White, 1941*a*). In each species one bivalent was heterozygous in some individuals but not in all. It is possible that small deficiencies or duplications were present in these cases, since the bivalents appear to be slightly unequal as well as asymmetrical.

Since crossing-over within a pericentric inversion or a centric shift will lead to the production of deficiencies and duplications, it is *a priori* likely that these types of rearrangements will only survive in organisms where the chiasmata are strictly confined to some other part of the chromosome. Klingstedt's figures

suggest that this is so in *Hemerobius*—each bivalent appears to have a single chiasma very close to one end. If it were otherwise the displacements of the centromere which have produced the asymmetrical bivalents could hardly have established themselves in the population.



Text-fig. 47. Three first metaphases of the mantid *Tenodera sinensis* (in side view). In *b* and *c* there is an unequal bivalent (*U*). The three sex chromosomes, X_1, X_2 and Y, form a trivalent. From White (1941*a*).

In a number of species of grasshoppers bivalents have been described which were 'unequal' but not asymmetrical, that is to say bivalents heterozygous for a large deficiency or duplication, but in which no displacement of the centromere had taken place. The behaviour of these unequal bivalents at meiosis was studied by Wenrich (1916) and Robertson (1915). The regions reduplicated or missing were probably heterochromatic in all these cases, so that the individuals with unequal bivalents were not phenotypically distinguishable from the homozygous types. Where individuals with unequal bivalents are present in a population we may, of course, expect to find two homozygous types as well—those having two large chromosomes and those having two small ones. Theoretically, if q and $1-q$ are the frequencies of the two kinds of chromosome, the three types of individuals should occur in the ratio $q^2 : 2q(1-q) : (1-q)^2$ if mating between them is at random.

Unequal bivalents of this type have been seen in the following species, but are doubtless present in many more:

Arphia simplex Carothers, 1913
Brachystola magna Carothers, 1913
Dissosteira carolina Carothers, 1913
Amphitornus bicolor Carothers, 1931
Mecostethus gracilis Carothers, 1931
Trimerotropis citrina Carothers, 1931
Phrynotettix magnus Wenrich, 1916
Arcyptera coreana Ch'en, 1942
Stauroderus bicolor Darlington, 1936

In all these cases only two types of individuals have been detected, one of the homozygous types being apparently missing. Whether it is really missing (i.e. lethal) or merely rare and undiscovered can usually not be decided from the rather meagre data given in the cytological papers dealing with unequal bivalents.

In *Trimerotropis citrina*, Carothers studied seventy-one individuals from Kansas, Texas and Florida. Sixty of these were structurally homozygous, but eleven had one of the smallest bivalents unequal (i.e. composed of a chromosome of normal size and one which, since it was much longer, presumably contained a duplication). No individual homozygous for the duplication was found, which may have been merely due to the small size of the sample.

An excellent example of an unequal bivalent has been described by Cappe de Baillon and de Vichet (1940) in the stick insect, *Leptynia attenuata*, but there is no information as to its distribution in natural populations of the species.

In three genera of grasshoppers belonging to the subfamily Oedipodinae (*Circotettix*, *Aerochoreutes* and *Trimerotropis*) asymmetrical bivalents are extraordinarily common, so that practically every individual contains one or more of them. These asymmetrical bivalents usually consist of an acrocentric chromosome paired with a metacentric, but in some instances two metacentrics with the centromere in different positions may form a bivalent. In extreme cases hardly any two individuals selected at random from a population have the same chromosome set.

These genera, which are widely distributed in the U.S.A. and the northern states of Mexico (*Trimerotropis* has a few species in South America), are closely allied. Kirby (1904–1910) listed thirteen species of *Circotettix* and seventy-one of *Trimerotropis* (some of which he included in a separate genus *Pseudotrimerotropis*). The whole group appears to be in need of taxonomic revision, and it is probable that a good many of the forms listed as distinct species by Kirby are synonymous. In *Circotettix* spp. there are only 11 pairs of chromosomes (instead of 12, as in most grasshoppers); one of the metacentrics has thus probably arisen through a centric fusion of two acrocentrics. In *Trimerotropis* (as far as is known) there are always 12 pairs of chromosomes, except in *T. cyaneipennis*, where there are 11, as in *Circotettix*.

In two species of *Trimerotropis* (*T. maritima* and *T. citrina*) the populations seem to be cytologically homozygous, all the chromosomes being acrocentric* (Carothers, 1931; White, unpublished observations). The species which are known to show structural heterozygosity are the following: *T. cyaneipennis*, *T. thalassica*, *T. caeruleipennis* (King, 1923); *T. suffusa* and *T. fallax* (Carothers, 1917); and three species of *Circotettix*, *C. lobatus*, *C. rabula* and *C. verruculatus*

* Unequal bivalents and a translocation have been described in some individuals of *T. citrina* (see pp. 112 and 116), but these are not comparable to the rearrangements that have occurred in other species of the genus.

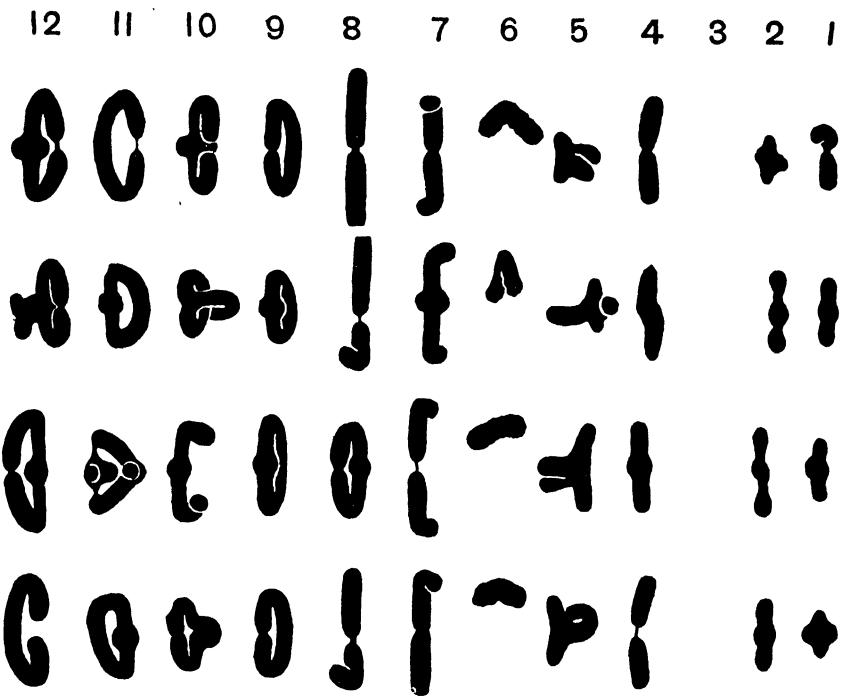
(Carothers, 1917, 1921; Helwig, 1929). No structurally homozygous species of *Circotettix* is known corresponding to the 'homozygous' Trimerotropi.

It is not quite clear exactly what type of structural rearrangements have led to the production of the asymmetrical bivalents which are found in these species. Their effect has been to convert acrocentric chromosomes into metacentrics. Most probably the rearrangements were pericentric inversions, one break being situated in the minute 'second limb', the other in the body of the chromosome; the possibility that centric shifts have occurred cannot, however, be entirely ruled out. There can be no doubt that originally all the chromosomes were acrocentric, since this is the type universally found in the short-horned grasshoppers, unless centric fusions have occurred, thereby diminishing the chromosome number (see p. 162). Thus *T. maritima* and *T. citrina* still preserve the original condition where all the chromosomes (including the *X*) are acrocentric; the other species represent various stages in a graduated evolutionary series. The situation in these other species can best be understood by an analysis of the three best sets of data.

(1) In *Circotettix verruculatus* which was studied by Helwig (1929) the *X* has become metacentric, the original acrocentric *X* having altogether disappeared from the species. There are ten pairs of autosomes ('1' being the longest, '10' the shortest). Chromosomes 1, 2, 3 and 4 are always metacentric: one of these has been derived from a fusion of two acrocentrics while the other three have become homozygous for a homosomal rearrangement. Chromosomes 7, 8 and 9 are always acrocentric, i.e. no rearrangement has yet occurred in them. The remaining chromosomes (5, 6 and 10) may be either metacentric or acrocentric. Individual grasshoppers can be homozygous or heterozygous for either position of the centromere in each of the three chromosome pairs. There are thus 3^3 ($=27$) possible chromosomal types in this species. Helwig examined 295 male individuals from five different localities in New England; his data are summarized in Tables 5 and 6. It will be seen that in chromosomes 5 and 10 the acrocentric type is almost five times as common as the metacentric one, whereas in chromosome 6 the reverse is the case, the metacentric type being about four times as common as the acrocentric. In the 295 individuals Helwig found all the 27 different combinations of acrocentrics and metacentrics, so that all of them are viable, although the data are insufficient to show whether they are equally so.

(2) In *Trimerotropis thalassica* (King, 1923) the *X* chromosome and the two largest autosomes (1 and 2) have become metacentric, the original acrocentric chromosomes having apparently disappeared altogether. The remaining nine autosomes may be either metacentric or acrocentric. If all combinations are viable there should be 3^9 ($=19{,}683$) possible types in this species. Actually the number is probably greater, since in several of the chromosomes more than one metacentric type exists (i.e. there are several alternative interstitial positions for the centromere). King examined twenty-five males from a single locality in

California, and found that they were all different in chromosomal constitution. Unfortunately, the size differences between the autosomes are relatively slight in this species, so that an identification of the individual chromosomes is in most instances not possible. King's data are summarized in Table 4. Most of

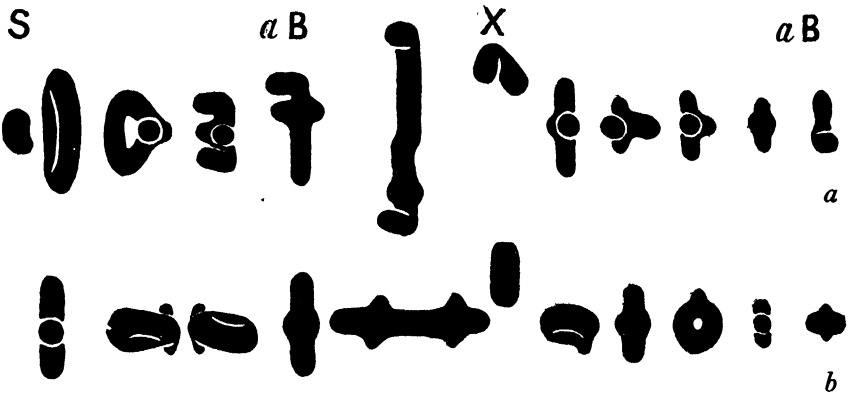


Text-fig. 48. Chromosome sets at first metaphase of four different individuals of the grasshopper *Circotettix verruculatus*, showing how bivalents 1, 7 and 8 are asymmetrical in some individuals but not in others. Chromosome 6 is the *X*. Column 3 is blank because the element occupying this place in the size-sequence has undergone a centric fusion and is included in chromosome 12. From Carothers (1921).

the bivalents recorded as heterozygous consist of an acrocentric and a metacentric chromosome; but at least eight of them were made up of two metacentric chromosomes that differed in the position of the centromere. In these bivalents there are often size differences between the two chromosomes, indicating that deficiencies and duplications are involved as well. If one adds together all the data for the variable autosomes (i.e. excluding chromosomes 1 and 2, which are always metacentric) one finds that metacentrics are distinctly commoner than acrocentrics.

(3) In *Trimerotropis suffusa* and *T. fallax*, Carothers (1917) studied eighty-two males from seven localities in California, Oregon, Washington and Idaho. The

two species were confused at first and Carothers divided her material into forms 'A' and 'B'; it is probable that 'A' was, in fact, *fallax* and 'B' *suffusa*. 'A' had an average of 13·94 metacentric autosomes per cell, the average number of acrocentric ones being 8·06. 'B' had an average of 8·9 metacentrics and 13·1 acrocentrics. In both forms a number of autosomes seem to have become



Text-fig. 49. Chromosome sets at first metaphase of (*a*) an individual of *Trimerotropis fallax*, (*b*) one of *T. citrina*. In *a* there is a supernumerary chromosome (*s*), two asymmetrical bivalents (*aB*) and a chain of four chromosomes resulting from a translocation. In *b* there is a similar chain of four chromosomes, but no asymmetrical bivalents or supernumeraries. From Helwig (1933).

completely homozygous for the median position of the centromere (the acrocentric type of chromosome having become extinct), and in both, but especially in form 'B', supernumerary chromosomes were present in some individuals.

In their general nature the asymmetrical bivalents of *Trimerotropis* and *Circotettix* do not seem to differ from those of some other forms such as *Hemerobius* and *Tenodera*. But certain special features deserve to be mentioned. In the first place there is no doubt that the original type of chromosome in the Trimerotropi was acrocentric, whereas in the other cases it was metacentric. Thus, unless we are dealing with 'terminal' rearrangements in the Trimerotropi, breaks must have occurred in the minute 'second arms'. Secondly, the occurrence and spread of structural rearrangements have taken place in the Trimerotropi on a scale which is unparalleled elsewhere. One chromosome after another has become metacentric, the new type gradually ousting the old. If the process had reached its logical conclusion all the chromosomes should have become homozygously metacentric, but this condition is not known in any species which has been investigated up till now. There is some suggestion that the process of converting acrocentrics into metacentrics started with the *X* and the longer autosomes, or at any rate that it has gone further in them than in the shorter members of the chromosome set.

All the populations of Trimerotropi which have been studied seem to be in a state of flux. Presumably heterozygosity cannot seriously decrease either viability or fertility; if it did we should expect that some, at any rate, of the populations would have become structurally homozygous as a result of selection. Possibly heterozygosis is definitely advantageous as in the case of *Drosophila subobscura*.

Since the natural populations of these grasshoppers are probably isolated fairly effectively in many instances by geographical barriers, we should expect on *a priori* grounds that different populations of the same species might represent different stages in the evolutionary conversion of acrocentrics to metacentrics. The only species that has been adequately investigated from this point of view is *Circotettix verruculatus*, and in this case the five populations studied by Helwig (1929) did differ significantly in the ratio $M : A$, at any rate in chromosome 1 and chromosome 8 (see Table 6). The most 'highly evolved' grasshopper of the whole group was an individual (no. 24 in Table 4) of *Trimerotropis thalassica* studied by King, which had 20 out of its 23 chromosomes metacentric.

TABLE 4. Trimerotropis thalassica—*King's data on 25 male individuals*

	Bivalents		
Individual	Homozygous metacentric	Heterozygous	Homozygous acrocentric
1	4	6	1
2	3	8	—
3	2	5	4
4	3	3	5
5	3	3	5
6	3	4	4
7	4	2	5
8	4	2	5
9	4	3	4
10	4	3	4
11	2	7	2
12	4	4	3
13	4	3	4
14	4	4	3
15	3	5	3
16	3	6	2
17	3	7	1
18	2	6	3
19	5	4	2
20	4	5	2
21	6	4	1
22	5	6	—
23	6	5	—
24	9	1	1
25	6	5	—
Total	100	111	64

TABLE 5. Circotettix verruculatus—*Helwig's data on* 295 *males*

No. of individuals	Locality		Bivalent 1	Bivalent 7	Bivalent 8
30	Mt Greylock, Mass.	Homozygous acrocentric	17	3	25
		Heterozygous	12	11	4
		Homozygous metacentric	1	16	1
73	Manchester, N.H.	Homozygous acrocentric	64	1	46
		Heterozygous	8	16	23
		Homozygous metacentric	1	56	4
64	Cheyboygan, Mich.	Homozygous acrocentric	29	4	34
		Heterozygous	26	24	21
		Homozygous metacentric	9	36	9
64	Mt Desert, Is. Maine	Homozygous acrocentric	51	5	58
		Heterozygous	13	21	6
		Homozygous metacentric	—	38	—
64	Mt Wachusett, Mass.	Homozygous acrocentric	54	—	48
		Heterozygous	9	21	13
		Homozygous metacentric	1	43	3
295	Total of 5 populations	Homozygous acrocentric	215	13	211
		Heterozygous	68	93	67
		Homozygous metacentric	12	189	17

TABLE 6. Circotettix verruculatus—*Helwig's data* (*continued*)

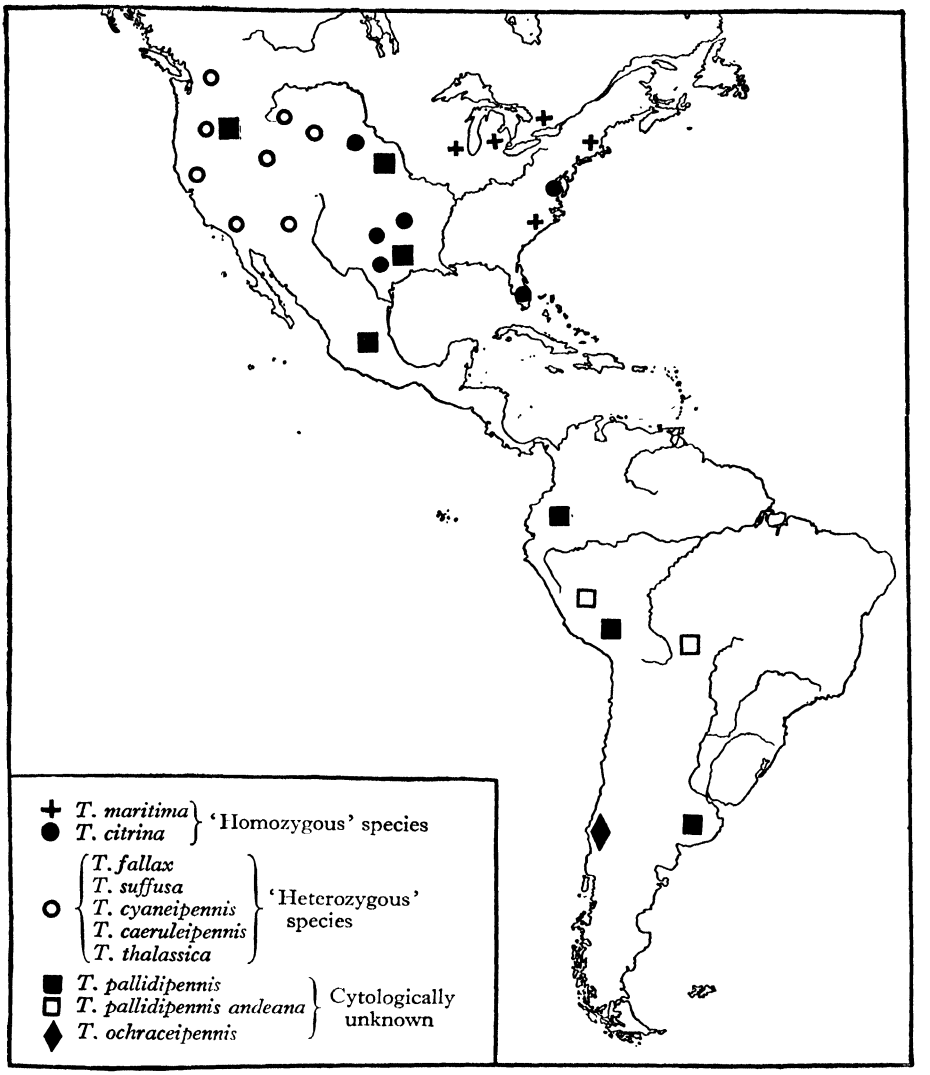
Frequencies of the two types of chromosome

Locality		Chromosome 1	Chromosome 7	Chromosome 8
Mt Greylock	Acrocentric	46 (76·7 %)	17 (28·3 %)	54 (90·0 %)
	Metacentric	14 (23·3 %)	43 (71·7 %)	6 (10·0 %)
Manchester	Acrocentric	136 (93·2 %)	18 (12·3 %)	115 (78·8 %)
	Metacentric	10 (6·8 %)	128 (87·6 %)	31 (21·2 %)
Cheyboygan	Acrocentric	84 (65·6 %)	32 (25·0 %)	89 (69·5 %)
	Metacentric	44 (34·4 %)	96 (75·0 %)	39 (30·5 %)
Mt Desert	Acrocentric	115 (89·8 %)	31 (24·2 %)	122 (94·3 %)
	Metacentric	13 (10·2 %)	97 (75·8 %)	6 (4·7 %)
Mt Wachusett	Acrocentric	117 (91·3 %)	21 (16·4 %)	109 (85·2 %)
	Metacentric	11 (8·7 %)	107 (83·6 %)	19 (14·8 %)

The 'homozygous' species of *Trimerotropis* (*maritima* and *citrina*) occur in the eastern and middle western states of the U.S.A., while the 'heterozygous' species are confined to the western states (particularly Washington, Oregon, California, Utah, Arizona and New Mexico). It is thus possible that the eastern species represent a more ancient stock that has never gone in for structural rearrangements in the way that the other species have. A cytological study of the species which have spread to South America might be of considerable interest.

No final answer can be given to the question: Why have some species of the Trimerotropi accumulated structural rearrangements in the course of their

phylogeny while in others all the chromosomes have retained the original acrocentric condition? Muller (1940*a*) has, however, suggested the following



Text-fig. 50. Distribution of the species of the grasshopper genus *Trimerotropis*. The 'cytologically heterozygous' species are restricted (as far as is known) to the western half of the U.S.A.

explanation: In most species of Acrididae chiasmata are formed near the centromere, being frequently localized in this region and in the distal parts. This is the state of affairs in *T. maritima* and *T. citrina*, in which no pericentric inversions

have occurred. In the remaining species that have been studied (and in all species of *Circotettix*) chiasmata are usually not formed in the centric regions, most of them being confined to the distal ends of the bivalents. Muller suggests that these species are, as it were, exempt from paying the usual penalty for pericentric inversions. Since no crossing-over usually takes place in their centric regions these segments can undergo structural changes of a type that could not possibly survive in other organisms.

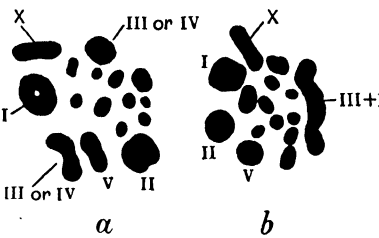
That *T. maritima* and *T. citrina* are fairly closely allied is shown by the fact that they can be crossed (Carothers, 1939, 1941). It would be extremely interesting to know how the difference in chiasma localization which separates these two species from the others arose in the first place. Muller's explanation is no doubt true, as far as it goes: pericentric inversions could hardly have survived save in the presence of a particular type of chiasma localization. But this type of localization seems to exist in many other species of Acrididae (e.g. in *Philocleon anomalus* (Helwig, 1941) and in *Paratylotropidia* (King and Beams, 1938)) without leading to the spread of pericentric inversions in the populations. The problem must therefore be regarded as only partially solved.

Although it is clear on general grounds that heterosomal changes (i.e. translocations of various types) must have taken place in the evolution of most groups of animals, they have only very rarely been found in the heterozygous state in wild populations. One exception must, however, be made to this statement—namely, that whole-arm transfers and particularly centric fusions are not uncommon in the heterozygous condition in wild populations of some groups. We have already seen that most types of translocation seriously diminish the fertility of the organism when heterozygous—so it is hardly surprising that they very rarely manage to establish themselves in nature. On the other hand, whole-arm transfers often do not lower fertility even when heterozygous, so that their occurrence in natural populations is not unexpected. Out of several hundred populations of *Drosophila pseudoobscura*, *azteca* and *melanogaster* that have been studied in detail by the salivary-gland technique, not a single one has been found to contain a translocation, but in *D. ananassae* Dobzhansky and Dreyfus (1943) found a reciprocal translocation between chromosomes II and III at one locality in Brazil.

In grasshoppers translocations seem to be equally rare in individuals caught in the wild state. Nevertheless, Carothers (1931) found one individual of *Trimerotropis citrina* which was certainly heterozygous for a mutual translocation: two acrocentric chromosomes had probably broken about midway along their length, and then interchanged the fragments. At meiosis the four chromosomes formed either a 'chain' or a 'ring', thus showing that the regions proximal and distal to the breakage points all had chiasma frequencies approaching or above unity. Unfortunately, Carothers does not seem to have found the condition in more than a single individual, so that it is uncertain whether the translocation had

persisted for any length of time in the population; it may have arisen in that particular individual. Helwig (1942) has recently described reciprocal translocations in an individual of *Podisma sapporoensis* and in one of *P. motodomariensis*.

In a population of the tettigoniid *Metrioptera brachyptera* from the New Forest, near Southampton, two pairs of chromosomes sometimes form a chain of four at meiosis (White, 1940*c*). The simplest interpretation of this condition would be to suppose that a mutual translocation was responsible, as in Carothers's case. If so, the regions distal to the break must be very much smaller than those proximal to it, or at any rate have a much lower chiasma frequency, since the chain of four is only found occasionally and a ring of four has never been observed (most cells show two separate bivalents). In this case it is clear that the translocation (if such it be) has existed for a number of years in the population, since it was found in many individuals both in 1933 and 1937.



Text-fig. 51. First metaphase in the tettigoniid *Metrioptera brachyptera*. *a*=a cell with 15 bivalents; *b*=a cell with a chain of four chromosomes, indicating that the individual from which it was taken was probably heterozygous for a translocation between chromosomes III and IV.

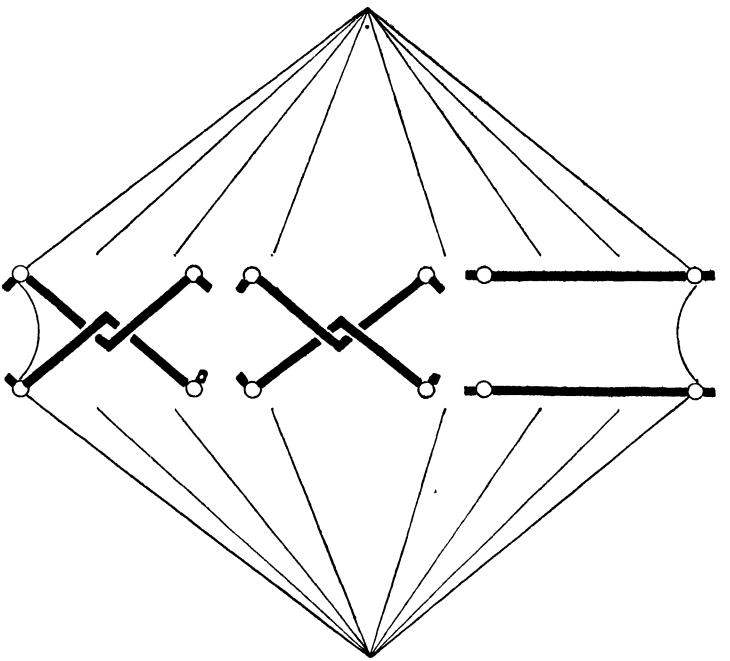
Populations in which centric fusions have occurred but have not stabilized themselves so that heterozygotes occur have been described by Woolsey (1915) in several species of the tettigoniid genus *Jamaicana* and by Ohmachi (1935*a*) in some cricket populations (see p. 168).

Piza (1939*a*, *b*, 1940*a*) has reported the existence of translocations in some individuals of the scorpion *Tityus bahiensis*. This species also shows unexplained variations in chromosome number—most individuals have six chromosomes in the spermatogonia and form three bivalents at meiosis, but one individual was found with 9 chromosomes in the spermatogonia and one with 18. The 9-chromosome individual was apparently heterozygous for two separate translocations.

The cytology of *T. bahiensis*, although extremely interesting, is thus very difficult to understand. It is doubtful whether chiasmata are formed in the male, and it is also possible that the chromosomes are polycentric, as in *Ascaris*. Piza (1941) has claimed that the chromosomes are dicentric, with one centromere at each end, but his evidence is unsatisfactory, since the centromeres have not been actually seen as morphological entities (it is worth noting that in another scorpion, *Opisthacanthus*, Wilson (1931) has figured one centromere in each chromosome).

Whatever the status of centromeres in *Tityus* two things are clear: translocations are extraordinarily common and rather drastic changes in chromosome number seem to have occurred in the history of the species. It is possible that the chromosomes undergo mechanical fragmentation rather frequently as a result

of their being polycentric (see Text-fig. 52 for an interpretation of the origin of translocations by this method). If this were so it might explain both the translocations and the variation in chromosome number. But the whole matter is far from clear. In *Ascaris megalocephala*, where the chromosomes are definitely known to be polycentric, variations in chromosome number in the germ-line have long been known to occur (Herla, 1895; Boring, 1909; Li, 1937)—it is



Text-fig. 52. Diagram showing how twisting of the chromatids round one another in an organism with polycentric chromosomes may lead to chromosome breaks. If two chromosomes in the same cell are broken, a mutual translocation may result. It is suggested that this mechanism may account for the translocation heterozygotes met with in *Tityus*.

possible that these are of similar nature to the variations found in *Tityus*. *Ascaris* embryos with three chromosomes have usually been assumed to be the result of hybridization between var. *univalens* and var. *bivalens*, but there is no really critical evidence on this point.

In wild populations of some species of animals so-called supernumerary chromosomes are present in addition to the usual chromosome set, the individuals in the population having different numbers of supernumeraries. We may define a supernumerary chromosome as one which is absent altogether in some individuals without noticeably affecting the appearance of the animal—a definition that excludes chromosomes which are essential to the life of the organism but

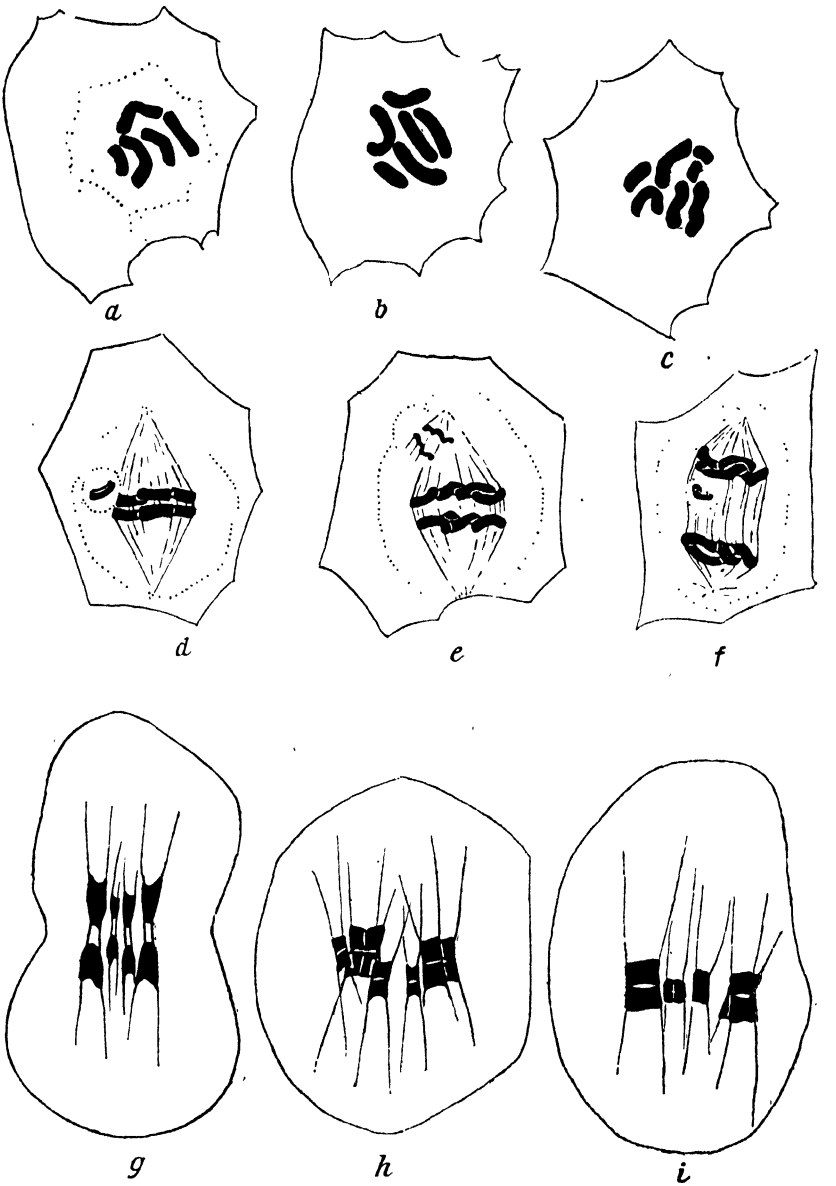
may, like the 'limited' chromosomes of *Sciara* spp. (see p. 201), be present in different numbers in different individuals. The genetical properties of supernumeraries must be so slight that individuals possessing several or none at all are fully viable and differ (if at all) in ways which are so subtle as to escape notice.

As typical examples of supernumeraries we may take those studied by Stevens (1908*a*, 1912*b*) and Hoy (1914) in the beetles *Diabrotica 12-punctata* and *D. soror*, by Carroll (1920) in the grasshopper *Camnula pellucida*, by Makino, Niiyama and Asana (1938) in a population of *Gryllotalpa africana* from Bengal, and by Hughes-Schrader (1942) in the scale insect *Nautococcus schraderae*.

It is probable on general grounds that supernumeraries represent duplications of regions present elsewhere in the chromosome set. In some instances they are very much smaller than any of the normal chromosomes, while in other cases they may be larger. Most supernumeraries probably arise from normal chromosomes by deletion of all, or nearly all, the euchromatic parts, the centromere, telomeres and inert regions being left behind. Some supernumeraries probably have a 'homosomal' origin (being derived from a single chromosome), while others have probably been derived from several chromosomes by a translocation which gave rise to a chromosome lacking euchromatic regions or only having short ones. Some supernumeraries may have become enlarged (by successive duplications) so that they now contain more heterochromatin than any of the other chromosomes which form the 'normal' set.

In many cases it has been suggested that supernumeraries have originated from either the *X* or the *Y* chromosomes. Since these are frequently heterochromatic or contain heterochromatic segments the assumption that heterochromatic supernumeraries have occasionally been derived from them is a very natural one, and there can be little doubt that in some cases it is correct. Thus in the grouse locust, *Tettigidea parvipennis*, Robertson (1917) found one individual which contained an extra chromosome similar to the *X* in appearance and behaviour, but somewhat shorter than a normal *X*. On the other hand, there are some supernumeraries which are fairly clearly of autosomal origin.

The pairing and chiasma formation of the supernumeraries are usually less regular than those of the normal chromosomes. A single supernumerary usually behaves as a univalent and may divide in either of the two meiotic divisions. Even where two or more are present, however, they are often unpaired at the first metaphase, either because they have failed to pair at zygotene or because their chiasma frequency is less than unity. The fact that supernumeraries are frequently univalent at meiosis no doubt explains many of the variations in number of supernumeraries as between one individual and another. Many supernumeraries are probably debarred from becoming regular members of the chromosome set (thereby increasing the chromosome number of the species) by the fact that they do not always form bivalents.



Text-fig. 53. Mitosis and meiosis in the scale insect *Nautococcus schraderae*. *a* = normal somatic set of male; *b* = same with large supernumerary; *c* = same with two small supernumeraries; *d*, *e* and *f* = behaviour of supernumeraries at mitotic anaphase, leading to variation of their number in the tissues of a single individual; *g* = first metaphase with a single supernumerary; *h* = same with two supernumeraries; *i* = same with one large supernumerary. From Hughes Schrader (1942).

Most individuals possessing supernumeraries have the same number in all their cells—but there are some interesting cases where supernumeraries may be present in varying numbers in different cells of the same gonad. This is notably the case in the grasshopper *Camnula* studied by Carroll (1920) and in some individuals of the common earwig (Callan, 1941*b*). These variations within the individual might theoretically be due to either of two causes: (1) supernumeraries might have arisen within the individual in question, or (2) mitotic non-disjunction of inherited supernumeraries might be responsible for the variation found. In *Camnula* there can be very little doubt that the second explanation is the correct one, but in *Forficula* Callan (1941*b*) believes that the *Y* chromosome may undergo fragmentation in some of the spermatogonial divisions, thereby giving rise to supernumerary fragments in some cysts of the testis but not in others.

Supernumeraries which undergo rather frequent mitotic non-disjunction present an interesting problem. There can be little doubt that they do so because they have got something wrong with their centromeres (mitotic non-disjunction of ordinary chromosomes is so rare that it has hardly ever been observed in the germ-track). Probably a centromere may be 'weakened' by a chromosome break near it or through it (see Darlington and Upcott, 1941; Rhoades, 1940; McClintock, 1941*b*), and it is possible that some supernumeraries have abnormal centromeres as a result of breaks of this kind.

We are badly in need of more exact data on the distribution and frequencies of supernumeraries in wild populations. Most of the authors who have studied them have merely recorded their presence in a few individuals from a single locality without attempting to determine their geographical distribution. It is thus impossible to tell what role they play in the population-dynamics of the species in which they occur. In *Locusta migratoria*, a species which is distributed over a great part of Asia, Africa and Europe, supernumeraries have only been found in a population from the island of Hokkaido (Itoh, 1934); in material from other localities they were absent (White, 1934, 1935*b*). In *Camnula* Carroll studied the testes of ten individuals and found supernumeraries in five. In this case the supernumerary had persisted for six years in the same locality, some of the individuals having been collected in 1909, some in 1915. In a Japanese population of *Trixalis nasuta* Minouchi (1934) found that nearly half the males bore supernumeraries, which sometimes formed bivalents at meiosis.

These very incomplete data merely suggest that once a supernumerary has arisen and spread to a fairly large percentage of the individuals in the population it may persist for a long while before it is either eliminated or established as a regular member of the chromosome set, present in the homozygous state in all individuals.

The genetical properties of supernumeraries have not been studied in any species of animal. An investigation of their effects (if any) on viability and fertility would be of considerable interest. In no case do we know what is the

upper limit to the number of supernumeraries that can be present in one individual without impairing viability to a serious extent. In maize the properties of supernumerary chromosomes (known as '*B*' chromosomes) have been investigated by a number of workers (Randolph, 1928*a*, *b*, 1941; McClintock, 1933; Darlington and Upcott, 1941). Here it is possible, by selection, to accumulate as many as 25 *B* chromosomes in one plant without noticeably affecting its appearance. This would seem to suggest that they must be almost entirely inert. Nevertheless, Darlington and Upcott have put forward an ingenious argument to prove that they are not completely functionless. They claim that the size and number of *B* chromosomes in a maize 'population' (i.e. culture or field, since the plant is not known in the wild state) are both constantly undergoing diminution, as a result of (1) the occurrence of deletions, (2) the loss of whole *B* chromosomes at meiosis. They then argue that since *B* chromosomes have not disappeared altogether there must be a positive selection which compensates for their loss. They therefore conclude that the *B*'s are only 'subinert'.

There may be several flaws in this argument. In the first place it is possible that duplications arise as often as 'deleted' *B* chromosomes. Secondly, the evidence that *B*'s are eliminated at meiosis is rather indirect. Nevertheless, it is *a priori* unlikely that any large heterochromatic chromosome is completely without influence on the cellular physiology of the organism, whether plant or animal. It is thus quite possible that a moderate number of supernumerary chromosomes may be advantageous in particular strains of certain organisms, and that these chromosomes may have been preserved and even accumulated in the course of evolution on that account. Some maize strains lack *B* chromosomes, and it is possible that in these they have been lost as a result of a *negative* selective pressure.

One interesting feature which the *B* chromosomes of maize probably share with many other supernumerary chromosomes is their variation in size. In a chromosome which is not, as a whole, essential to the life of the organism all duplications and deletions as well as shifts and other types of structural change will be preserved and may give rise to further increases or decreases in size by crossing-over. Thus wherever a supernumerary is present we may expect to find that it varies in size from one individual to another.

We have dealt with the subject of supernumeraries at some length for several reasons. Their properties are in some respects similar to those of other heterochromatic chromosomes and chromosome regions, but a comparison between the *Y* chromosomes of *Drosophila* and true supernumeraries shows that the former are much less completely inert.* The 'limited' chromosomes of *Sciara*,

* In some Heteroptera of the genus *Metapodius* (Wilson, 1907, 1909*a*, 1910) the distinction between *Y* chromosomes and supernumeraries really breaks down, since the number of *Y*'s varies from 0 to 4 in different individuals and populations of the same species.

on the other hand, vary in size in the manner that we have seen to be characteristic of many supernumeraries—nevertheless, they cannot be completely dispensed with in those species in which they occur (although some species seem to have got rid of them in the course of evolution).

The formation of supernumeraries is probably the chief method whereby chromosome numbers become increased in the course of evolution. Once a supernumerary has become established, portions of other chromosomes may become translocated to it, so that eventually it becomes an essential and permanent part of the chromosome set (see Chapter VIII).

CHAPTER VII

CHROMOSOMAL EVOLUTION IN THE GENUS *DROSOPHILA*

The genus *Drosophila* is a large one: Sturtevant (1921*b*) mentioned 202 species known at that time, and since then a large number of new forms have been described, mainly by Duda (1924, 1925, 1926, 1935), Sturtevant (1942), Kikkawa and Peng (1938), Patterson and Wheeler (1942) and Patterson (1943). It is probable that several hundred species still remain undiscovered, and new ones are still being described from Europe and the U.S.A., where the dipteran faunas are relatively well known. It is therefore quite probable that when the drosophilids of the more remote parts of the world have been properly studied the genus may be found to contain well over a thousand species. We may regard it as a flourishing group which is probably evolving fairly rapidly at the present time. To a considerable extent the geographical distributions of the species seem to depend on the habits of the larvae, which are very diverse, those of some species living on rotten fruit, while others inhabit decaying vegetation, fungi, oozing sap of trees, mammalian faeces and so on. The genus includes forest and woodland species, desert forms and swamp dwellers, and is represented in all the continents. Oceanic islands frequently have specialized *Drosophila* faunas: thus Hawaii has been stated to possess more species of the genus than the whole of continental North America (Zimmerman, 1942). There are several other genera belonging to the family Drosophilidae (*Scaptomyza*, *Chymomyza*, *Gitona*, *Leucophenga*, etc.), but *Drosophila* itself is by far the largest genus.

Some species of *Drosophila* (such as *melanogaster*, *simulans*, *funebris* and *busckii*) have become almost completely cosmopolitan in distribution, feeding on refuse dumps and other products of human activity. It is unlikely that the country of origin of these widely distributed forms will ever be known with certainty. Other species, whose larvae are restricted to specialized habitats such as rotting cactus stems, corollae of flowers or the exudates of particular species of trees, have 'natural' distributions which have not been seriously affected by man. Even here, however, a word of caution is necessary; *D. buzzatii* seems to have been imported into Sicily with the cactus *Opuntia*, both being originally native in America. Patterson and his collaborators distinguish between 'domestic' and 'wild' species, but a form which is wild in one part of its range may be domestic in another region.

In temperate climates the populations of most species are reduced to a very few individuals in the winter, being 'regenerated' in early summer from flies that have accidentally managed to survive the cold weather in sheltered places. In the tropics and subtropics, on the other hand, the natural populations of

many species consist of almost astronomical numbers of individuals at all seasons of the year.

Various attempts have been made to split up *Drosophila* into subgenera. Sturtevant (1939, 1942) has tabulated a large number of taxonomic characters for many species. On the basis of these tabulations he concludes that the genus can be divided into six subgenera which he calls Hirtodrosophila, Pholadoris, Dorsilopha, Phloridosa, Sophophora and Drosophila. There are a few species of uncertain relationships, so that the number of subgenera may eventually be increased to accommodate them. The first four subgenera include very few species, more than 90% of the total falling into Sophophora and Drosophila.*

The subgenera are distinguished by a number of characters such as whether the posterior pair of Malpighian tubules are free or fused, the shape of the dark bands on the abdomen, the number of filaments on the egg, the shape of the ventral receptacle in the female and of the testis in the male, and so on. This classification agrees with the habits and ecology of the species. Thus all members of Hirtodrosophila are fungus-feeders, while those of Phloridosa live in flowers. The distribution of some of the better known species between the subgenera may be gathered from Text-figs. 54–58. Each subgenus can be further split up into a number of species groups, which in their turn may in some cases be subdivided into subgroups. This elaborate hierarchy is both necessary and desirable in view of the large amount of information we now possess bearing on the relationships of the species and the mechanisms of speciation within the genus.

Even a superficial examination of the metaphase chromosomes of about a hundred species of *Drosophila* reveals a great variety of visibly different chromosome sets. In some species all the chromosomes are acrocentric, while in others they are all metacentric; in some species there is a minute, dot-like microchromosome pair, while in others this is absent. On the other hand, the general morphology of the salivary gland chromosomes is considerably more uniform, a large proportion of the species (67 out of the 87 studied by Wharton, 1943) having five long euchromatic arms and one very short one. The diversity of the mitotic chromosome sets is in part due to two factors which do not show up in the salivary nuclei, the fact that centric fusions have occurred in some species but not in others, and the presence in some species of heterochromatic arms which are wholly embedded in the chromocentre, so that they are not distinguishable in the salivary nuclei.

This number of 6-chromosome pairs is possibly the primitive one for the genus as a whole; it is not exceeded by any species of *Drosophila* so far studied, although in a good many species the number of chromosomes has been reduced to 5, 4 or 3.

* In the following pages *Drosophila* in italics means the genus, if in roman type it means the subgenus.

An investigation of the mitotic chromosomes is, of course, only a preliminary stage towards the complete cytological analysis of a group possessing salivary chromosomes, since it is certain that only a very small part of the cytological differences between the species are revealed in such a study; many of the structural changes in gene-sequence which have occurred in the phylogeny of the genus must have been of types which did not alter the visible morphology of the metaphase chromosomes and would only be detectable by a detailed study of the salivary chromosomes. Nevertheless, the great range in form of the mitotic chromosomes in *Drosophila* does lead to some general conclusions about their chromosomal evolution: it is a rather striking contrast to the situation in some other dipteran genera, such as *Culex* or *Chironomus*, where the evidence so far available suggests that there is much less of this type of variability, the mitotic chromosome sets of the different species being mostly very similar and often indistinguishable.

As soon as a number of species of *Drosophila* began to be studied genetically it became obvious that many of the mutations in *pseudoobscura*, *virilis*, *willistoni* and other species showed resemblances to one another and to mutations previously known in *melanogaster* and *simulans*. Some of these resemblances are probably spurious (i.e. between different and non-homologous genes with similar effects), but there can be little doubt that many of them do represent mutations of homologous genes. Thus the well-known mutations *yellow*, *achaete*, *dusky* and *bobbed* have been found in a large number of species. One fact of general significance which has emerged from linkage studies on different species of *Drosophila* is that, if we consider species not too distantly related to one another, there is a definite tendency for genes which are linked in one species to be linked

TABLE 7. *Homologies of the chromosome arms in various species of the subgenus Sophophora*

(Based on the tables of Muller (1940*a*) and Sturtevant (1940))

Muller's terminology ...	*A*	*B*	*C*	*D*	*E*	*F*
			Usual terminology			
melanogaster and *simulans*	*X*	II *L*	II *R*	III *L*	III *R*	IV
pseudoobscura	*X L*	IV	III	*X R*	II	V
miranda	$X_1 L$	IV	X_2	$X_1 R$	II	V
affinis subgroup	*X L*	IV	III	*X R*	II	V

in others as well. Two qualifications must, however, be made to this statement: (1) a metacentric chromosome in one species may be represented by two separate linkage-groups (i.e. two acrocentrics) in another, and (2) although the linkage-groups are largely the same throughout each species-group, the sequence of the genes within the linkage-groups varies considerably from species to species.

These facts have led to the drawing up of tentative homologies between the

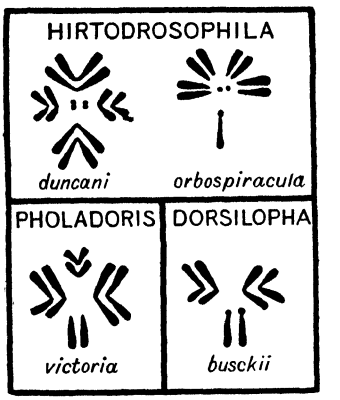
chromosome arms in some sections of the subgenus Sophophora (Crew and Lamy, 1935; Donald, 1936; Sturtevant, 1937*a*; Muller, 1940*a*; Sturtevant and Novitski, 1941*a*). Muller has designated the six chromosome arms which are found in most species of Sophophora A, B, C, D, E and F (not counting the *Y*-chromosome which is acrocentric in some species, while in others it consists of two arms designated *YS* and *YL*). Of these A is the *X*-chromosome of *melanogaster* and the 'left' limb of the *X* of *pseudoobscura*, while F is the 'dot-chromosome', i.e. IV in *melanogaster* and V in *pseudoobscura*.

The existence of these homologies between the chromosome arms of related species shows that translocations and heterobrachial changes have been much less frequent than homobrachial rearrangements in the evolution of *Drosophila*. Thus, although the sequences of the genes are continually changing in the course of evolution, the linkage groups are rather more permanent. On the other hand, it is unlikely, although not impossible, that the chromosome arms can be homologized between species so distantly related that they fall in different subgenera: heterosomal rearrangements *have* occurred in the phylogeny of *Drosophila*, although perhaps a hundred or more homosomal changes become established for every heterosomal one that does so (excluding heterosomal changes where both breaks are in the heterochromatin, i.e. whole-arm transfers).

In general, the sequence of genes within the linkage groups is entirely different, except in very closely related species. Thus in *melanogaster* and *simulans* the sequence is mostly the same (except for one large inversion and a number of small rearrangements), but in *melanogaster* and *pseudoobscura* (which belong to different groups of the same subgenus) no similarities in banding pattern could be observed in the salivary chromosomes (Dobzhansky and Tan, 1936*b*), and linkage studies confirm the conclusion that a very large number of homobrachial rearrangements (probably several hundred) have taken place since the evolutionary separation of these two species. It has been pointed out by Sturtevant and Novitski (1941*a*), however, that a few pairs of closely linked genes (e.g. *yellow-scute*, *Notch-white* and *miniature-dusky*) have remained associated over a long period of time, since they are found together in many species belonging to both the two main subgenera (*yellow* and *scute* are separated, however, in *D. hydei* and *D. affinis*).

In our systematic review of chromosome morphology in *Drosophila* (based mainly on the figures and descriptions of Wharton, 1943) we shall consider first the smaller subgenera. Hirtodrosophila includes two species with very different chromosome sets. *D. orbospiracula* has four acrocentric autosomes, a 'dot' and an acrocentric *X*. It is almost unique among the species of *Drosophila* in that the male lacks a *Y* altogether. Presumably the functions which the *Y* performs in other species of the genus have been transferred to one or more heterochromatic regions in the autosomes or the *X* (either by actual translocation of *Y* substance or as a result of one set of genes taking over functions previously

carried out by those in the *Y*). In the other species of the subgenus which has been studied cytologically, namely, *duncani*, there are three metacentric autosomes, a metacentric 'dot' and a metacentric *X*. Here there is a *Y* in the male (also a metacentric element). One of the autosomes of *duncani* probably represents two chromosomes which are separate in *orbospiracula*, while the other chromosomes of *duncani* (including the *X*) have all undergone internal rearrangements which have transferred the centromere to a median or submedian position. Thus *duncani* has eight long arms and a 'dot' in the salivary nuclei, instead of five and a dot as in *orbospiracula*.



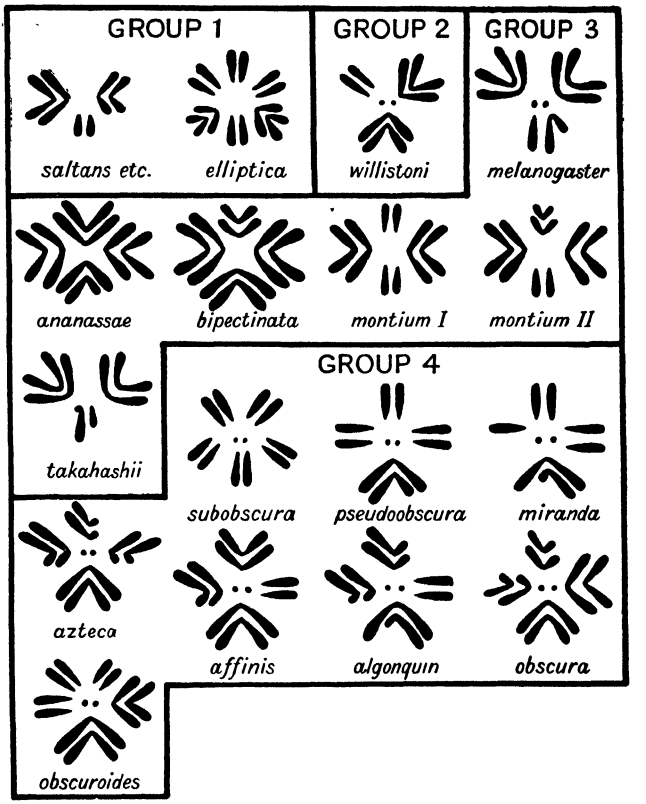
Text-fig. 54. Diagrams of the male chromosome set in the subgenera Hirtodrosophila, Pholadoris and Dorsilopha. Mainly after Wharton (1943), but redrawn.

D. (*Pholadoris*) *victoria* appears to have two large metacentrics, a small metacentric and an acrocentric *X*. There is no separate dot chromosome, but since a short arm is present in the salivary nuclei together with six long arms, it is probable that the dot has been translocated to one of the other chromosomes. Possibly it forms a 'short arm' to the *X*, in which case one autosomal arm must be entirely heterochromatic. *D. coracina* probably also belongs to the subgenus Pholadoris: it is reported by Kikkawa and Peng (1938) to have a chromosome set of the same type as *melanogaster*.

In *D.* (*Dorsilopha*) *busckii* the dot chromosome also appears to have been translocated to the short arm of the *X*. The latter has been described as 'rod-shaped', but the detailed descriptions of Sirotina (1938, 1939) and Eloff (1940) make it clear that the 'short arm' is considerably longer than in *melanogaster*. Very similar fusions of the IVth chromosome and the *X* have been obtained experimentally by Stone and Griffen (1940) in *melanogaster*, thus leading to an artificial reduction in chromosome number and a new genic balance in the male, the IVth chromosome being present once only instead of twice. There are only two autosomes in *busckii*, both large metacentrics. One further peculiarity of the *busckii* chromosome set is that in the salivary nuclei the chromocentre is practically absent, although the centric regions of all the chromosomes seem to be connected to the nucleolus by thin strands. It is thus probable that the heterochromatic regions round the centromeres are very short although they may all contain nucleolar organizers. The acrocentric *Y* of *busckii* shows about 14 bands in the salivary nuclei, according to Sirotina.

The subgenus Sophophora may be divided into four groups of species. Group 1 (*saltans* group) includes a number of forms from Central and South America whose larvae have the curious habit of skipping into the air. Most of

these species have two metacentrics and an acrocentric, and in *D. sturtevanti*, at any rate, the *X* is one of the metacentrics. *Elliptica* apparently has an aberrant chromosome set consisting of four acrocentrics and two metacentrics (Sturtevant, 1942, p. 36). The dot chromosome has probably been translocated to the short



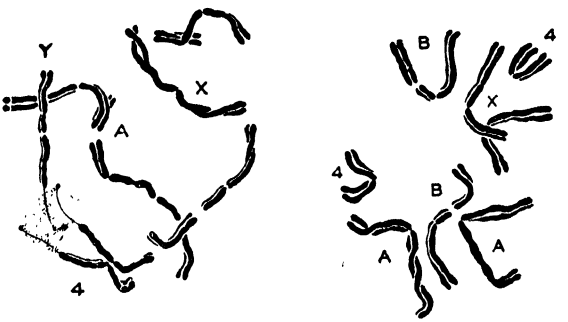
Text-fig. 55. Diagrams of the male chromosome set in the subgenus Sophophora. In group 1 most of the species (e.g. *sellata*, *prosaltans*, *sturtevanti* and *biopaca*) *appear* to have the same type of chromosome set as *saltans*, but the arrangement of the chromosome arms is known to be different in *prosaltans* (see Text-fig. 61). In group 2 the *nebulosa* set resembles that of *willistoni*. Based on various authorities: some of the figures are from verbal descriptions only, so that the lengths of the chromosome limbs may not be accurately shown.

arm of the acrocentric in the *saltans* group, but until more detailed descriptions of the chromosomes have been published it is impossible to be certain. In *D. prosaltans*, studied by Dobzhansky and Pavan (1943), a whole-arm transposition has apparently taken place and has led to the production of an $X_1X_2Y_1Y_2$ sex chromosome mechanism (Text-fig. 61). Just how this mechanism functions at meiosis is not clear, but apparently three bivalents are formed in the male

(an autosomal one and two sex bivalents, X_1Y_2 and X_2Y_2). One might expect that such a species would produce 50% inviable sperms or sperms which led to the death of the eggs they fertilized, but it is not definitely known if such is the case.

Group 2 includes *willistoni* and *nebulosa*, Caribbean and neotropical species with a chromosome set which outwardly resembles that of *melanogaster*. The resemblance is deceptive, however, since Lancefield and Metz (1921) showed that the acrocentric element is one of the autosomes, the *X* being V-shaped as in *sturtevanti*. One arm of the *willistoni X* is homologous to the *melanogaster* one, the other being an arm which is autosomal in most of the species of Sophophora.

Group 3 contains *melanogaster*, *simulans*, *takahashii*, *montium*, *bipectinata*, *ananassae* and a number of Asiatic species described by Kikkawa and Peng (1938).



a *b*

Text-fig. 56. *Drosophila ananassae*. *a* = a somatic prophase from a male larva, showing the association of the *Y* and the two IVth chromosomes with the nucleolus; *b* = a somatic metaphase from a female larva. From Kaufmann (1937).

Many species of this group have two pairs of metacentrics, an acrocentric *X* and a dot chromosome (as in *melanogaster*), but in *ananassae* and *bipectinata* the *X* has had its centromere transferred to a position in the middle of the chromosome which has thus been converted into a metacentric. In these species the IVth chromosome is relatively quite large since it has acquired extensive heterochromatic regions (Kikkawa, 1936*a*, *b*, 1937, 1938). In *ananassae*, at any rate, this is quite clear: the IVth chromosome is a metacentric which is almost entirely heterochromatic and bears the nucleolus, which in *melanogaster* arises from the *X* (Kaufmann, 1937; Kikkawa, 1937, 1938). The *X* of *ananassae* plays no part in the formation of the nucleolus, but one limb of the *Y* appears to be partly homologous to that region of the IVth chromosome which bears the nucleolar organizer. Thus in somatic prophases of male larvae three chromosomes (two IVths and the *Y*) are attached to the nucleolus, while in female larvae only two are connected to it. The partial homology between IV and *Y*, as well as the

fact that the *X* lacks a nucleolar organizer, suggests that the heterochromatic proximal part of the *melanogaster X* has in *ananassae* been translocated to the IVth chromosome. It is definitely known that the *bobbed* gene, which lies in this region, is carried in the IVth chromosome in *ananassae*. It is not easy to understand how the *X* and *Y* pair at meiosis in *ananassae*, since the heterochromatic region of the *X* acts as a 'pairing segment' in *melanogaster*. Most probably the region which has become translocated to the IVth chromosome in *ananassae* includes part of the inert segment of the *melanogaster X*, but not the whole of it, the remaining region still serving as a 'pairing segment'.

In salivary nuclei of *ananassae* chromosome IV is entirely embedded in the chromocentre; although heterochromatic it is not wholly inert, since haplo-IV individuals of *ananassae* are smaller than normal (Kikkawa, 1938).

Montium resembles *ananassae* in that the IVth chromosome is much larger than in other species of Sophophora. Kikkawa (1936*b*) has shown that there are two races of this species, in one of which this chromosome is acrocentric, while in the other it is a metacentric element. The IVth chromosome of *montium* is largely heterochromatic, so that it has probably received a part of one of the sex chromosomes by translocation, as has happened in *ananassae*; it is attached to the chromocentre at both ends (Text-fig. 15), but there is a euchromatic region between the two heterochromatic segments (a point of difference from *ananassae*, in which the IVth chromosome is entirely embedded in the chromocentre). In *takahashii* a centric fusion has apparently occurred between the *X* and the dot chromosome (Sturtevant, 1942): this arrangement, since it also seems to occur in *busckii*, may be a relatively primitive one.

The members of group 3 seem to have relatively short linkage-maps. The total known genetic length is 280 units in *melanogaster*, 311 in *simulans* and 326 in *ananassae* (as compared with 420 in *pseudoobscura* race A, 570 in *subobscura* and 788 in *virilis*). It is thus probable (as suggested by Philip, Rendel, Spurway and Haldane, 1944) that the members of group 3 have lower chiasma frequencies than most of the species of the genus.

Group 4 includes a number of darkly coloured species from the north temperate zone. It may be divided into several subgroups. The European *D. subobscura* occupies a somewhat isolated position in the group: it has five pairs of acrocentric chromosomes and a 'dot'. There is no recognizable chromocentre in *subobscura*, the proximal ends of all the chromosomes being merely joined together by thin strands very much as in *busckii* (Emmens, 1937). The *obscura* subgroup includes *D. obscura* itself and a number of other imperfectly known European species (Frolova and Astaurov, 1929; Buzzati-Traverso, 1940). *Obscura* has a metacentric *X*, three large metacentric autosomes and a dot. One of the four metacentrics must have arisen by a centric fusion, the other three by some sort of homosomal rearrangement whereby the centromere lost its original position near the end of the chromosome and acquired a new one

near the mid-point. In an unnamed form close to *obscura* one metacentric has been replaced by two acrocentrics (Frolova and Astaurov). *D. bilineata* and *D. tristis*, briefly described by Buzzati-Traverso, seem to have the same type of chromosome set as *obscura*, while *obscuroides* is said to have three metacentrics, an acrocentric and a dot (the *X* chromosome has not been identified with certainty).

In the *pseudoobscura* subgroup, which includes the A and B races of *pseudoobscura* itself and the closely related *miranda* (all from western North America), an autosomal arm which linkage studies have shown to be homologous to III *L* of *melanogaster* has become attached by a centric fusion to the *X*, which is accordingly metacentric. We shall deal with the cytology of this group in further detail later (p. 141).

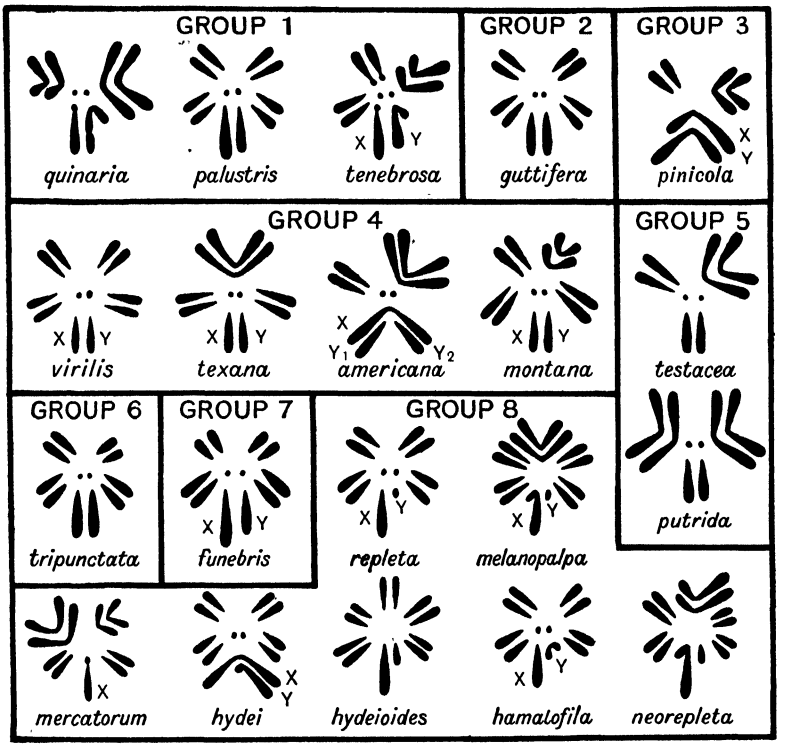
In the *affinis* subgroup (also confined to North America) the *X* has the same composition as in *pseudoobscura*, but in *azteca* and *athabasca* the three long autosomes have become metacentric through some kind of homosomal rearrangement, while in *affinis* and *algonquin* only two of them have done so. The relative proportions of the various chromosome arms differ somewhat from species to species, but the general type of chromosome set is the same in all of them (Sturtevant and Dobzhansky, 1936*b*; Wharton, 1943). Owing to these rearrangements the salivary nuclei show seven long arms and a dot arising from the chromocentre instead of five and a dot as in *pseudoobscura* (in *azteca* and *athabasca* one arm is completely heterochromatic).

Whereas group 3 of Sophophora seems to lead on to the related genera *Chymomyza* and *Scaptomyza* (*Ch. amoena* and *S. graminum* have mitotic chromosome sets which outwardly resemble that of *melanogaster*), group 4 forms, according to Sturtevant, a connecting link with the subgenus Drosophila.

Drosophila is a more complex subgenus than Sophophora, and has been subdivided by Sturtevant into no less than fifteen species-groups. Some of these contain at least 20–30 species while others are monotypic. Doubtless, a great many more species-groups will eventually be recognized, when species of uncertain relationships have been studied in detail. Group 1 (the *quinaria* group) includes a large number of species whose chromosome sets are all rather similar, although centric fusions have occurred in some but not in others. All have an acrocentric *X* and an independent dot chromosome which is never fused with any of the other elements. The remaining four chromosome arms are separate in *transversa*, *palustris*, *subpalustris*, *occidentalis*, *suboccidentalis*, *subquinaria* and *innubila*, fused to form two metacentrics in *quinaria* and *munda*, while in *tenebrosa* there is only one metacentric, the other two large autosomes being acrocentric. Minor differences in the proportions of the various chromosome arms may be due to differences in the lengths of the heterochromatic segments and their distribution throughout the chromosome set.

In groups 2 and 4 (*guttifera* and *virilis* groups) the same conditions prevail (four acrocentric autosomes, an acrocentric *X* and a dot), but in some members

of the *virilis* group various centric fusions have occurred (see p. 145), and in *montana* one of the autosomes has become converted into a metacentric by a complex rearrangement, reminiscent of those which we have inferred in *duncani*, *victoria* and some members of the *obscura* group.

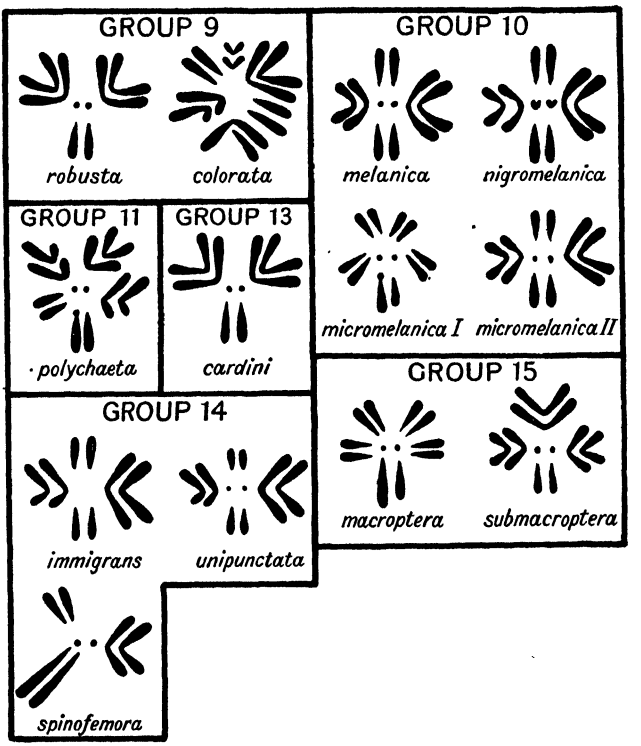


Text-fig. 57. Diagrams of the male chromosome set in the subgenus Drosophila (groups 1–8).

Group 3 includes only *pinicola*, a Californian species with a very aberrant chromosome set consisting of a J-shaped *X*, one acrocentric autosome and one metacentric. Patterson (1943) states that of all species of Drosophila it is nearest to Sophophora and to *Scaptomyza*. He is inclined to consider it as a very primitive form in spite of its peculiar chromosome set, which is difficult to compare with that of any other species.

Group 5 includes the fungus-feeder *testacea* and *putrida*. The first named has apparently lost one chromosome arm in comparison with other members of the subgenus Drosophila, since it only possesses one metacentric autosome, one acrocentric, a 'dot' and an acrocentric *X*. The second species has a chromosome set like that of *melanogaster*.

Groups 6 and 7 (*tripunctata* and *funebris* groups) show four acrocentric autosomes, a dot and an acrocentric X; there are minor differences between the species in regard to the relative lengths of the chromosomes, so that there have probably been changes in the distribution of the heterochromatin. We shall deal with the *funebris* group later (p. 148) when we come to consider interspecific hybridization.



Text-fig. 58. Diagrams of the male chromosome set in the subgenus Drosophila (continued). In group 10 *paramelanica* has the same chromosome set as *melanica*.

Group 8 (*repleta* group) is a large and complex assemblage including at least thirty species which has been specially studied by Wharton. It seems to have its headquarters in Mexico and the south-western United States. Except for *D. annulimana*, an aberrant species placed by Dobzhansky and Pavan (1943) in group 8, all the species have five long arms and a dot in the salivary nuclei, but the mitotic chromosome sets are very dissimilar. *Annulimana* has eight long arms and a dot in the salivary nuclei. The X is acrocentric in nearly all the species so far studied except *hydei*, in which it is a large metacentric as in the *obscura* group. The composition of this X is, however, entirely different, since the 'extra'

arm is entirely heterochromatic (it may possibly have been derived, by translocation, from the *Y*). In *mercatorum* and *neorepleta* the *X* also has an extra arm fused to it, but a very much shorter one than in *hydei*.

A separate dot chromosome is found in most of the group 8 species, but is absent in *melanopalpa*, *neorepleta*, *fuliginea*, *mercatorum*, *nigrohydei*, *hydeioides* and *leonis*; in these species it either has a long heterochromatic arm fused to it so as to convert it into a 'macrochromosome' or else it forms a 'short arm' to the *X*.

The *Y* varies greatly in size and shape in the *repleta* group. It may be large or small, acrocentric or metacentric, or even absent altogether, as it is in *D. annulimana* and in some strains, at any rate, of *mercatorum*. Even in the single species *D. repleta* several types of *Y* are known (Bauer, 1936*a*). It is interesting to note that some species of the *repleta* group with very different chromosome sets have been successfully crossed (e.g. *repleta* and *melanopalpa*). The shape of the chromosomes at metaphase is thus an unreliable index of phylogenetic relationship in this group (we assume that the latter is strongly correlated with crossability).

Group 9 includes *robusta* and *colorata*, two species with very different chromosome sets (Text-fig. 58). The first shows five euchromatic arms and a dot in its salivary nuclei, the second seven euchromatic arms and a dot. *Colorata* has apparently converted several of its chromosomes (including the *X*) into metacentrics by means of homosomal changes.

Group 10 (*melanica* group) includes several species with six euchromatic arms and a dot in the salivary nuclei. The *X* is acrocentric in all of them. Wharton (1943) has described two very dissimilar chromosome sets in different strains of *micromelanica*. One of these has a chromosome set very similar to that of *repleta*, while in the other there are two large metacentric autosomes, one presumably derived by centric fusion, the other by a homosomal rearrangement. Whereas the first has five long euchromatic arms the second has six, resembling *melanica* in this respect.

Group 11 includes only one species (*polychaeta*) which has been studied cytologically. It has seven euchromatic arms and a dot in the salivary nuclei.

Group 12 consists of *carbonaria*, whose chromosomes have not yet been studied.

Group 13 includes *cardini*, a species whose chromosome set outwardly resembles that of *melanogaster*.

Group 14 is the *immigrans* group. *Immigrans* itself has five euchromatic arms and a dot in the salivary nuclei, but the dot does not exist as a separate element in the mitotic chromosome set (Metz, 1916*a*, *b*; Stella, 1936; Spencer, 1940*c*; Wharton, 1943). *D. komaii*, a Japanese species, is said to have the same chromosome group and is probably closely related to *immigrans* (Kikkawa and Peng). *Spinofemora*, from Hawaii, has a very aberrant chromosome set with only four long euchromatic arms and a dot. One of the acrocentrics in this species is

extraordinarily long. It may have arisen by a translocation in which two acrocentrics were joined together end to end or by a pericentric inversion in a large metacentric.

Group 15 includes *macroptera* and *submacroptera*, two species with rather different chromosome sets (Text-fig. 58). The first has five long arms and a dot in the salivary nuclei, the second one seven long arms and a dot.

Group 16 includes *D. pallidipennis* from Brazil, studied by Dobzhansky (1944). This species has a very anomalous chromosome set, consisting of four pairs of acrocentrics, a pair of dots and a pair of huge metacentrics whose length is greater than the combined length of all the other chromosomes. These great V's are the *X* and *Y*, and their size is due to the large heterochromatic regions they contain.

Certain general conclusions can undoubtedly be drawn from this survey of chromosome morphology in *Drosophila*, but until detailed studies have been made on the salivary chromosomes of a large number of species it would be unwise to speculate too far as to the types of rearrangements which have occurred in phylogeny. The most generalized chromosome set (although not necessarily the most primitive at any particular level of evolution or in any particular section of the genus) seems to consist of an acrocentric *X*, four acrocentric autosomes and a dot. This type of chromosome set occurs in *D.* (Hirtodrosophila) *orbospiracula*, in *D.* (Sophophora) *subobscura* and in at least eight out of the fifteen species-groups belonging to the subgenus Drosophila.

Apart from fusions with the dot chromosome in *busckii*, *takahashii*, *melanopalpa*, *neorepleta*, the *X* appears to have become metacentric on at least nine different occasions in the phylogeny of the genus:

(1) in *duncani* by homosomal rearrangement;

(2) in *sturtevanti* and presumably in other members of the *saltans* group, by fusion with an unidentified autosomal element;

(3) in *willistoni* and *nebulosa*, by fusion with an unidentified autosomal element;

(4) in *ananassae* and *bipectinata* by homosomal rearrangement;

(5) in the whole of the *obscura* group except *subobscura* by fusion with element *D*;

(6) in *americana* by fusion with chromosome IV;

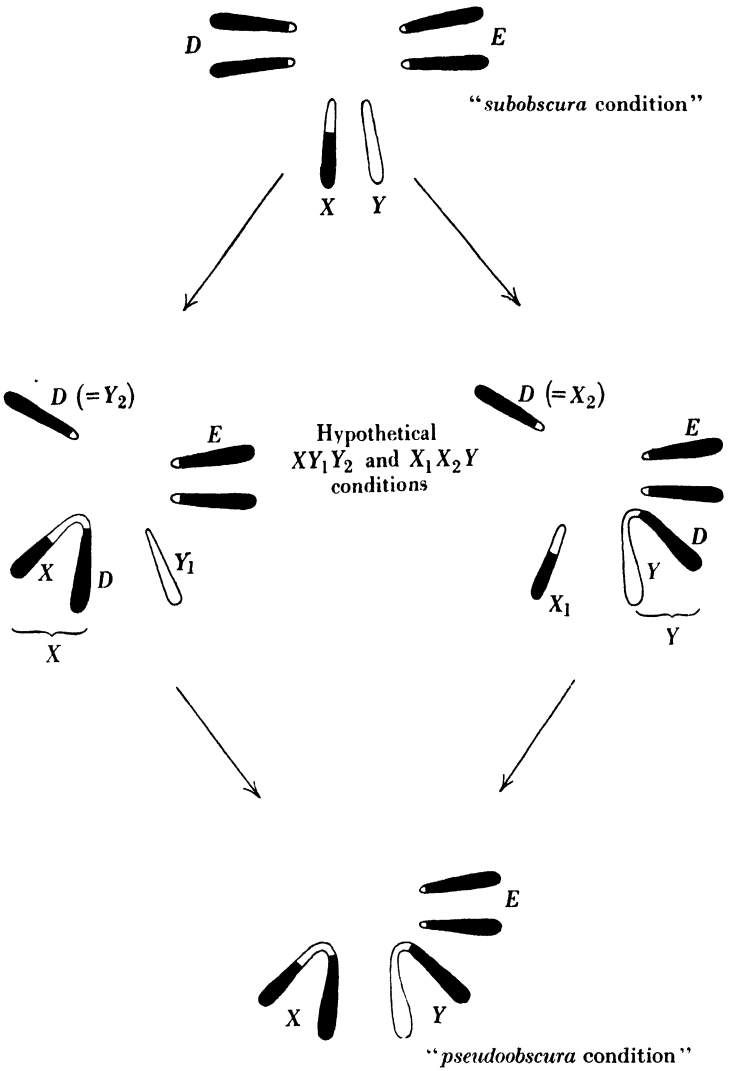
(7) in *hydei* by fusion with a heterochromatic arm (possibly derived from the *Y*);

(8) in *colorata* by a homosomal rearrangement.

(9) in *pallidipennis*.

We have assumed that in the subgenus Sophophora the condition in which the *X* is acrocentric is the primitive one, the fusion with the *D* element being secondary. Sturtevant and Novitski (1941*a*) have, however, suggested that the sequence of events was reversed. If *D* was part of the *X* and subsequently broke away to become autosomal (as they suppose), then it must have been originally

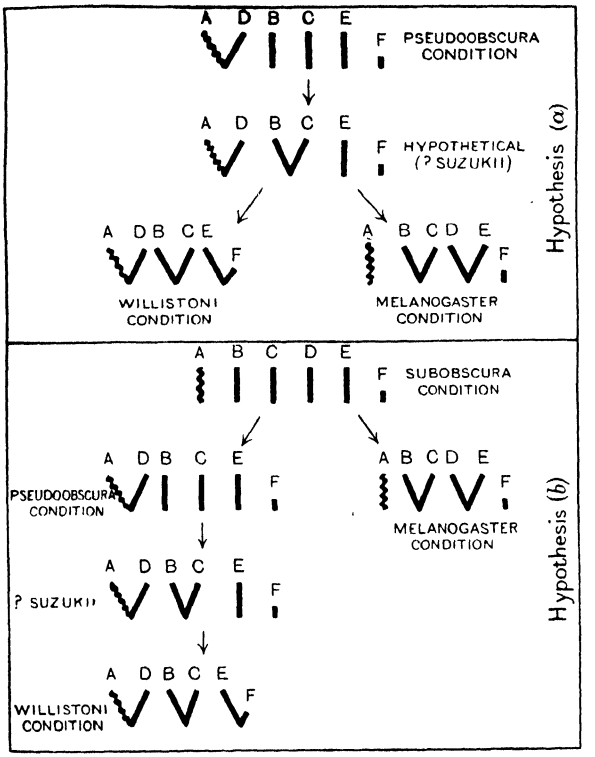
present once only in the male and later became diploid in both sexes. Conversely, if the *D* element was originally autosomal and later became included



Text-fig. 59. Diagram showing two alternative ways in which the metacentric *X* and *Y* of the *pseudoobscura* subgroup could have been derived from the *subobscura* condition in which both sex chromosomes are acrocentric.

in the *X* during the early history of the *obscura* group, then it must at the same time have become adapted to being haploid in the male.

Although it is not possible to decide with absolute certainty between the two alternatives, Sturtevant and Novitski's hypothesis seems very improbable, since a chromosome limb which is part of the *X* will almost certainly upset the genic balance upon which sex determination depends, if it becomes autosomal. The reverse process (incorporation of an autosomal arm in the *X*) is known to have

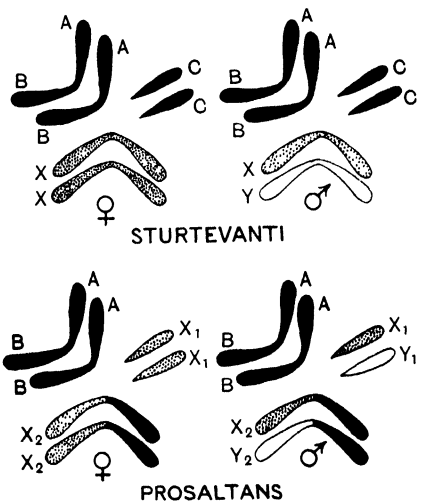


Text-fig. 60. Diagrams of two alternative hypotheses of chromosomal evolution in the subgenus Sophophora. Hypothesis *a* is that favoured by Sturtevant and Novitski, hypothesis *b* seems more probable for various reasons explained in the text.

occurred in several genera of grasshoppers, such as *Machaerocera*, *Philocleon*, *Hesperotettix* and *Mermiria*, without upsetting the sex-determining mechanism (see p. 250) and has occurred also in *D. americana*.

If we accept the view that the *obscura* condition is secondary, what has happened to the other *D* element in the male? It might, of course, have been suddenly dropped out of the chromosome set, but this would have produced a considerable upset in the genic balance of the fly, and hence seems unlikely on general grounds. If one *D* chromosome became fused to the *X* the other would presumably persist for a while as a separate element, as has happened in the case of the IVth chromosome

in *americana* (see p. 145). It might then become gradually inert or be lost by a succession of deletions (the effect of each of which would be less drastic than the loss of the whole chromosome at once). McKnight (1939) has suggested that the other *D* chromosome was translocated to the *Y* and that it then became gradually heterochromatic. This suggestion makes it unnecessary to assume any sudden and improbable loss of a large chromosome element. In the *saltans* group a similar translocation of an autosomal element to the *X* seems to have taken place and, as in the *obscura* group, this element has become haploid in the male. In *willistoni* and *nebulosa*, according to Wharton (1943), a different condition is met with—one member of the autosomal element has become fused to the *X*, the other to the *Y*, so that no change in genic balance need have occurred.



Text-fig. 61. Diagrams of the mitotic chromosome sets in two species of the *saltans* group of *Drosophila* to show the change in the sex-chromosome mechanism which has taken place in *prosaltans*. Based on the work of Dobzhansky and Pavan (1943).

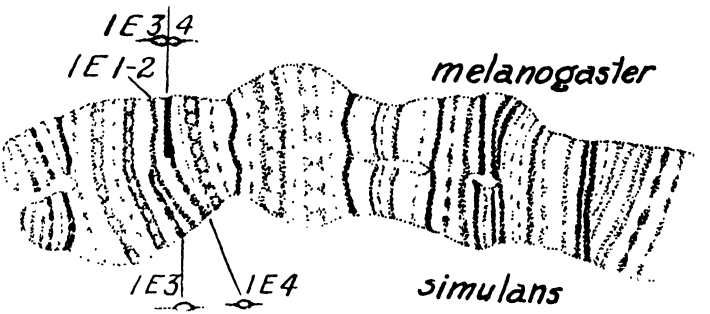
The conversion of acrocentric elements into metacentrics by homosomal rearrangements seems to have occurred independently in many species-groups of *Drosophila*. The simplest way for such a change to occur would be by a pericentric inversion, but it is by no means certain that this is what has actually happened in species like *duncani*, *affinis*, *colorata*, *annulimana* and *montana*. Thus, until detailed studies on the salivary chromosomes have been carried out, it would be unwise to follow Wharton (1943) in labelling all such changes as necessarily due to pericentric inversions.

The 'standard' number of six chromosome pairs is not exceeded by any species of *Drosophila* so far studied, although, as a result of fusions, the number of centromeres (i.e. of chromosome pairs) may be reduced to 5, 4 or even 3. The fact that the chromosome number has not been increased above 6 may be correlated with the extreme rarity of supernumerary chromosomes in wild individuals of *Drosophila*. Apart from an old record of a supernumerary in *ornatipennis* the only undoubted instance is a stock of *putrida* which was found by Wharton to be carrying some very small supernumeraries.

For a long time the only two species of *Drosophila* that had been successfully hybridized in the laboratory were *melanogaster* and the very closely related *simulans*. More recently it has been found that many species can be induced to mate in captivity, and in many cases hybrid offspring have been obtained.

Experimental hybridization has become, in fact, a most important technique for studying the taxonomic relationships of the various forms. By studying the salivary nuclei in the hybrids a very accurate picture of the structural rearrangements which have occurred since the evolutionary divergence of the two forms can be obtained.

Hybridization is only possible in *Drosophila* between closely allied species belonging to the same group. Even within a species-group not all forms can, as a rule, be crossed, all but the most nearly related ones being completely cross-sterile (Patterson, 1942*c*).



Text-fig. 62. Distal end of the *X* chromosomes in a salivary nucleus of a hybrid between *Drosophila melanogaster* and *D. simulans*. Pairing is incomplete at the tip and in two other short regions. A small inversion including the bands 1E1-2 and 1E3 has occurred since the evolutionary separation of the two species. From Painter (1939).

The best-known case of interspecific hybridization is that between *melanogaster* and *simulans*. These two species are very similar in appearance. Their original home is unknown, but was probably in tropical Asia, where group 3 of Sophophora seems to have its headquarters; they have now become largely cosmopolitan, breeding in rubbish dumps and similar places. The two species form large populations and often occur together, apparently without interbreeding. The cross *melanogaster* ♀ × *simulans* ♂ gives only female offspring (with a few rare males that have arisen as a result of non-disjunction), while the reciprocal cross gives offspring of both sexes, although the males are in a majority (Sturtevant, 1921*a*; Biddle, 1932). All the hybrids are entirely sterile, having underdeveloped gonads in which the germ cells never undergo meiosis, remaining as oogonia and spermatogonia.

It was shown by Sturtevant and Plunkett (1926) and Sturtevant (1929*b*) that the alinement of the genes in the two species is similar, but that in the right limb of the IIIrd chromosome there is a long section which is inverted in *simulans* as compared with *melanogaster*. This conclusion was arrived at by genetical methods and has since been confirmed by the salivary chromosome studies of Pätau (1935) and Kerkis (1936, 1937), who also found that although

the pairing of the chromosomes is fairly complete in the salivary nuclei of the hybrid larvae, there are a few regions which regularly fail to pair, particularly in the IVth chromosome and at the distal end of the *X*. The analysis has been carried a stage further by the work of Horton (1939), who finds that a number of 'minute' rearrangements have occurred since the divergence of the two species and that these differences are concentrated in the regions where Pätau and Kerkis had observed failure of pairing. Horton distinguished ten clear cases of structural change, including five very short inversions in addition to the long one seen by other workers. In addition, four structural changes involving one or two bands were detected at the free ends of certain chromosomes. There were also fourteen short regions where no pairing took place in the hybrids, but where no structural changes could be detected; Horton suggests that in these segments rearrangements have occurred which are too minute to be detected cytologically. Slizynski (1941) has later made a detailed comparison between the IVth chromosome of *melanogaster* and that of *simulans*. He finds that the dot chromosome has two arms, one of which (IV *L*) is very short. In IV *R* there is a region containing about 24 bands which is inverted in *simulans* as compared with *melanogaster*. In IV *L* a single conspicuous band which is present in *melanogaster* is apparently wanting in *simulans* (this may represent a true deletion, or the missing band may be 'inserted' somewhere else in the chromosome set). We shall deal with the nature and causes of the sterility of the *melanogaster-simulans* hybrids in a later chapter (pp. 217 and 223).

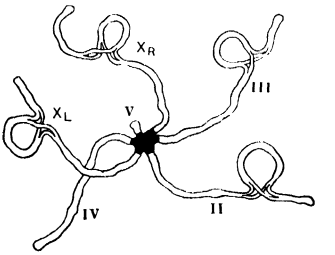
The *pseudoobscura* subgroup includes three forms—the A and B races of *pseudoobscura* itself and the closely related *miranda*. The group extends from Alaska to Guatemala: *pseudoobscura* occurs in all the Pacific and Rocky Mountain states of the U.S.A., being represented in Alaska, British Columbia, Washington, Oregon, California, Montana, Utah, Nevada, New Mexico, Arizona and Colorado by both races, and in Texas, Mexico and Guatemala only by race A. The subgroup as a whole seems to belong to the 'Vancouveran' fauna, race A having extended its range eastwards and southwards beyond the Vancouveran area.

We have already described the situation which exists in wild populations of *pseudoobscura*, in which large numbers of different gene-sequences are known, particularly in the IIIrd chromosome. Hybrids between the two races show at least four different inversions, but no 'minute' structural differences. The total number of inversion loops present in the salivary nuclei of A × B hybrids may, of course, be more than four, owing to the presence of intraracial inversions, as well as the interracial ones. The male hybrids are entirely sterile, but the female ones produce a few offspring when backcrossed to males of either parent race (see p. 222).

The morphological differences between the A and B races of *pseudoobscura* are so slight that they cannot be detected except by careful measurements and statistical analysis (Mather and Dobzhansky, 1939). The sharpest difference

recorded is in wing-beat frequency, which may be important as a sexual stimulus. No ordinary taxonomist would regard these forms as even subspecifically distinct. Nevertheless, if we adopt the definition of a species laid down in Chapter I, we must consider them as worthy of specific rank, since they probably never interbreed in nature, and if wild hybrids ever do occur they would almost certainly be completely sterile under natural conditions. Boche (see Dobzhansky, 1937*d*) has shown that there is a definite sexual isolation between the two forms, interracial matings taking place less frequently than intraracial ones in mixed cultures. This case illustrates the extreme difficulty of reconciling taxonomic practice with a 'dynamic' evolutionary standpoint.*

The third member of the *pseudoobscura* complex is *D. miranda*, known only from the Puget Sound area, north-western California, and a single locality (Mt Whitney) in the Sierra Nevada (central California). In external appearance it resembles *pseudoobscura* very closely; Dobzhansky (1941*a*) states that the visible differences are smaller than those between *simulans* and *melanogaster*.



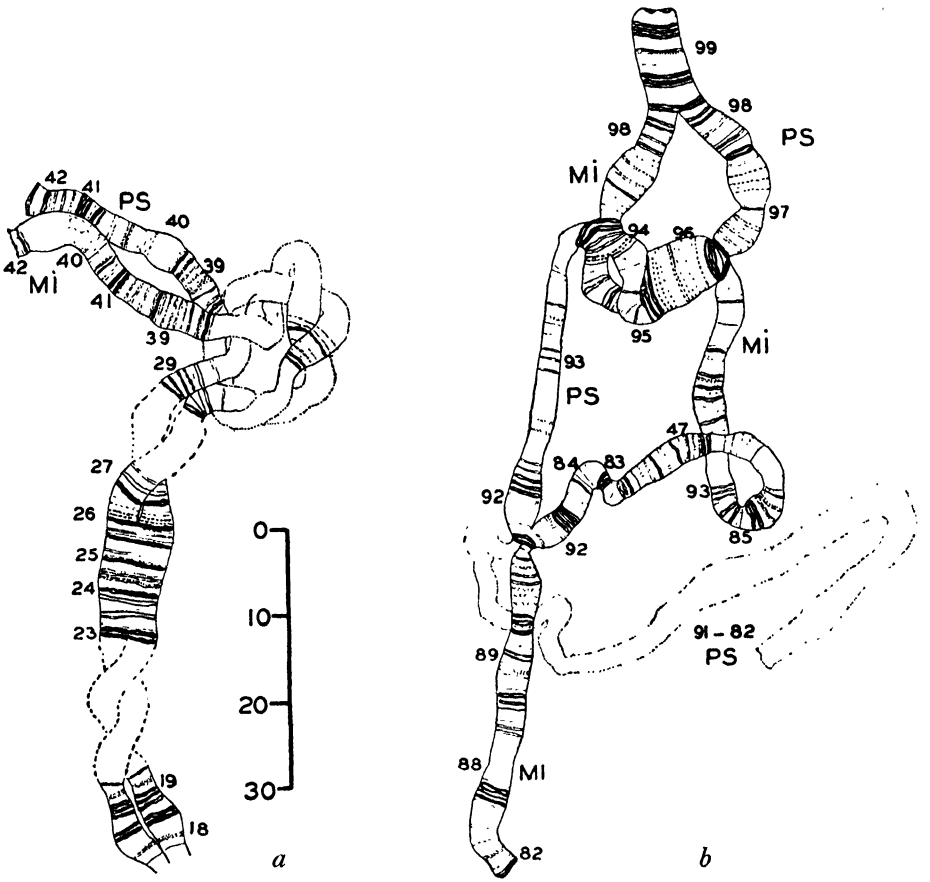
Text-fig. 63. The salivary chromosomes of a hybrid between races A and B of *Drosophila pseudoobscura*, showing inversions in *XR*, *XL*, II and III. Based on the work of Koller (1936*e*).

The metaphase chromosome set of the female *miranda* is indistinguishable from that of *pseudoobscura*. In the male, however, there is one chromosome less, i.e. the male *miranda* has 9 chromosomes instead of 10. The missing element is one member of the third pair of autosomes (element *C* in Muller's terminology); the male *miranda* has thus become haploid for this chromosome (Text-fig. 55). There is both genetical and cytological evidence that the single IIIrd chromosome always passes to the same pole as the *X* at meiosis in the male (Dobzhansky, 1935; Koller, 1939). It has thus become, in effect, a sex chromosome (just what role it plays in the physiology of sex determination does not concern us for the moment). We may call the original *X* (which is homologous to that of *pseudoobscura*) X_1, the IIIrd chromosome of *miranda* being designated X_2. The female *miranda* has four sex chromosomes ($X_1X_1X_2X_2$) which form two separate bivalents at meiosis. Since three out of five long chromosome elements are included in X_1 and X_2 the male *miranda* is haploid for more than half its genes.

It has been shown by McKnight (1939) that the *Y* of *miranda* differs from that of *pseudoobscura* in containing a number of short euchromatic segments. These he supposes to have been derived from the 'missing' IIIrd chromosome. Thus in the evolution of the *miranda* sex mechanism what probably happened was that one member of the IIIrd pair of autosomes became translocated to the

* Dobzhansky and Epling (1944) have recently raised race B to full specific rank under the name *D. persimilis*, reserving the name *pseudoobscura* for race A only.

Y, being subsequently broken up into a number of short regions by successive inversions. Mutations in these active regions of the *Y* are inherited, of course, exclusively through the male line, from father to son. The fact that the *Y* contains some material homologous to X_2 explains why the latter chromosome



Text-fig. 64. Incomplete pairing between chromosomes in salivary nuclei of hybrids between *Drosophila miranda* and *D. pseudoobscura*. $a = X\,R$ in a *miranda* ♀ × *pseudoobscura* race B male hybrid; *b* = IVth chromosome in a *miranda* ♀ × *pseudoobscura* race A male hybrid. Scale of micra attached. From Dobzhansky and Tan (1936*b*).

passes to the same pole as X_1 at the anaphase of the first division—both *X*'s being paired with parts of the *Y* to form a 'sex-trivalent' as shown in the figures of Koller (1939).

Hybrids between *miranda* and some strains of *pseudoobscura* can be obtained without great difficulty, but they are almost completely* sterile (Dobzhansky,

* In crosses between certain strains a very small number of backcross hybrids can be obtained.

1937*b*; Dobzhansky and Tan, 1936*a*, *b*), so that it is not possible to rear an F_2 or backcross generation. The cross *miranda* ♀ × *pseudoobscura* ♂ gives an approximately normal sex ratio in the offspring, but the reciprocal cross produces practically nothing but females (Dobzhansky, 1935)—yet another example of 'Haldane's rule' (see p. 225).

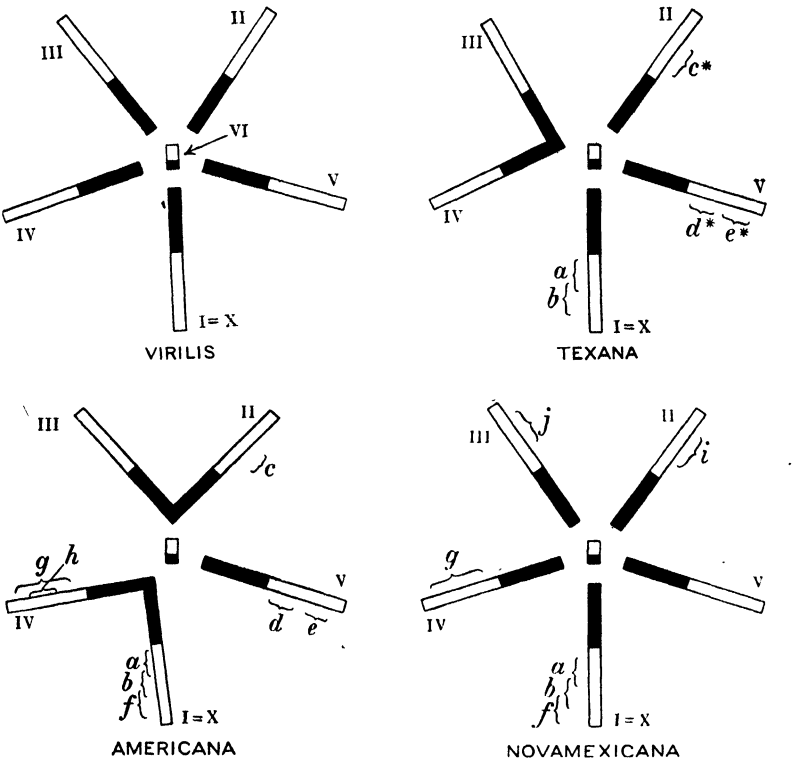
In the salivary nuclei of the hybrids the pairing of the *pseudoobscura* chromosomes with those of *miranda* is variable but usually very incomplete. In most nuclei each *miranda* chromosome or chromosome arm is loosely coiled round its approximate homologue in the *pseudoobscura* set, true pairing only occurring at a few points. A careful examination of the sequence of bands in the salivary chromosomes has shown that a great many structural rearrangements must have taken place since the evolutionary divergence of the two species, so that it is only in certain segments that the band sequence has remained identical. These homologous regions are fairly extensive in *XR* and chromosome II; on the other hand, in *X L*, III, IV and the small Vth chromosome the band sequences of the two species are very different. Dobzhansky and Tan (1936*b*) have estimated that at least 49 and more probably as many as 100 chromosome breaks must be assumed to have occurred during the divergence of the *miranda* and *pseudoobscura* gene-sequences in the course of evolution. They also claim that a number of the rearrangements which have occurred since the separation of the two species were heterosomal, i.e. transferences of short regions from one chromosome to another—a conclusion which has been questioned by Sturtevant and Novitski (1941*a*). There are a number of regions in which no similarities of banding pattern could be made out; they presumably represent sections in which the sequence of bands has been very greatly changed since the divergence of the two forms, as a result of multiple rearrangements in one or both species. Patterson and Crow (1940) have suggested that the small size of the populations of *miranda* may account for the large number of rearrangements that have undergone fixation.

The *pseudoobscura-miranda* cross is interesting because it shows how very different the gene-sequences of two species may be, even when the forms are almost indistinguishable to a taxonomist working solely on external characters. An even more striking example is the *azteca-algonquin* cross (Dobzhansky, 1937*d*). In this case the hybrid larvae show almost no pairing in the salivary nuclei, and the number of rearrangements which must have occurred since the separation of the two species is even greater than in the case of *pseudoobscura* and *miranda*.

The *virilis* group includes a number of forms whose exact status as subspecies or species is a matter of dispute. Patterson and his collaborators regard them all as species, while Sturtevant and some other workers consider *D. virilis virilis*, *D. virilis americana*, *D. virilis texana* and *D. virilis novamexicana* as geographical subspecies of a single Rassenkreis, '*D. virilis*'. We shall adopt the former course in the following account, since all these forms seem to be effectively isolated in nature.

D. virilis is widely distributed in Japan, China and Korea and has been found on a number of occasions in the U.S.A. and Mexico, where it is a purely 'domestic' species and has almost certainly been introduced, as suggested by Spencer (1940*a*). It differs from *D. americana* in at least seventeen different morphological and physiological characteristics.

D. americana, discovered by Spencer in 1936, is widely distributed in the U.S.A., occurring in a broad belt of territory from Ohio to Texas, but is nowhere



Text-fig. 65. Diagrams of the haploid chromosome sets of four members of the *virilis* group of *Drosophila*. Each of the letters *a* to *j* represents an inversion (*virilis* itself being taken as the standard). No attempt has been made to show the exact limits of the inversions, but where they overlap this has been indicated. Heterochromatic regions in black. Based on the work of Patterson (1941).

a common species (Patterson, 1942*d*). Whereas *virilis* has all its chromosomes of the acrocentric type, *americana* has acquired two centric fusions, one between autosomes II and III, the other between the *X* and autosome IV (Spencer, 1940*a*, *b*; Stalker, 1940; Patterson, Stone and Griffen, 1940, 1942). The effect of this second fusion is to convert *americana* into an XY_1Y_2 form, the

'Y_2' chromosome being simply the original acrocentric IVth chromosome, now confined to the male line and thus no longer able to undergo crossing-over with its homologue (owing to the absence of crossing-over in the male sex). The male *americana* naturally has one chromosome more than the female, although the same number of chromosome limbs. A peculiarity of the chromosomes of both forms is that the heterochromatic regions are very extensive and occupy almost the whole of the proximal halves of the mitotic chromosome limbs, but in spite of this the chromocentre is not particularly large.

Americana is further distinguished from *virilis* by no less than eight inversions, three in the *X*, two in chromosome IV, two in V and one in II. In the salivary nuclei of the hybrids pairing is very incomplete (Hughes, 1938, 1939).

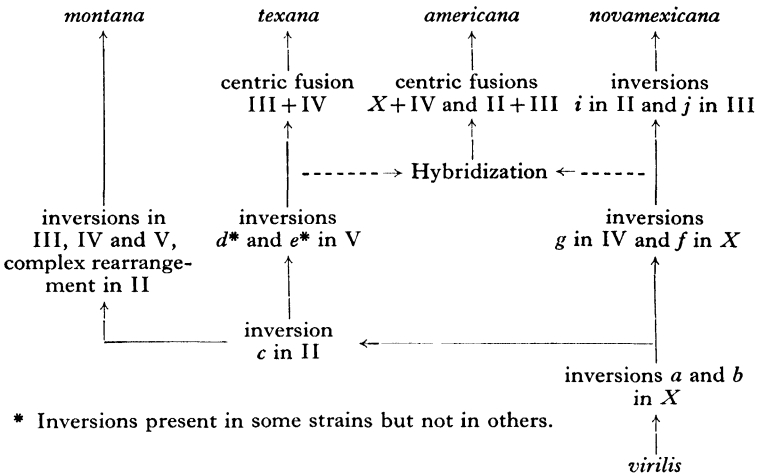
Texana was first described by Patterson, Stone and Griffen (1940), while *novamexicana* was discovered by Patterson (1941). *Texana* possesses a centric fusion, but it is between chromosomes III and IV, i.e. it is not the same as either of the fusions present in *americana*. *Novamexicana* has no metacentric chromosomes, its mitotic set resembling that of *virilis*.

A careful study of the inversions in these four different forms has enabled Patterson (1941) to put forward some hypotheses as to their phylogenetic relationships. In comparison with *virilis* the three New World forms all possess a couple of inversions (which we shall call *a* and *b*) in the *X* chromosome. They are also distinguished from *virilis* by the colour of the pupa (which is reddish instead of grey) and by a number of other morphological characters. We may thus regard them as more closely related to one another than to *virilis*. Apart from the *a* and *b* inversions, *texana* has three further inversions lacking in *virilis*, while *novamexicana* has *a*, *b* and four others. Of the eight inversions in *americana* three are also found in *texana* and two in *novamexicana* (apart from *a* and *b*, which are present in all forms except *v. virilis*). There is thus reason to believe that *americana* probably arose by hybridization between *texana* and *novamexicana*, or at any rate between stocks that subsequently gave rise to those forms. It probably acquired its centric fusions and a further inversion (*h*) after the hybridization. The only alternative to this theory of hybridization is to suppose that two identical inversions had arisen independently in *americana* and *texana*, a highly unlikely series of events.

Morphologically, *virilis* and *americana* differ more than the *pseudoobscura-miranda* pair, but the closeness of pairing of the hybrid salivaries and the partial fertility of the F_1 individuals would seem to indicate that they are more closely related than the latter pair of species.

The existence of yet another form (*D. montana*) belonging to the *virilis* group has been reported by Stone, Griffen and Patterson (1942). No centric fusions have occurred in *montana*, but the mitotic chromosome set differs from that of the other members of the *virilis* group in that chromosome II is a small metacentric. Thus some time after *montana* separated from the *virilis* stock a complex

structural rearrangement must have transferred the centromere of this chromosome to an interstitial position in the middle of the euchromatic region. Preliminary cytological studies of the salivary chromosomes in *montana-texana* hybrids have shown that in addition to this rearrangement chromosome II in *montana* contains inversion *c* which is found in *texana* but not in *novamexicana*. Chromosome III of *montana* has two included inversions not found in any other



Text-fig. 66. Diagram showing the presumed relationship of the various forms in the *virilis* group of *Drosophila*. After Patterson (1941), but modified and extended so as to include *D. montana*.

members of the *virilis* group. The *X* of *montana* contains two inversions (*a* and *b*) which occur in all the 'wild' species of the *virilis* group but not in *virilis* itself. The general conclusion from these data is that *montana* is nearest to *texana* and most widely separated from *virilis*. According to Patterson (1942*a*, *b*) there is a high degree of sexual isolation between *montana* and the other members of the group, so that hybrids are not easy to obtain.

In addition to the *melanogaster*, *pseudoobscura* and *virilis* complexes a number of other groups of closely related forms have recently been studied by Spencer (1940*a*, *b*, 1941) in Ohio and by Patterson and his collaborators in Texas (see especially, Patterson, 1941, 1942*a*, *b*; Patterson and Crow, 1940; Crow, 1942; Wharton, 1941, 1942; Griffen, 1941, 1942; and Mainland, 1941, 1942*a*, *b*). Unfortunately, in most of these cases the salivary-gland analysis has not been carried to completion. Thus the statement is several times made that 'there are no large inversions or other structural differences' between the forms under consideration, leaving open the possibility that minute rearrangements (of the type shown by Horton to exist between *simulans* and *melanogaster*) may be present.

One interesting pair of species consists of *D. palustris* and *D. subpalustris* from swamps in Ohio (Spencer, 1940*b*—the species were unnamed at the time when his paper was written). Hybridization is possible if large numbers of flies are used and the F_1 flies are partially fertile. The salivary chromosomes of the hybrids are very incompletely paired. These two species are obviously closely related and seem to have undergone speciation in a very restricted and specialized ecological habitat.

The *funebris* group (Mainland, 1941, 1942*a*, *b*) includes the cosmopolitan *D. funebris* (a 'domestic' species in the U.S.A.), *D. subfunebris* from California and *D. macrospina*. The last has been divided by Mainland into three subspecies, *D. m. limpiensis*, *D. m. macrospina* and *D. m. ohioensis*. The first of these is a Rocky Mountain form (Texas, New Mexico, Sonora, Arizona and Utah), the second is mid-western (Texas, Oklahoma, Missouri, Arkansas, Louisiana, Tennessee, Mississippi, Alabama, and Florida), while the last occurs in Ohio. They are thus true geographical subspecies whose ranges only overlap slightly, if at all. There are no major cytological differences between the last two subspecies, but *limpiensis* is distinguished by the presence of two inversions in the *X* chromosome.

Limpiensis females when crossed with either of the other two forms produce an F_1 consisting of sterile males and fertile females; the reciprocal crosses give offspring which are fertile in both sexes. Apparently there is a factor in the *limpiensis Y* which is necessary for the fertility of the male *if a limpiensis X is present* (compare the situation in crosses between *virilis* and *americana* or *texana*).

D. funebris will not cross with either of the other species of the group, so that its exact relationship to them is obscure. The Californian *subfunebris* will cross with *limpiensis*, however—readily with strains from Utah, less readily with ones from Texas. It can be crossed with strains of *macrospina* from western Texas, but not with stocks from eastern Texas, Ohio or Florida. We seem to have here a clear example of a 'cline of crossability' extending across the south-western states from California to the Mississippi. The F_1 males from all *subfunebris* × *macrospina* crosses are sterile, while their sisters are fertile.

The *mulleri* group, studied by Patterson and Crow (1940), Crow (1941, 1942) and Patterson (1942*a*), contains *D. buzzatii* from South America and Sicily (where it has probably been accidentally introduced with the cactus, *Opuntia*), *D. aldrichi* and *D. arizonensis* from the U.S.A., and two subspecies of *mulleri* itself, *D. m. mulleri* and *D. m. mojavensis*. *Mulleri* and *aldrichi* both occur in Texas, where their distribution areas overlap considerably; *mojavensis* is found in the Californian deserts, and is not known to exist in any locality where either of the other two forms occurs. *Mulleri*, *aldrichi*, *arizonensis* and *mojavensis* are probably all found in Mexico, but their distribution south of the border has not been determined.

The cross *mulleri* ♀ × *aldrichi* ♂ gives a few sterile offspring, while the reci-

procal cross could not be carried out at all. Nevertheless, Patterson and Crow report that a few male hybrids were found in the wild—the first natural hybrids to be recorded in *Drosophila*.

Crosses between *mulleri* and *aldrichi* on the one hand and *mojavensis* on the other have been carried out with the following results: *mulleri* females when crossed with *mojavensis* males produce female offspring which are partially fertile in backcrosses and male offspring which are entirely sterile; the reciprocal mating does not succeed. Crosses between *aldrichi* females and *mojavensis* males gave a few sterile sons.

All these three forms have five pairs of acrocentric chromosomes and a pair of 'dots' in the diploid set. The hybrid salivaries have not been studied in detail, but apparently there are no large inversions between *mulleri* and *aldrichi*, while *mojavensis* is distinguished by the possession of several inversions. Pairing is very incomplete in the *aldrichi-mulleri* hybrids, rather less so in those between *mojavensis* and the other two forms.

Mulleri and *aldrichi* are regarded as distinct species, although they seem to have differentiated very little further than the A and B races of *pseudoobscura*; they have somewhat different habits—*aldrichi* feeding almost exclusively on the prickly pear, while *mulleri* is a much more omnivorous species which lives on many kinds of rotting fruit (Patterson, 1942*a*). *Mojavensis* seems to be a true geographical subspecies, adapted to a desert life (it is considerably lighter in colour than *mulleri*).

Fairly closely related to the *mulleri* group are *D. melanica* and *D. micromelanica*. The former consists of a number of strains which may be divided on the basis of body colour into a 'light' and a 'dark' group (Griffen, 1941). A 'light' strain from Madison, Wisconsin, was found to show some cross-fertility with all the other 'light' strains, and was slightly cross-fertile with the Texas 'dark' strain. There seem to be no cytological differences between all these various races (if they deserve the name), except that the Texan strain has one inversion in comparison with the rest. A subspecies, *D. melanica paramelanica*, should perhaps be regarded as specifically distinct, since it shows a high degree of cross-sterility when mated with *melanica*, only very few offspring being produced. Similar results were obtained when the closely related *nigromelanica* was crossed to either *melanica* or *paramelanica* (Griffen, 1942). Somewhat unexpectedly, the few F_1 hybrids from these crosses which were obtained proved to be fertile, thus showing that cross-sterility and hybrid-sterility do not always go together.

In *D. micromelanica* crosses between two strains, one from Texas, the other from south Arizona, were made by Sturtevant and Novitski (1941*b*). When a Texas female was crossed with an Arizona male the sons were sterile, due to an interaction between the Texan *X* chromosome and the Arizona *Y*. All other hybrids were fertile. *Micromelanica* is completely cross-sterile to *melanica*, *paramelanica* and *nigromelanica*.

The cases where strains or geographical races show incipient cross- or hybrid-sterility are especially interesting, because they show us the initial stages of the speciation process, i.e. the first appearance of isolation mechanisms, as yet incomplete and only partially effective. Where geographical isolation is fairly complete a considerable amount of morphological divergence may have developed, while the isolation mechanism is still very incomplete. Thus in *D. hydei*, Spencer (1940*a*) has described a very distinct subspecies from the Yucatan peninsula. In spite of the differences in external morphology there are said to be no cytological differences between *D. h. yucatanensis* and the typical *hydei*, and hybrids between them are perfectly fertile. On the other hand, some very similar or indistinguishable strains may show almost complete cross-sterility. Thus in *D. repleta*, Wharton (1941) has distinguished as many as ten different strains which are prevented by some sort of sexual isolation from effective crossing. In some instances crosses which were successful in one direction failed completely when the reciprocal cross was attempted, the females having no sperm in the genital tract when dissected. Here again there are no large inversions or other structural differences between the chromosomes of the various strains.

As a result of these and other investigations of the same general type, it is becoming clear that, even in the single genus *Drosophila*, it is impossible to state that any particular degree of morphological divergence entitles a form to be regarded as a distinct species. Some geographical subspecies like *mojavensis* and *yucatanensis* still show a considerable degree of cross-fertility and hybrid-fertility with the 'type' subspecies, in spite of being very different in external appearance. Conversely, *miranda* and *pseudoobscura* produce almost completely sterile hybrids but are extremely similar in general appearance. Cytological differences between the chromosome sets are a useful guide, but should not be regarded as the sole criterion, or even the main criterion of evolutionary divergence, since it is certain that they have occurred far more frequently in some species groups than in others. Thus changes of gene-sequence which imply a considerable amount of evolutionary divergence in one section of the genus may have a lesser significance in another. In some sections (e.g. the *virilis* group) centric fusions may occur more readily than in others (e.g. the *mulleri* group). The morphology of the chromosome set is only one aspect of the general structure of the organism, and in estimating the degree of divergence between two forms it should not be considered apart from differences in eye shape, wing venation, length of bristles, structure of genitalia and other recognized taxonomic characters. The only advantages that changes in gene-sequence have over the usual type of systematic characters are (1) that they sometimes enable one to build up a phylogenetic tree which cannot be challenged (see p. 102), and (2) that it is sometimes possible to work out the actual number of breaks involved in a particular change of sequence, so that the degree of cytological divergence can be stated in a quantitative way.

Both these methods of investigation will, no doubt, be used extensively in the future.

It must be admitted that we have very little reliable information as to how frequently 'minute' changes (of the type seen in *simulans-melanogaster* hybrids) have occurred in *Drosophila* evolution. Where the salivaries do not pair at all (or very incompletely) in the hybrid nuclei, it is an extremely laborious task to work out the homologies of the various regions. Yet it is precisely in these cases (where the gene-sequences are very different) that we should expect to find the greatest number of minute rearrangements. At present one gets the impression from the published accounts of hybrid salivaries that the *simulans-melanogaster* pair of species show cytological differences of a type that is extremely rare in other species-groups: but it is likely that even more painstaking investigations than those already carried out will eventually reveal 'minute' differences in other sections of the genus. In *miranda-pseudoobscura* hybrids (Dobzhansky and Tan, 1936*b*) and also in those between *virilis* and *americana* (Patterson, Stone and Griffen, 1940) a few 'minute' differences certainly exist.

No pair of subspecies or species is known in *Drosophila* which differ in respect of a repeated segment. It is probable that cases of this kind will eventually be discovered, but at the moment it appears as if repeats only established themselves very rarely, so that one will not often find two closely related forms, one of which possesses a repeat, while the other lacks it. It is possible, however, that duplications of heterochromatic regions are in a special category and establish themselves more easily than euchromatic repeats. Something of this sort must have happened in the evolution of the *virilis* group, in which the heterochromatic regions are much more extensive than in other species of *Drosophila*. In the *repleta* group it is definitely known that some species have extensive heterochromatin, while in others the inert regions are much shorter.

All the work that has been carried out recently on *Drosophila* hybridization seems to suggest that most isolation mechanisms are in the beginning 'genic' rather than 'chromosomal', and that differences in gene-sequence between species or subspecies only begin to accumulate after the initial divergence has taken place. But all degrees of isolating mechanisms occur, some more effective, some less so. When dealing with forms that are rapidly 'speciating' it is often very difficult to state the degree of cross-fertility between two races or subspecies, since each may be subdivided into a number of local strains which differ in their degree of cross-fertility or sterility when hybridized.

CHAPTER VIII

THE EVOLUTION OF CHROMOSOME NUMBERS AND CHROMOSOME FORM

Until recently it did not appear likely that chromosome numbers were of any particular evolutionary importance. Thus Morgan, Bridges and Sturtevant (1925) wrote that 'To a geneticist many of these comparisons [i.e. between the chromosome sets of different species] will seem of little significance, because to him it is not the shapes and sizes of chromosomes which are important, but the genes contained in them'. Similarly, Wilson (1925) considered that 'Both cytological and genetic evidence prove that the chromosomes are compound bodies, containing many different components. So long as the sum total of these remains the same, or nearly so, it seems immaterial whether they be grouped to form few or many aggregates.'

These views are quoted here because they are still frequently expressed, although by now quite out-of-date. They belong to the period in the history of genetics when the gene was looked upon as an absolutely discrete and independent body exercising no influence on its neighbours. Whatever precise interpretation of the phenomena covered by the term 'position-effect' ultimately prevails, it is already clear that alterations in gene-sequence (such as commonly occur when changes of chromosome number take place) are of considerable genetical significance. The newer conception of the chromosome as an organized body whose parts stand in a definite functional relationship to one another has replaced the crude and atomistic idea of a row of entirely independent chromomeres like beads on a thread. The view that changes in chromosome number can take place by simple 'fragmentation' and 'fusion' died when it was realized that each chromosome possesses a centromere, and that centromeres do not arise *de novo* but only from pre-existing centromeres (Navashin, 1932). Thereafter it was clear that an increase in chromosome number must involve duplication of a centromere together with a region (large or small) around it; while a decrease in chromosome number must involve the permanent loss of a region containing a centromere. Thus both increases and decreases lead to concomitant changes in the total amount of genetic material, and must hence be expected to produce genetical changes, quite apart from the position-effect. Whether these laws apply to groups like the Heteroptera and Homoptera, where centromeres cannot be detected cytologically, is still uncertain; but there can be no doubt that they apply in the vast majority of organisms.

Before considering the problem of the evolution of chromosome numbers it is necessary to examine the extent and nature of the available data. The number of described species of animals is not far short of a million, and it is certain that

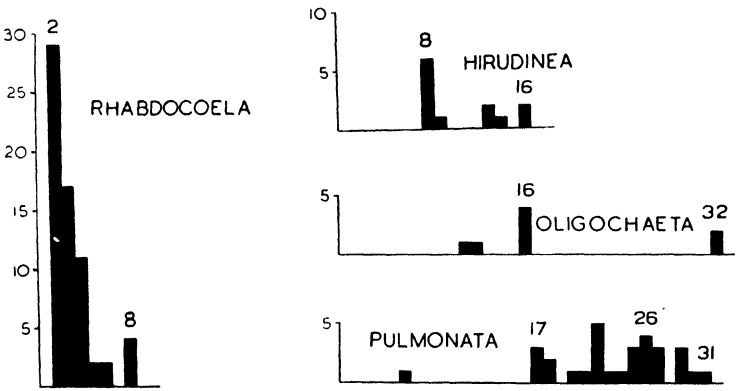
many more remain to be discovered. Of the total only about 1,500 (i.e. approximately 0·1%) have had their chromosome numbers determined. No doubt some of these determinations are erroneous, but if we exclude some of the very early work it is probable that the numbers catalogued by Harvey (1917, 1920), Bresslau-Harnisch (1927), and Oguma and Makino (1932, 1937) represent a reasonably accurate set of data upon which to base general conclusions.* Except in some groups such as the birds, where the chromosome numbers are very high and other special technical difficulties exist, there is little justification for the distrust sometimes shown by non-cytologists in the data which have been compiled on chromosome numbers. On the other hand, it is quite true that the chromosome number of an organism is merely the first thing that one needs to know about its cytology: it is much more useful to know the number of chromosome arms, the extent and position of heterochromatic regions, the location of nucleolar organizers, the chiasma frequencies of the arms, and so on. In many groups, however, all this information is likely to be unavailable for a long while, so that we have to base tentative conclusions upon the data we possess.

The haploid numbers of most species of animals lie between 6 and 20, numbers above or below these limits being rare except in a few groups. The only organism with a haploid number of 1 is *Ascaris megalocephala* var. *univalens*, although this instance is complicated by the fact that the number of chromosomes in the somatic cells is very much higher. The highest haploid number recorded for any metazoan is 112 in the geometrid moth, *Phigalia pedaria* (Regnart, 1933). The most notable example of a group in which all the chromosome numbers are low is the Diptera, while the birds probably all have high numbers (i.e. above 20 in the haploid set). It is not very easy to see why the range of chromosome numbers should be so restricted, but it is possible that in some groups the mechanism of mitosis is best suited to accomplish the separation of a moderate number of bodies, the spindle being unable to deal efficiently with very high or very low numbers (other explanations are, of course, quite possible).

In groups where metacentric and acrocentric chromosomes can easily be distinguished it is possible to compare the number of chromosome limbs, rather than the number of whole chromosomes. This is obviously a more satisfactory procedure, but in many groups it cannot be applied, since all the chromosomes look spherical at metaphase and it is not possible to determine the position of the centromere. This is the case in several insect orders such as the Heteroptera, Lepidoptera and Trichoptera, where some recent workers have even questioned the existence of individualized centromeres (see p. 22). It is possible that future work may enable us to analyse the structure of the chromosomes in these groups, but until then a discussion of their chromosomal evolution must be on an unsatisfactory basis.

* The later catalogue of McClung (1940) is very incomplete and contains many errors of compilation.

The extent of variation in chromosome numbers that is met with in various groups of animals can be grasped from an inspection of the histograms of Text-figs. 67–72. No doubt there are errors and omissions in the lists of chromosome numbers upon which these histograms are based, but they show the general nature of variation in chromosome number sufficiently clearly. It will be seen that in some groups nearly all the species have the same chromosome number, while in others there is a great range of variation. Harvey (1917, 1920) and some later authors have spoken of the most frequently occurring number in a group as

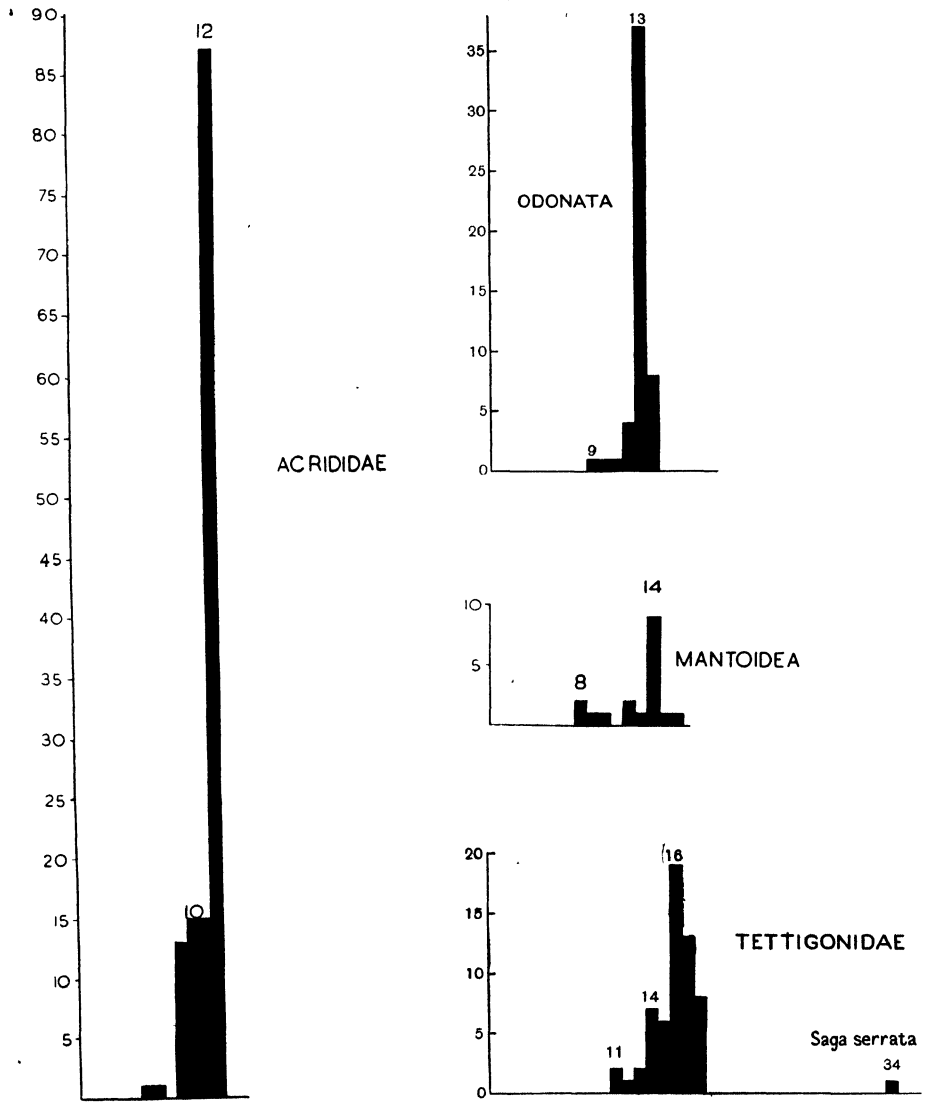


Text-fig. 67. Haploid numbers of various groups of invertebrates in which all the species are hermaphrodite. Figures on the ordinates represent numbers of species.

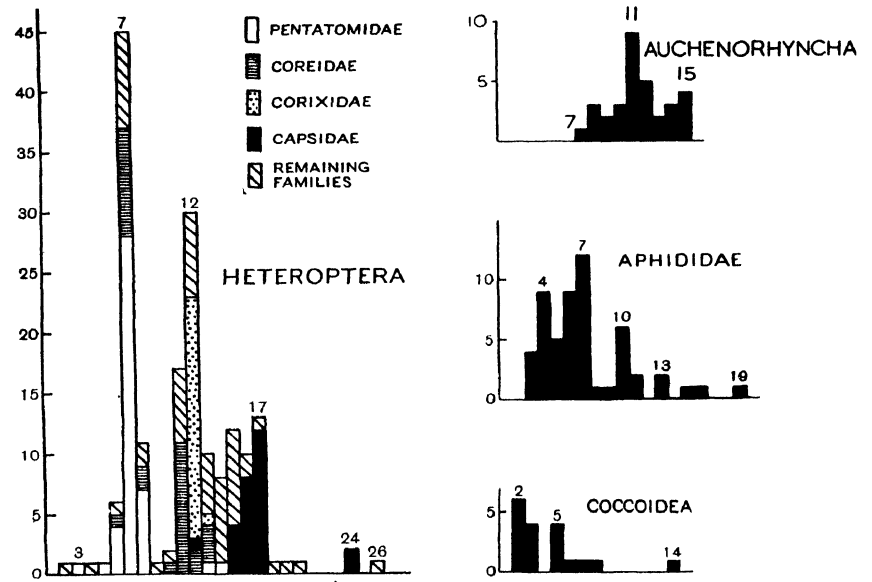
the 'type number'. This term has often been used with the implication that it is the ancestral number for the group in question, the other numbers having all been derived from it. If this were true for most groups it would be a generalization of the utmost importance. Apart from a few instances, however, it is an unproven hypothesis, so that it is better to use the term (if at all) without any evolutionary implications. Generally speaking it becomes more and more difficult to distinguish clearly defined type numbers the higher one goes in the systematic hierarchy; on the other hand, in the smaller units (families, subfamilies and genera) the species which have been studied by cytologists usually do not represent a random sample, particular sections of the group having been investigated more extensively than others.

In many groups below the rank of class or subclass, however, the concept of a type number is probably a useful one. To speak of a type number for the Insecta or the Vertebrata would be absurd; but to regard 13 as typical for the dragonflies (Odonata) seems legitimate, since it is the commonest number in both suborders (Anisoptera and Zygoptera) and the other numbers do not deviate far from it (Text-fig. 68). Other groups which show fairly well-defined type numbers are the Coleoptera (10 occurs in many different families), the Tettigoniidae (16 is

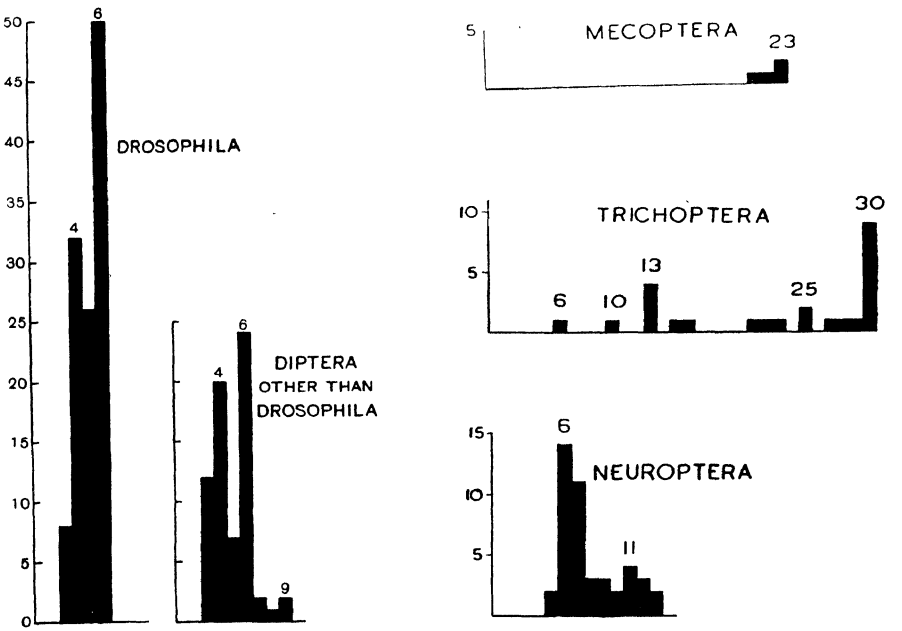
the commonest number in several large subfamilies, but higher or lower numbers are characteristic of other subfamilies) and the snakes (18 in most families). Some groups may appear to have more than one type number. Thus the histogram for the Heteroptera (Text-fig. 69), whose complete range is from 2 to 26, shows peaks at 7, 12 and 17. In this instance it is possible to demonstrate that



Text-fig. 68. Haploid numbers of various groups of Exopterygote insects.



Text-fig. 69. Haploid numbers of various groups of Hemiptera.



Text-fig. 70. Haploid numbers of various groups of Endopterygote insects.

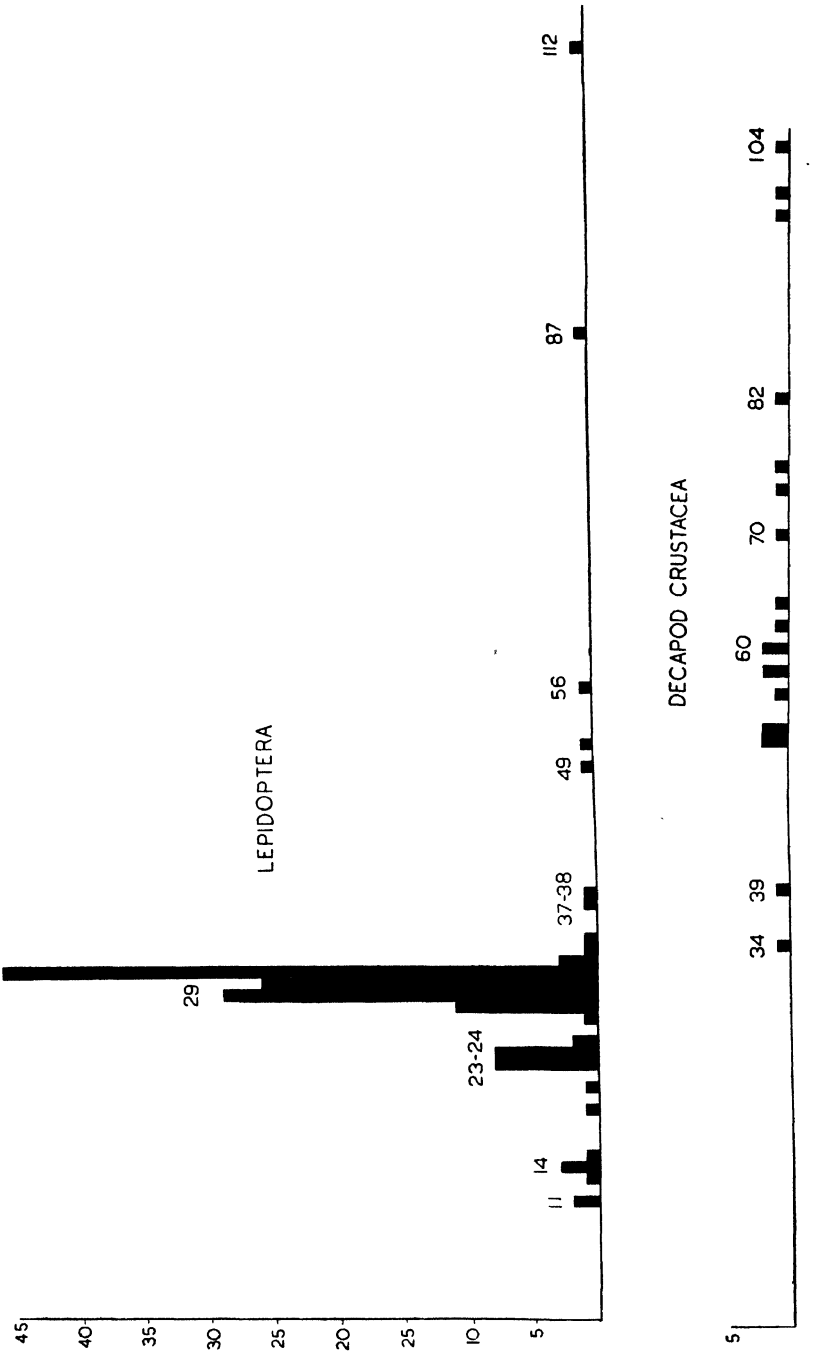
each of these peaks is, in fact, the type number of one of the chief families of which the order is composed. Thus the peak at 7 is due to the Pentatomidae, that at 12 to the Corixidae, while that at 17 is mainly due to the Capsidae. If some of the other families of Heteroptera had been investigated as extensively as these three the histogram for the order as a whole might have had a very different shape. It has sometimes been said that the Urodeles have a type number of 12. This is, in fact, only true of the dominant family Salamandridae. The Hynobiidae and Cryptobranchidae (Makino, 1934*b*, 1935, 1939*b*; Iriki, 1932) have a type number of 28 (Text-fig. 72), so that it is quite impossible to tell whether a high or a low number was present in the common ancestor of the modern families of Urodeles. Where there is no reason to believe that the commonest number is particularly primitive or ancestral for the group as a whole one might speak of it simply as the *modal number*, a term with no special implications.

Many authors seem to have used the idea of a type number far too loosely. Thus Shinji (1931) concluded that in the aphids the number 3 was the primitive one from which all the others had been derived. There is, of course, no means of proving or disproving statements of this kind, but it is probable that the evolutionary changes which chromosome numbers have undergone have been rather more complex than has been realized by most writers on the subject.

In the Lepidoptera, Beliajeff (1930) considered that 30 was the ancestral number for the whole order. He was undoubtedly influenced towards this conclusion by the work of Pchakadze (1928, 1930) who had shown that it was the most frequent one in the caddis flies (Trichoptera), an order believed by morphologists to be more or less ancestral to the Lepidoptera. In point of fact 31 is the most frequent number in the 151 species of Lepidoptera whose chromosome numbers have been determined (Text-fig. 71); but 29, 30 and 31 are so nearly equally common that it does not seem legitimate to consider any one of them as the type number in preference to the others. The only family of the Lepidoptera which seems to have a special 'type number' of its own is the Lycaenidae, nearly all of which have a haploid number of 23 or 24 (Federley, 1938).

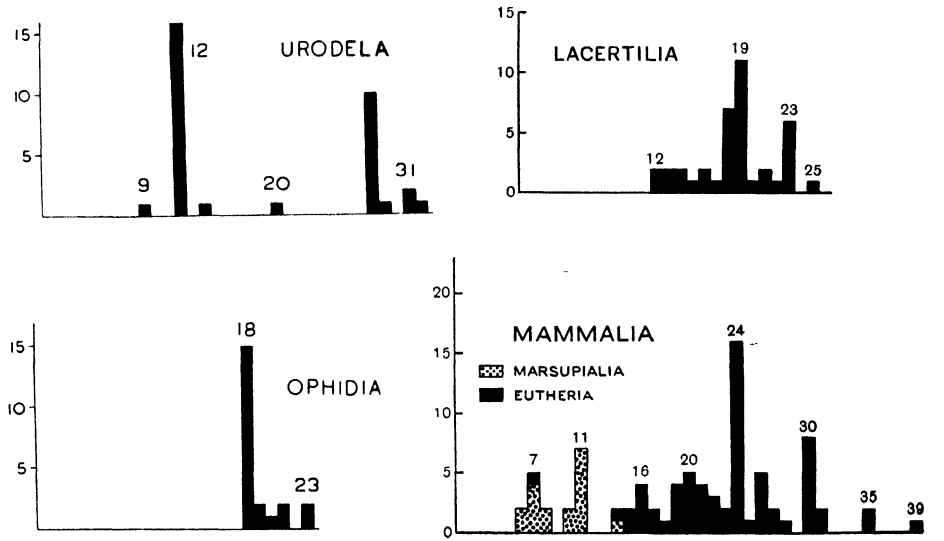
When we find that a particular species has a chromosome number which deviates very widely from those of all its near relatives (see Table 8 for examples), there must be a strong presumption that its chromosome number has been derived from a more 'normal' one, unless there is any reason to suspect, on morphological grounds, that the species occupies a particularly isolated or primitive position in regard to the rest of the group.

It is, of course, to be expected that groups which are characterized by high numbers should show more variation in chromosome number, on the whole, than groups with low numbers. This is, in fact, just what we find. Thus the Lepidoptera, which mostly have high numbers, are also an outstanding example of a group which shows an extreme range in chromosome number, since species



Text-fig. 71. Haploid numbers of the Lepidoptera and the decapod Crustacea.

occur with 11, 13, 14, 15, 19, 21, 23, 24, 25, 27, 29, 30, 31, 32, 33, 34, 37, 38, 49, 51, 56, 87 and 112 pairs of chromosomes. Most of the species with aberrant numbers belong to the family Geometridae, but the one with 87 is *Dasychira pudibunda*, a member of the Lymantridae. Since there is no particular reason to look upon these species with aberrant numbers as archaic or ancestral forms, they have probably been derived from species whose chromosome numbers lay

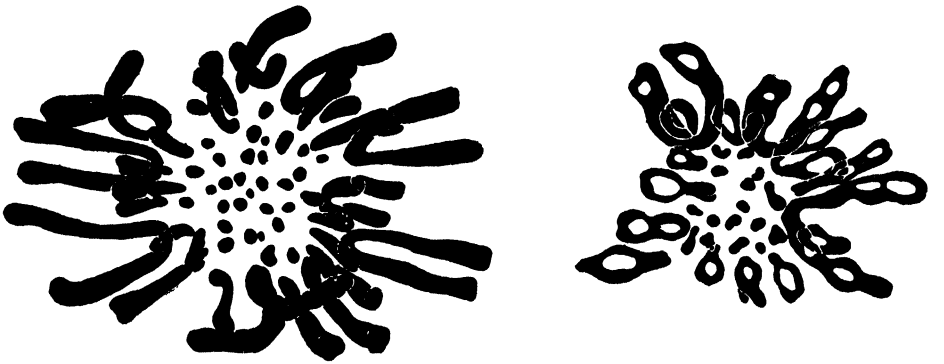


Text-fig. 72. Haploid numbers of several groups of vertebrates.

between 20 and 32. It is most unlikely that the very high and very low numbers arose suddenly—probably they represent the end-products of evolutionary processes, each step of which was an increase or decrease of the chromosome number by one element.

The decapod Crustacea (Text-fig. 71) are another group exhibiting an extreme range in chromosome number (37 to 104, as far as is known at present). Unfortunately, only a few species have been studied cytologically (Fasten, 1914, 1918, 1924, 1926; Delpino, 1934; Leopoldseder, 1934; Niiyama, 1934, 1935*a*, *b*, 1936, 1937, 1938, 1939, 1941; Rathnavathy, 1941), so that the histogram is a less interesting one than that for the Lepidoptera, although it is probably of the same general type, with a peak somewhere about 60. The scorpions are a third group which would probably show a striking range of chromosome number if more species were studied. Several have haploid numbers of 12–13 (Wilson, 1931; Sato, 1936, 1940), but *Tityus serrulatus* has 6 (Piza, 1940*b*) and *T. bahiensis* only 3 (Piza, 1939*a*, *b*, 1940*a*), and some species have haploid numbers of over 50, which have not been accurately counted.

In contrast to groups like the Lepidoptera and decapods there are others in which the chromosome number is almost or completely constant. Thus with one exception all the Corixidae so far studied have 12 chromosomes in the haploid set (Prokofieva, 1933; Slack, 1938). In this case it is clear that structural changes have taken place during the evolution of the group, since some species such as *Corixa fabricii* have a pair of minute chromosomes which are much smaller than the rest, while in other species like *Macrocorixa dentipes* all the chromosomes are about the same size.



Text-fig. 73. Spermatogonial metaphase and first meiotic metaphase in the Urodele *Cryptobranchus allegheniensis*. Haploid number 31; the chiasma frequency of the longest chromosomes is about 8 or 9. From Makino (1935).

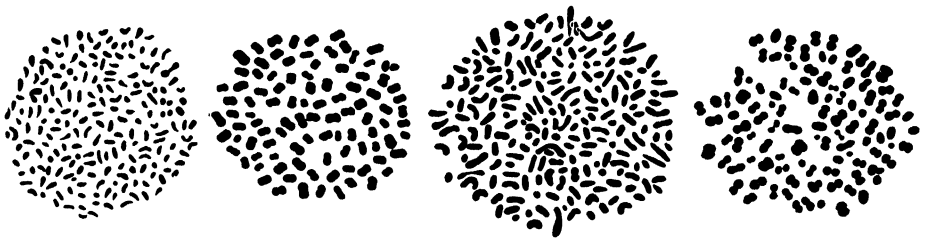
Among the Vertebrata the snakes show very little variation in chromosome number, the Lacertilia rather more (Text-fig. 72). This is perhaps what one would expect, since the lizards are a more diversified group from the morphological standpoint. The mammals show a rather considerable range in chromosome number; 24 is the commonest haploid number and occurs in several orders, but there is no reason to regard it as a particularly primitive one, as Painter (1925) did. The most interesting thing about the histogram for the Mammalia is the sharp gap between the marsupials and the Eutheria, the former having much lower chromosome numbers (i.e. below 15). *Echidna* resembles the birds and the reptiles rather than the mammals in having a very high chromosome number; some of the elements are of moderate size, but most of them are very minute (White, unpublished).

The graph for the Diptera (Text-fig. 70) is an outstanding example of one showing a small range of variation. This is not unexpected, since the chromosome numbers are unusually low. The majority of the 'higher' Diptera seem to have a haploid set of 6 metacentric chromosomes.

Turning now to groups where the number of chromosome arms can easily

be determined, we find that in the Acrididae the number of arms is extremely constant. Owing to the great size of the chromosomes in this group they have been studied by many investigators, and the chromosome sets of many species have been figured, mainly by Brunelli (1910, 1911), McClung (1905, 1914, 1928, 1932), Davis (1908), Saez (1930, 1932), Nolte (1939), Asana, Makino and Niiyama (1939), Eisentraut (1926), Carlson (1936), Rao (1937), Helwig (1941, 1942), Robertson (1916) and Wenrich (1916, 1917).

On the basis of their chromosome number the Acrididae can be divided into two sections, one of which includes the Pamphaginae (Granata, 1910; Chen,



Text-fig. 74. Chromosomes of some Decapod Crustacea. *a* = *Cambaroides japonicus*, spermatogonial set (196 chromosomes); *b* = the same, first metaphase (98 bivalents); *c* = *Paralithodes camtschatica*, spermatogonial set (208 chromosomes); *d* = the same, first metaphase (104 bivalents). From Niiyama (1934, 1935).

1937) and the Pyrgomorphinae (Rao, 1937), while the second includes the subfamilies Truxalinae, Oedipodinae, Ommexechinae and Catantopinae (Cyrtacanthacrinae). This subdivision of the family is also satisfactory from the general taxonomic standpoint. The first section may be called the 10-chromosome group, the second the 12-chromosome group, those being the characteristic haploid numbers (there is no *Y* in most species, so that the diploid number is odd in the males, i.e. 19 in the first section and 23 in the second). Roberts (1941), who has made a detailed study of the male genitalia, splits the family into two groups which he calls Chasmosacci and Cryptosacci; these correspond exactly to our 10- and 12-chromosome groups, so that the cytological evidence fits in well with that derived from a study of external morphology. Unfortunately, students of the group are not in agreement as to which of the two groups should be regarded as the more primitive (Roberts considers the Chasmosacci as ancestral, but Uvarov (1943) has made out a strong case for regarding them as having been derived from the Catantopine stock). There are several American genera, such as *Brachystola*, *Romaleum* and *Phrynotettix*, whose position within the family is uncertain. Uvarov considers some of them as Pamphaginae, others as Catantopinae, while Roberts unites them in his subfamily Romaleinae within the Cryptosacci. The latter course is the more satisfactory one from the cytological standpoint, since they all have 12 chromosomes (Sutton, 1900, 1902;

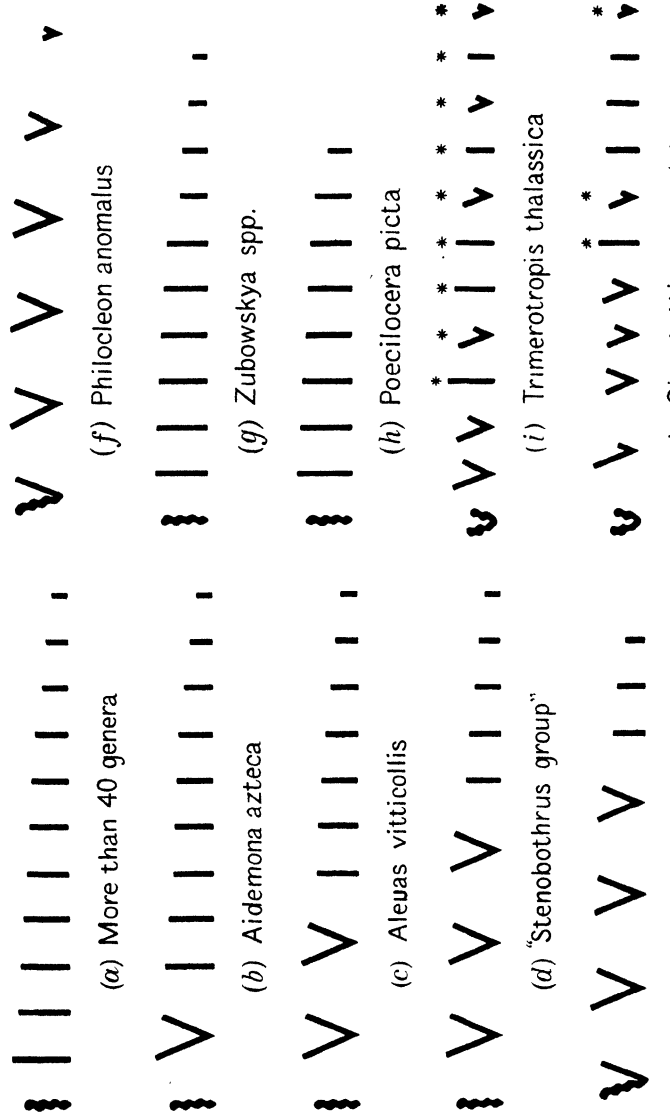
Pinney, 1908; Carothers, 1913; Wenrich, 1916); they may be directly ancestral to the 10-chromosome group. Since a reduction in chromosome number is known to have taken place independently in several genera of the Cryptosacci (see p. 164), while an increase does not seem to have occurred in any of them, it is likely on cytological grounds that the 10-chromosome sections have been derived from the Cryptosacci, two chromosomes being lost in the process.

Usually the chromosomes of the Acrididae are acrocentric, and the numbers we have quoted really refer to chromosome arms, since in both sections the actual chromosome number may be reduced, owing to centric fusions having taken place. Most of these fusions are between two autosomes, but in no less than fourteen genera (according to Helwig, 1941) fusions have occurred between the *X* and one member of a pair of autosomes, thus converting the diploid number of the male sex into an even one (most of these cases have not been published in detail).

We may place the Truxaline, Oedipodine and Catantopine grasshoppers with less than 12 chromosomes in a graduated series, according to the number of centric fusions that have occurred (we do not, of course, imply that this series is a phylogenetic one). Thus the Mexican species *Aidemona azteca* (Catantopinae) has only 11 chromosomes, but one of these is metacentric (Text-fig. 75). The South American *Aleuas vitticollis* (Truxalinae) has 10 chromosomes, two being metacentric (Saez, 1932), and a whole section of the Truxalinae, including the genera *Stenobothrus*, *Chorthippus*, *Stauroderus*, *Gomphocerus*, *Chloëaltis* and *Chrysochraon*, all have 9 chromosomes, three being metacentric (McClung, 1914, 1932; Robertson, 1916; Bělař, 1929; Carlson, 1936; Darlington and Dark, 1932; Klingstedt, 1939). Lastly, in *Philocleon anomalus* (Helwig, 1941) the process of reduction in chromosome number through centric fusions reaches its limit: there are 6 chromosomes, the *X* being fused to one member of an autosomal pair and the remainder of the autosomes forming 5 pairs of metacentrics. It is interesting that nearly all these centric fusions have taken place between chromosomes of similar length, so that the V's produced have approximately equal arms. Thus in *Aidemona*, *Aleuas* and the members of the '*Stenobothrus* group' it is only the longer chromosomes which have united to form metacentrics, while in *Philocleon*, where the process has extended right down the series, the two limbs of the smallest metacentric are about equal in length, i.e. this chromosome has been formed by centric fusion of the two smallest members of the ancestral chromosome set.

In some species of grasshoppers centric fusions have occurred, but have not become completely established, so that the 'unfused' acrocentric chromosomes still exist in some individuals. Thus *Chortophaga viridifasciata* (Oedipodinae) usually has 12 acrocentrics, but in some individuals there are as many as four metacentrics, the chromosome number being correspondingly reduced (McClung, 1905). The same kind of situation also exists in some species of *Hesperotettix* (McClung, 1917).

In the 10-chromosome section of the Acrididae the tendency to form metacentrics is apparently less marked, but in certain individuals (or subspecies?) of



Text-fig. 75. Diagrams of the haploid chromosome sets of various members of the Acrididae (12-chromosome group). *X* chromosomes in each case on the left, the 'original' *X* being represented with a wavy outline. Chromosomes of *Trimerotropis* and *Circotettix* marked with asterisks may be either acrocentric or metacentric.

Sphenarium mexicanum (one of the Pyrgomorphinae) there are only 9 chromosomes, one of them being metacentric (McClung, 1932).

Apart from centric fusions, several other kinds of evolutionary change may reasonably be inferred to have taken place in the chromosomes of the Acrididae.

It is probable that the general rule that homosomal changes are more frequent than heterosomal ones applies in this group, as it does in the genus *Drosophila*. In the Pyrgomorphinae, at any rate, the careful measurements of Rao (1937) suggest that one can probably homologize the nine autosomal pairs, not only from species to species, but from genus to genus. This would not be the case if heterosomal changes were of frequent occurrence. The even more detailed measurements of Powers (1942) confirm the view that the Pyrgomorphinae have an extraordinarily uniform chromosome set (far more so than the other subfamilies of Acrididae).

The main heterochromatic regions of grasshopper autosomes are usually adjacent to the centromere and sometimes at the distal end of the chromosome as well. The extent and location of these heterochromatic blocks varies, however, from species to species. They can be seen very clearly during the prophase of meiosis. In *Mecostethus grossus* (White, 1936*a*) each autosome has a conspicuous heterochromatic 'block' next to the centromere, and one of the smaller chromosomes has one at the distal end as well. In this species the remaining ten autosomes either have no distal heterochromatic regions or only very short ones. An essentially similar arrangement of heterochromatic regions exists in other species of *Mecostethus* and in the related genus *Arcyptera* (Ch'en, 1942). *Schistocerca gregaria*, on the other hand, has proximal and distal heterochromatic regions of about the same size in most of the autosomes. The proximal heterochromatic regions are very highly developed in *Stauroderus scalaris* (Corey, 1933) which may be compared with *Drosophila virilis*, in which it will be remembered that the proximal half of each autosome is heterochromatic.

After studying the extent of the heterochromatic regions in a large number of grasshopper species one is driven to the conclusion that these regions have repeatedly undergone duplications and deficiencies in the course of evolution. This view is strengthened by the fact, already discussed in Chapter VI, that in many species duplications and deficiencies of heterochromatic regions occur in natural populations. The general significance of this type of variation will be discussed in Chapter XIV.

In a few members of the 12-chromosome group a genuine reduction in the number of chromosome arms has taken place (Helwig, 1942). Thus in the group Podismae (which includes a number of Palaearctic genera) the members of the 'main stock' (e.g. species of *Podisma* itself) have 12 acrocentrics, but in *Miramella* and *Zubowskya* the smallest chromosome seems to have been lost (Makino, 1936; Corey, 1938). The missing chromosome has probably been translocated on to another member of the set, its centromere being lost in the process.

In *Niitakacris rosaceanum* there are likewise only 11 chromosomes, but Helwig claims that in this species it is one of the medium-sized pairs of chromosomes that has been 'lost'.

In species of the genus *Indopodisma* there are likewise only 11 chromosomes, but it is rather uncertain whether these should be regarded as acrocentric in the

strict sense, since the 'short arms' are unusually large in comparison with related genera, and in some bivalents chiasmata may be formed in them. Whereas in most grasshopper genera these short arms are about one-twentieth or less of the length of the long arms, in *Indopodisma* they appear to form about one-fifth of the length of the chromosome at mitosis. Whether this condition has been attained by some type of pericentric rearrangement, or by successive duplications in the short arms must remain conjectural for the present.

Other species of grasshoppers in which the number of chromosome arms has been reduced to 11 include *Perixerus squamipennis* (where a centric fusion between the *X* and an autosome has also occurred), the neotropical *Coscineuta virens*, and lastly *Machaerocera mexicana*, where no less than four separate centric fusions have occurred, one of which involves the *X* (Helwig, 1942).

In *Dactylotum pictum*, an aberrant member of the Catantopinae, there are only 9 acrocentrics, i.e. no less than three pairs of autosomes have disappeared as independent entities.

We have already described the state of affairs in the genera *Circotettix* and *Trimerotropis*, where large numbers of originally acrocentric chromosomes have become metacentric as a result of some sort of homosomal change. This is a very special kind of chromosomal evolution, but it has apparently taken place in some individuals of *Podisma sapporoensis* (Helwig, 1942).

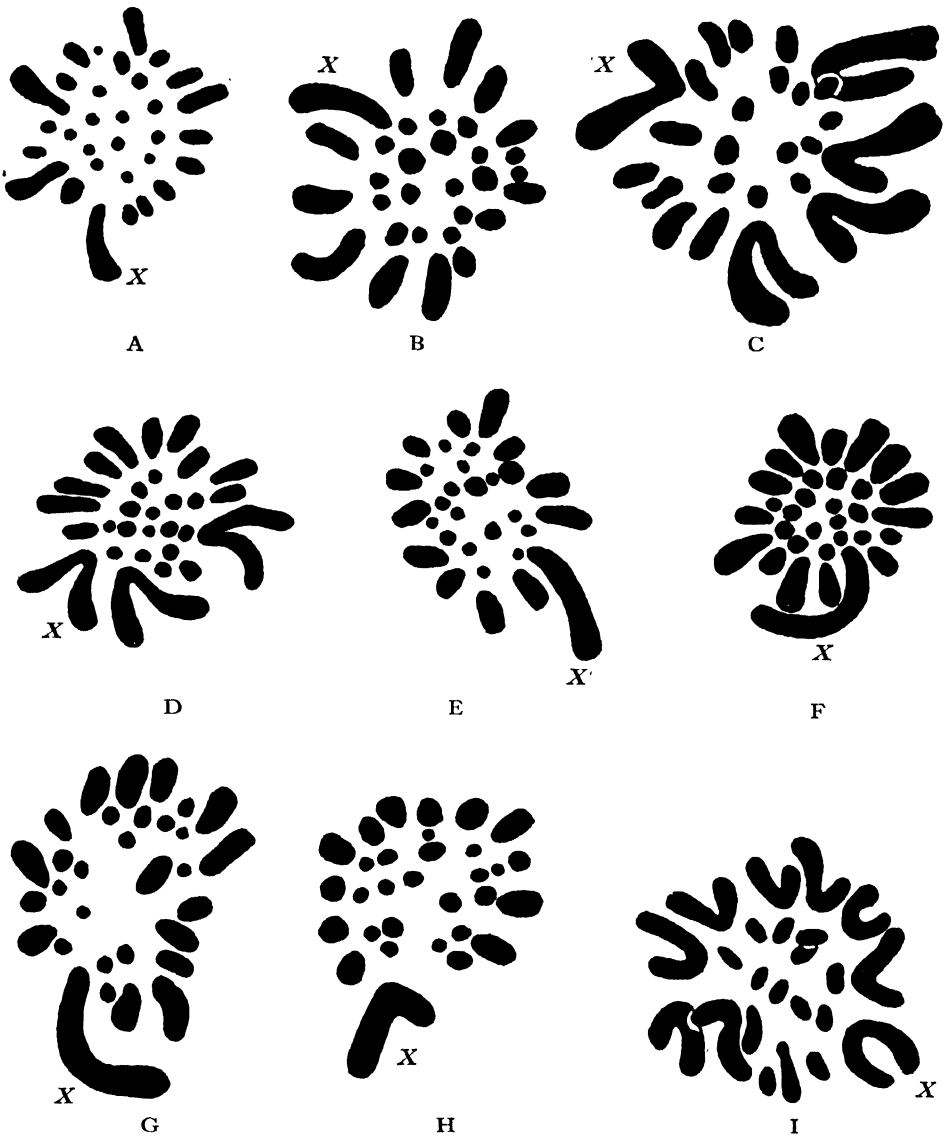
The earlier workers on orthopteran cytology were hopeful that it would eventually be possible to establish direct correlations between the comparative morphology of the chromosomes and the taxonomy of the group. If this expectation has not been fully realized, it is nevertheless clear that a number of such correlations have been made. Thus the genera of the Truxalinae which possess three pairs of metacentric chromosomes probably do represent a natural group. The body of facts about the cytology of the 12-chromosome Acrididae is quite compatible with the view that the same types of structural rearrangement have occurred in the phylogeny of this group as in that of the genus *Drosophila*. It is not necessary to suppose that the different kinds of rearrangement have taken place with the same relative frequencies in the two groups, but there is a general similarity. In both *Drosophila* and the grasshoppers paracentric inversions have probably been the commonest type of rearrangement, but they are not easily detectable in the Acrididae, owing to the absence of salivary chromosomes. In *Drosophila* inversions of this kind do not necessarily lead to a loss of fertility, since there is no crossing-over in the male, and the inviable chromatids resulting from crossing-over within the inversion are cast out in the polar bodies and never pass into the egg nucleus (see p. 96). In the Acrididae inversions certainly lead to the formation of some 'lethal sperms' if they occur in regions where chiasmata are formed: it is not known whether the *Drosophila* mechanism whereby dicentric and acentric chromatids are got rid of in the polar bodies operates during the oogenesis of grasshoppers—if it does not then some eggs of inversion-carrying females will be inviable.

On the whole the 12-chromosome grasshoppers show a more uniform chromosome set than the species of *Drosophila*: but since this comparison is merely based on the gross morphology of the chromosomes as revealed at metaphase, it may be a deceptive uniformity, and we have no right to assume that fewer structural rearrangements have taken place in grasshopper speciation than in *Drosophila* speciation. In the case of whole-arm transpositions, however, it really does seem as if they had occurred more often in *Drosophila*; there are probably many large genera of grasshoppers in which all the chromosomes of all the species are acrocentric. We may compare the species of *Zubowskya* and *Miramella* which have lost one pair of chromosomes with those species of *Drosophila* (*willistoni*, *saltans* and others) in which the microchromosome pair is absent; but loss of a chromosome pair seems to be a relatively infrequent event in evolution, both in Diptera and Orthoptera. Lastly, the fusions between the *X* and an acrocentric autosome which have occurred independently in a number of genera of grasshoppers (see above, pp. 162, 165) may be compared with the fusion between elements '*A*' and '*D*' in *Drosophila pseudoobscura* or *X* and IV in *D. americana*.

It is worth noting that in none of the Acrididae hitherto studied is the chromosome number more than 12. Several instances have been described in which 'supernumerary' chromosomes were present in wild populations of grasshoppers (Minouchi, 1934; Itoh, 1934; Carroll, 1920), but in no case have they become established as permanent members of the chromosome set. It would seem therefore, that there is a real barrier which prevents the chromosome number from rising above 12 in the Acrididae, just as no species of *Drosophila* has more than 6 chromosomes. This barrier (whatever its precise nature) seems to operate against the acquisition of extra centromeres, since in both cases a number of species are known in which the number of chromosome arms has been increased (e.g. *Drosophila obscura* and the 'heterozygous' Trimerotropi).

The grouse locusts (Tettigidae or Tetrigidae), which are now regarded as a separate family, allied to the Acrididae, have a very uniform chromosome set, consisting of 7 acrocentrics in the haploid set (Robertson, 1916, 1930; Rayburn, 1917; Harman, 1915, 1920; Nabours and Robertson, 1933; Misra, 1937*b*).

In the long-horned grasshoppers (Tettigoniidae) there is a much greater variety of chromosome number and form than in the Acrididae and Tetrigidae (McClung, 1902, 1908; Woolsey, 1915; Mohr, 1915, 1916; de Winiwarter, 1931; King, 1924; Asana, Makino and Niiyama, 1938; Asana, 1940; White, 1941*b*; Li, 1931; Hareyama, 1932; Favrelle, 1936; Pearson, 1929). The haploid numbers vary from 11 to 18 (*Saga serrata* has a somatic number of 68 (Matthey, 1939*a*, 1941), but it is parthenogenetic and therefore possibly tetraploid). Generally speaking, the species with low chromosome numbers (e.g. *Neoconocephalus* sp. with 12) have a certain number of large metacentric chromosomes—but it is not possible to ascribe all the variations in chromosome number to centric fusions. As in the Acrididae it is the longer chromosomes which are liable to



Text-fig. 76. Spermatogonial chromosome sets of various Tettigoniidae. From White (1941*b*). A = *Platycleis grisea*; B = *Metrioptera brachyptera*; C = *Atlanticus pachymerus*; D = *Tettigonia viridissima*; E = *Insara tolteca*; F = *Insara gracillima*; G = *Microcentrum* sp.; H = *Leptophyes punctatissima*; I = *Neoconocephalus* sp.

become metacentric, the smaller ones being always acrocentric. The *X*-chromosome may be of either type (Text-fig. 76), but the differences between acrocentric and metacentric *X*'s seem to depend on structural rearrangements within a single chromosome rather than on heterosomal changes (White, 1941*b*). The metacentric *X*'s of species such as *Tettigonia viridissima*, *Atlanticus pachymerus* and *Leptophyes punctatissima* are thus comparable to those which have arisen in the acrididid genera *Trimerotropis* and *Circotettix* by a transposition of the centromere. One interesting point about the tettigoniids with metacentric *X*'s is that they nearly always have a number of metacentric autosomes as well. It is difficult to understand the reason for this correlation, since the autosomal metacentrics have almost certainly arisen by a totally different mechanism, namely, by centric fusion. Possibly the coèxistence of a number of large V-shaped elements in the chromosome set is an arrangement which is mechanically more satisfactory at mitosis than the situation where there is only one such element or a pair of them.

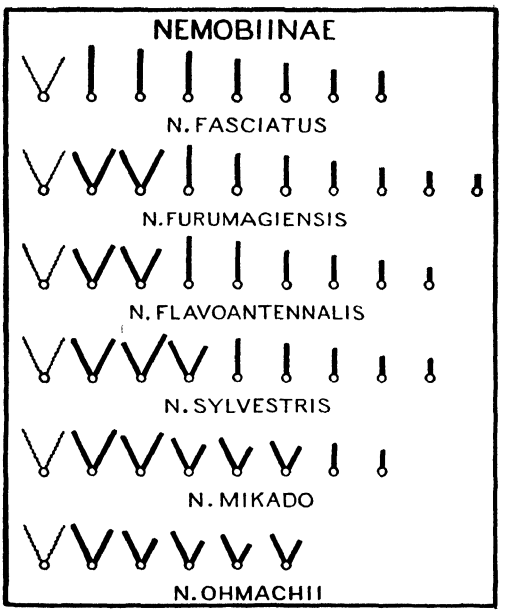
The Tettigoniidae are a more diversified family, from the morphological point of view, than the Acrididae. Moreover, they are possibly a more ancient group (Zeuner, 1939), so that it is not surprising that their chromosome morphology is less uniform than that of the Acrididae. Some sections of the Tettigoniidae have a very uniform chromosome set, but the uniformity is never as great as in the Acrididae. Thus in the subfamily Decticinae the Old World genera *Decticus*, *Metrioptera*, *Gampsocleis* and *Platycleis* all have 15 pairs of acrocentric autosomes and an acrocentric *X*, but *Pholidoptera griseoaptera* (White, 1942*b*, frontispiece) has one more pair of autosomes, and the American genera *Atlanticus* (White, 1941*b*) and *Anabrus* (McClung, 1905, 1914), with one or more pairs of metacentrics, diverge still more widely from the 'standard' chromosome set of the Old World genera.

The crickets (Gryllidae) have not been studied by cytologists to the same extent as the other two great groups of the Orthoptera, but the chromosome sets of a number of species have been investigated by Baumgartner (1917, 1929), Brunelli (1909), Tateishi (1931, 1932), Honda (1926), Honda and Iriki (1932, 1938), and especially Ohmachi (1927, 1929, 1932*a*, *b*, 1935*a*). The numbers, both of chromosomes and chromosome arms, vary even more than in the Tettigoniidae. On the other hand, the *X* always seems to be a metacentric chromosome, except perhaps in *Cyrtoxiphus ritsemae* and *Homoeogryllus japonicus* (Ohmachi, 1927, 1935*a*).

In some crickets centric fusions which have not spread completely through the species are responsible for variations in chromosome number. Thus in *Loxoblemmus arietulus* the diploid number in the male may be 15, 14 or 13, but the number of chromosome arms is always 20 (Honda, 1926; Ohmachi, 1927, 1935*a*).

Before concluding this brief review of chromosome sets in the Orthoptera Saltatoria some mention should be made of the minor groups. The cave- and camel-crickets (Rhaphidophorinae), the 'Wetas' of Australasia, the tropico-

politan Gryllacrinae and the curious Indian *Schizodactylus* are usually regarded as members of a single family (variously called Stenopelmatidae or Gryllacrididae) allied to, but distinct from, the Tettigoniidae and Gryllidae. Among the Rhaphidophorinae, *Ceuthophilus* spp. have 18 pairs of autosomes (Stevens, 1912*a*; Thompson, 1911), two species of *Diestrammena* (= *Tachycines*) both have 28 autosomes and a metacentric *X* (Makino, 1931; Mohr and Eker, 1934), while *Stenopelmatus* sp., with a lower number of chromosomes (18 autosomes), has an even higher number of chromosome arms, since all the chromosomes are



Text-fig. 77. Diagrams of the chromosome sets in various crickets of the subfamily Nemobiinae, showing the numbers of acrocentric and metacentric chromosomes. *X* chromosomes on the left. Based on the work of Baumgartner (1929) and Ohmachi (1935*a*).

metacentric (Stevens, 1909). On the other hand, *Gryllacris signifera* has only 5 acrocentric autosomes (Heberer, 1937), while *Schizodactylus monstrosus*, an *XY* : *XX* form, has 6 metacentric autosomes (McClung and Asana, 1933). It is difficult to draw any conclusions from these meagre facts, but they do suggest that the group as a whole is probably a rather unnatural assemblage, the various subfamilies having little in common with one another.

The occurrence of centric fusions, with its corollary that in many groups the number of chromosome arms is nearly constant, although the actual number of chromosomes may vary, was first clearly stated by Robertson (1916), and is hence referred to by some authors as 'Robertson's law'. It is not, of course, a 'law' in the physical sense, and was never intended to be. Many cytologists

have been content with the statement that two acrocentrics in one species correspond to a single metacentric in another, without considering whether the evolutionary change has been in the direction $A+A \rightarrow M$ or $M \rightarrow A+A$. It seems fairly certain that the former process (centric fusion) is a single event, while the latter is a two-step process, requiring the establishment of a supernumerary chromosome as a preliminary to the translocation (see p. 56). If this is so we should expect centric fusions to be much more frequent than the reverse process. The evidence so far available does seem to bear out this view: it can hardly be doubted that the metacentric chromosomes in *Drosophila americana* and *D. texana*, as well as those in *D. pseudoobscura* and in various grasshoppers, have arisen by the process $A+A \rightarrow M$; while there does not seem to be a single instance in which it can be positively asserted that an $M \rightarrow A+A$ transformation has occurred (although no doubt such instances will eventually be discovered).

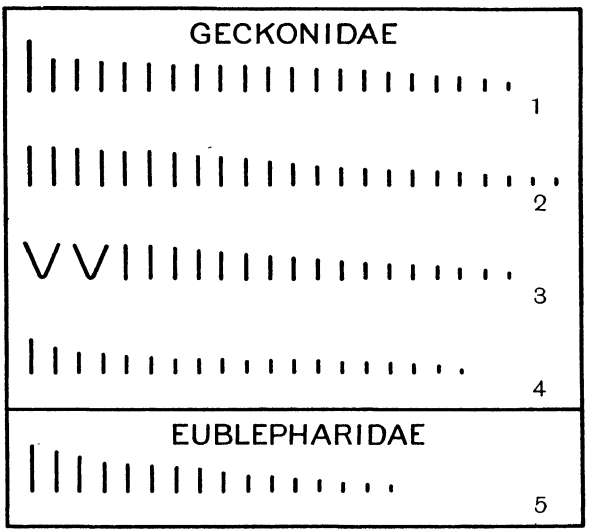
The grasshoppers *Trimerotropis* and *Circotettix*, the *obscura* group of *Drosophila* and several other similar cases, show us clearly that not all metacentrics have arisen by centric fusion—a point that has sometimes been overlooked. The distinction between metacentrics which have arisen by homosomal rearrangements and those which have resulted from centric fusion is, of course, solely a phylogenetic one, so that it is only by comparing a species with its nearest relatives that one can decide which type any particular metacentric belongs to. It has recently been pointed out (White, 1941*b*) that if one considers only homosomal rearrangements within a single chromosome the most stable position for the centromere should, on *a priori* grounds, be almost at the end of the chromosome. The reason for this is as follows: in order for the centromere to undergo a change in position a break must occur on either side of it. When the centromere is almost at the end of the chromosome the chance of a break occurring distal to it will be minimal. This is probably one reason why many groups like the Acrididae have almost all their chromosomes of the acrocentric type.

In certain groups 'Robertson's law' explains many of the more obvious changes in chromosome shape, but in others it is not so applicable. Thus in the crickets of the subfamily Nemobiinae the number of chromosome arms varies from 9 to 14 (Text-fig. 92). Here it is clear that processes other than $M \rightarrow A+A$ and $A+A \rightarrow M$ have been at work, although a detailed analysis is not possible at present.

The most ambitious attempt to apply 'Robertson's law' to chromosome phylogeny on a large scale is due to Matthey (1931, 1932*a*, *b* and *c*, 1933, 1939*b*), who has studied the chromosomes of a considerable number of Lacertilia belonging to all the more important families. His survey has recently been extended by Asana and Mahabale (1940, 1941), who have studied the chromosomes of some Asiatic lizards. There is usually a great range in size of chromosomes in this group, and in many species there is a break in the middle of the series, so that there are two rather sharply defined types, the 'macrochromosomes'

(which are arranged round the periphery of the spindle at mitosis and meiosis) and the 'microchromosomes' (which occupy the central region of the spindle). This condition is also found in the birds, but there the two types are not so sharply defined and tend to intergrade. It is possible that in the lizards the centromeres of the 'macros' and 'micros' differ in size or in some other way, although there is no definite evidence on this point.

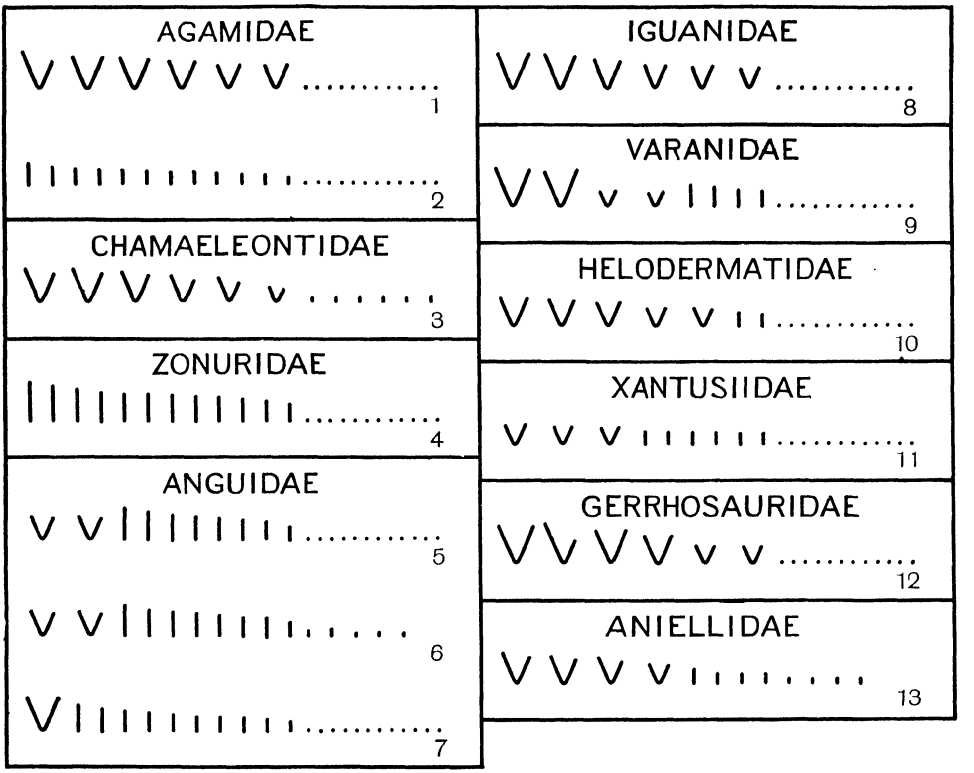
On the basis of his cytological work Matthey has divided the Lacertilia into three main groups: (1) the 'complexe geckonoïde', which includes the Geckos and the Eublepharidae, (2) the 'complexe iguanoïde', which consists of the families Agamidae, Iguanidae, Zonuridae, Anguidae, Helodermatidae, Varanidae,



Text-fig. 78. Diagrams of the haploid chromosome sets of some Lacertilia. Based on the work of Matthey (1931, 1933). 1 = *Tarentola mauritanica*; 2 = *Hemidactylus bowringi*; 3 = *Gekko japonicus*; 4 = *Hemidactylus milliousi*; 5 = *Eublepharis variegatus*.

Xantusiidae, Aniellidae and Chamaeleontidae, and (3) the 'complexe scinco-lacertoïde', with the families Scincidae and Lacertidae. In the first 'complexe' there is no sharp distinction between the larger and the smaller chromosomes; the number of chromosome arms varies between 16 and 23 in the haploid set, and there are relatively few metacentrics (*Gekko japonicus* has two pairs (Nakamura, 1932), four other species have none). In the 'complexe iguanoïde' there is usually a sharp distinction between macro- and microchromosomes. Typically there are 12 macrochromosome arms and 12 microchromosome arms in the haploid set, but centric fusions may have occurred in either group. Thus *Heloderma suspectum* has 5 pairs of large metacentrics, 2 pairs of large acrocentrics and 12 pairs of acrocentric microchromosomes. *Anolis carolinensis* has all its macrochromosomes but none of its microchromosomes metacentric, while the

process of centric fusion seems to have been carried farthest in *Chamaeleon vulgaris* where there are 6 metacentric 'macros' and 6 metacentric 'micros'. In none of the species studied by Matthey had a centric fusion between a 'macro' and a 'micro' occurred.



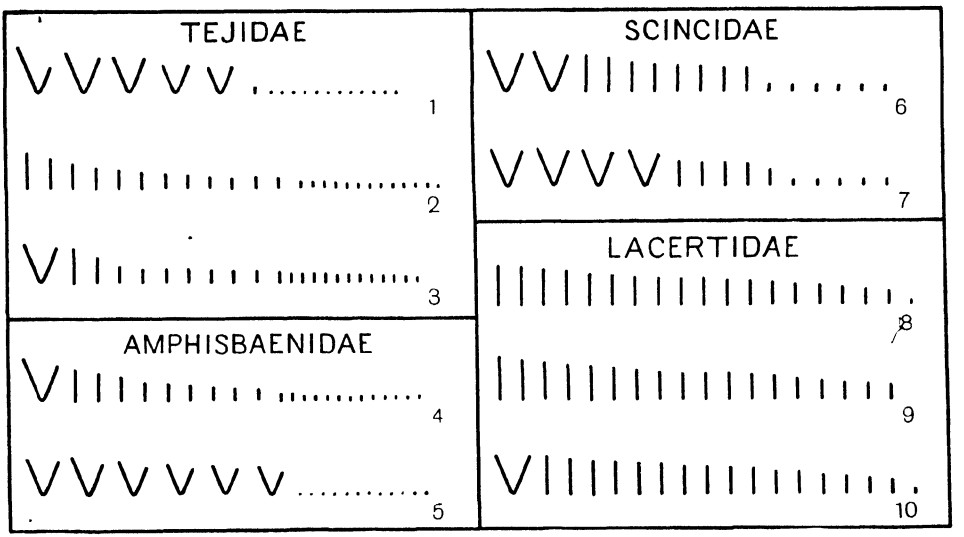
Text-fig. 79. Diagrams of the haploid sets of some more Lacertilia. Based on the work of Matthey (1931, 1933). 1 = *Agama stellio* and *Uromastix hardwicki*; 2 = *Japarula swinhonis*; 3 = *Chamaeleon vulgaris*; 4 = *Zonurus catephractus*; 5 = *Pseudopus apus*; 6 = *Ophisaurus ventralis*; 7 = *Gerrhonotus scincicauda*; 8 = *Anolis carolinensis*; 9 = *Varanus gouldi*; 10 = *Heloderma suspectum*; 11 = *Xantusia henshawi*; 12 = *Gerrhosaurus flavigularis*; 13 = *Aniella pulchra*.

In the 'complexe scinco-lacertoïde' there are typically 18 pairs of acrocentric 'macros' together with a single pair of 'micros'. This is the condition in most of the members of the genus *Lacerta*, but *L. vivipara* has lost the microchromosome pair (Oguma, 1934; Matthey, 1934). In the Scincidae, *Scincus officinalis* has 14 acrocentrics and two metacentrics, while *Chalcides tridactylus* has 10 acrocentrics and 4 metacentrics.

To sum up, therefore, we may say that Matthey's work has definitely shown that centric fusions (possibly together with the reverse process $M \rightarrow A+A$) account for a large part of the visible differences between the chromosome sets

of allied species in the Lacertilia. Clearly these are not the only kinds of structural rearrangements that have occurred in this group, any more than they are the only ones in *Drosophila* or the Acrididae.

Certain more general conclusions may, however, be drawn from Matthey's work and from other similar surveys of the cytology of particular groups. It is



Text-fig. 80. Diagrams of the haploid sets of some more Lacertilia. Based on the work of Matthey (1931, 1933). 1 = *Tupinambis teguixin*; 2 = *Ameiva surinamensis*; 3 = *Cnemidophorus sexlineatus*; 4 = *Rhineura floridana*; 5 = *Trogonophis wiegmanni*; 6 = *Scincus officinalis*; 7 = *Chalcides tridactylus*; 8 = *Lacerta* (most species), *Psammodromus hispanicus* and *Tachydromus* spp.; 9 = *Lacerta vivipara*; 10 = *Lacerta ocellata*.

obvious that the lengths and shapes of chromosomes in a set are not at random. In species after species we find that the chromosome set consists of members which are alike in size and in the position of the centromere. Alternatively, there may be two size classes, each with definite characteristics. Such conditions would not be encountered if the structural changes which become established in phylogeny were of all possible types. It seems, rather, that in many groups chromosome after chromosome has undergone the same types of structural change, so that they have all retained a similar morphology. The special kind of transformation which has occurred in the grasshopper genera *Circotettix* and *Trimerotropis* is merely one example of the general tendency. Tendencies of this kind probably do not occur in all groups of organisms; some chromosome sets are composed of elements which are very heterogeneous, both in length and shape. Nevertheless, uniformity is very significantly commoner than heterogeneity. The structural changes which are successful in the face of selection seem to obey what we may call the *principle of homologous change* (i.e. one

chromosome after another undergoes the same type of change in the same phyletic line). This would be unintelligible if the crude mechanical views quoted at the beginning of this chapter were entirely true. But we must now consider chromosomes, not as mere linear assemblages of genes, but as organized bodies whose sequence of centromere, hetero- and euchromatic regions determines the mechanical relations of the chromosome to the spindle, the amount and position of crossing-over, and a variety of position effects. It is thus natural that the structural rearrangements which become established in evolution should tend to be of one or two main types in all the chromosomes of a particular group, thus leading to the very usual situation where all the chromosomes or chromosome limbs are about the same length and have a similar distribution of heterochromatic segments.

Where more than one type of chromosome exists in the set (as, for example, when there are 'macros' and 'micros') it is probable that the arrangement is mechanically satisfactory, the small elements occupying the centre of the spindle at mitosis, the larger ones the periphery. No doubt countless structural changes have failed to establish themselves in evolution because they upset the genic balance of the animal or because they were incompatible with a normal meiosis. But even if a rearrangement is satisfactory from this point of view it still has to be one which does not diminish the efficiency of the mitotic or meiotic mechanisms in a purely mechanical way. In an organism whose chromosomes are all of a particular size the dimensions of the spindle (and possibly also of the cell) will be adapted to ensure the efficient division of such chromosomes. Thus a rearrangement which gave rise to a chromosome twice the normal length might impair the disjunction process quite seriously, since any particular type of spindle probably cannot cope efficiently with more than a certain length of chromosome. In general, it is probable that the whole architecture of the cell imposes a certain degree of limitation and canalization on the types of structural chromosomal changes which can be expected to survive and establish themselves. Unfortunately, very little attention has been paid to the shapes and sizes of cells and spindles in different tissues and organisms in relation to the morphology of the chromosome sets. Where a pair of chromosomes has apparently vanished in the course of evolution (as in *Drosophila willistoni*, the grasshoppers *Zubowskya* and *Miramella* and the lizard *Lacerta vivipara*) it is often the smallest. This suggests that the smaller the chromosome the easier it is for it to become incorporated in another member of the set.

Although many rearrangements are known in laboratory stocks of *Drosophila* in which one break is in euchromatin and the other in heterochromatin, it is probable that rearrangements of this type are particularly liable to lead to deleterious position-effects. It is thus not surprising that the main heterochromatic blocks do not, in general, become broken up and distributed at random throughout the euchromatin in the course of evolution.

The occurrence of centric fusions and other whole-arm transpositions is probably facilitated by the existence of heterochromatic regions round the centromeres. Small deficiencies and duplications of inert material will not affect the viability of the individual as much as would a corresponding deficiency or duplication of active material. Some authors (e.g. Darlington, 1939*b*) have suggested that groups in which no whole-arm interchanges are known to have occurred or in which the chromosome numbers are very constant may be ones in which there are no heterochromatic regions around the centromeres. But this is probably carrying the argument too far. It seems probable that *all* centromeres lie in heterochromatic regions, and that whole-arm interchanges can consequently occur in all groups. It would be unwise to assume that the frequency of occurrence of such rearrangements depends on the length of the inert regions until we know far more about the factors which allow or prevent the establishment of structural rearrangements in natural populations. It is at any rate certain that in many sections of the Acrididae large heterochromatic segments exist round the centromeres without a single centric fusion being known in the whole genus or group of genera. In many of the families of Orthoptera and vertebrates the longer acrocentrics seem to be more apt to undergo centric fusion than the shorter ones, but there is no explanation of this at present. In many large groups of the animal kingdom chromosomes of the acrocentric type seem to be altogether unknown, so that the only whole-arm transfers that can take place are of the $M_1+M_2 \rightarrow M_3+M_4$ type (see p. 56).

In considering the evolution of chromosome numbers particular interest is naturally attached to those instances where closely related species or subspecies possess widely different numbers. There are not very many such cases in animals, and some of the more interesting are set out in Table 8. Unfortunately, most of these cases have not been subjected to a critical analysis.

In the Pentatomidae, where most species have 7 chromosomes, *Thyanta custator* and *calceata* are so similar that they were not recognized as distinct species until they were studied cytologically by Wilson. Here it would seem that the form with the higher number (*calceata* with 14 chromosomes) has been derived from the one with the lower number. Not only is 14 a higher number than any other pentatomid is known to possess; *calceata* also has a complex sex-chromosome mechanism of the X_1X_2Y type which is not known to occur in any other member of the group. There is thus indirect evidence that *calceata* has probably undergone a rather drastic reorganization of its chromosome set since it split off from *custator* or from a common ancestor of both forms.

In another pentatomid genus, *Rhytidolomia*, the situation is probably the other way about. *R. senilis* has a haploid number of 3, while *R. saucia* shows the 'type number' of 7. Thus *senilis* has probably undergone a diminution of its chromosome number. This viewpoint is strengthened by Schrader's (1940*a*, *b*) demonstration that the *X* and *Y* chromosomes of *senilis* both possess a euchro-

TABLE 8. *Examples of nearly related species with widely different chromosome numbers*

	Haploid number	Author
CRUSTACEA		
COPEPODA		
Cyclops strenuus	11	Braun, 1909
C. insignis	11	,, ,,
C. bicuspidatus	9	,, ,,
C. dybowskii	9	,, ,,
C. fuscus	7	,, ,,
C. albidus	7	,, ,,
C. leukarti	7	,, ,,
C. viridis	6	,, ,,
C. diaphanus	6	,, ,,
C. vernalis	5	,, ,,
C. gracilis	3	,, ,,
AMPHIPODA		
Gammarus chevreuxi	13	Palmer, 1926
G. annandalei	27	Niiyama, 1935*b*
INSECTA		
HETEROPTERA		
(1) Pentatomidae		
Thyanta custator	8 (XY)	Wilson, 1911
Th. calceata	14 (X_1X_2Y)	,, ,,
Rhytidolomia saucia	7	Schrader, 1940*a*
Rh. senilis	3	Wilson, 1913; Schrader, 1940*a*
(2) Belostomatidae		
Lethocerus sp.	2	Chickering, 1927, 1932; Chickering and Bacorn, 1933
L. americanus	4	
L. uhleri	15	
TRICHOPTERA		
Limnophilus affinis	6	Pchakadze, 1930
L. decipiens	10	Klingstedt, 1931
L. lunatus	13	,, ,,
L. centralis	13	Pchakadze, 1930
L. nigriceps	16	,, ,,
L. rhombicus	30	,, ,,
L. politus	30	,, ,,
L. stigma	30	,, ,,
L. flavicornis	30	,, ,,
LEPIDOPTERA		
(1) Notodontidae		
Cerura bicuspis	30	Federley, 1939
C. furcula	29	,, ,,
C. bifida	49	,, ,,
Dicraneura vinula vinula	21	,, ,,
D. vinula delavoiei	31	,, ,,
(2) Geometridae		
Biston (*Lycia*) *hirtaria*	14	Harrison and Doncaster, 1914
B. (*Nyssia*) *pomonaria*	51	Malan, 1918
B. zonaria	56	Harrison and Doncaster, 1914
Phigalia pedaria	112	Regnart, 1933
(3) Pieridae		
Pieris napi	25	Federley, 1938
P. rapae	25 or 26	Beliajeff, 1930; Federley, 1938
P. brassicae	15	Beliajeff, 1930; Federley, 1938

TABLE 8 (*cont.*)

LEPIDOPTERA (*cont.*)		
(4) Satyridae		
Erebia ligea and *E. disa*	29	Federley, 1938
E. lappona	28	,, ,,
E. medusa var. *polaris*	11	,, ,,
MAMMALIA		
RODENTIA		
Cricetus auratus	19	Koller, 1938
Cricetulus griseus	7	Pontecorvo, 1943
Sciurus carolinensis carolinensis	24	Cross, 1931
S. carolinensis leucotus	14	Koller, 1936*b*

matic region which forms a 'pairing segment' at meiosis; it seems probable that this region is one which was originally autosomal and later became translocated to the sex chromosomes.

In the genus *Lethocerus* (Heteroptera, family Belostomatidae) it is clear that species with very different chromosome numbers exist, but the data do not permit us to speculate as to whether high numbers have been derived from low ones or vice versa. However, the species (or variety) with a haploid number of 2 has almost certainly arisen from one with a higher number, since it has lost the separate sex chromosomes which are found in other members of the group (see p. 242).

In the scorpion *Tityus bahiensis*, which normally has a somatic number of 6, Piza (1940*a*) has found individuals with 9 and 18 chromosomes. It is probable that this is a species with polycentric chromosomes (like *Ascaris megalocephala*), but the details are not yet fully worked out (see p. 117).

A number of species with 'exceptional' chromosome numbers are found in the Lepidoptera. Instances are known in the Pieridae, Satyridae, Notodontidae and Geometridae, the best-studied cases occurring in the subfamily Bistoninae of the Geometridae. The chromosomes of *Biston* (*Lycia*) *hirtaria* are much more massive than those of *B.* (*Nyssia*) *zonaria*, so that it is probable that each *hirtaria* chromosome corresponds to several *zonaria* ones; but it is unlikely that this is the only difference between them—*hirtaria* may also have more heavily nucleinated chromosomes or more extensive heterochromatic regions. In the hybrids between the two forms the chromosomes retain their characteristic sizes, but there is practically no pairing between the *zonaria* and *hirtaria* chromosomes at meiosis.

It is difficult to analyse the processes of chromosomal evolution in the Heteroptera and Lepidoptera, since we do not yet know anything about the centromeres in these groups (if indeed they possess localized centromeres at all!). In the Mammalia, however, this difficulty does not exist, since it is generally quite easy to determine the position of the single centromere in each chromosome. In the squirrels (family Sciuridae) the species which have been

studied differ quite considerably in chromosome number, and in *Sciurus carolinensis* forms which are generally regarded as subspecies of the same species are said to have haploid numbers of 14 and 24. If the facts, as stated, are correct, this is a most interesting example of an evolutionary change in chromosome number. It is not known whether the two forms can be hybridized or not. Cross (1931) stated that about 15 out of the 24 pairs of chromosomes in his subspecies were metacentric, but an inspection of his figures suggests that probably they were all of this type. Since Koller's figures show that in the other subspecies all the chromosomes are likewise metacentric the position seems clear—one form has 28 chromosome limbs in its haploid set, the other 48. An even more extreme difference in chromosome number occurs in another group of rodents, namely, the hamsters, *Cricetus auratus* having 19 chromosomes while *Cricetulus griseus* has only 7.

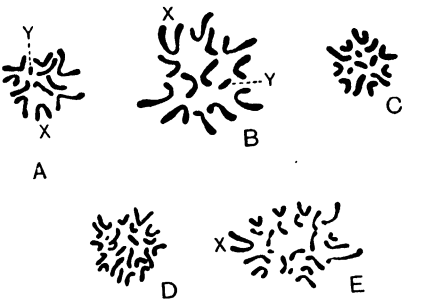
We cannot know how many structural rearrangements have led to these great differences in chromosome morphology, but the *minimum* number of rearrangements is equal to the difference in number of chromosome arms (unless we suppose whole chromosome arms to have been entirely lost, which is unlikely, unless they were completely heterochromatic). Thus a single rearrangement is sufficient to account for the loss of an acrocentric chromosome pair in the grasshopper *Zubowskya*, while in the praying mantids *Sphodromantis viridis*, which lacks two pairs of metacentrics that occur in all its near relatives (White, 1941 *a*), must have undergone at least four translocations since it diverged from the stock that gave rise to *Sphodromantis gastrica*. Although *Sciurus carolinensis* is a complex 'polytypic' species, not all mammalian species of this type have a variable chromosome number. Thus, as far as we know, all races of man have the same chromosome set of 24 pairs of metacentrics (Evans and Swezy, 1929; Shiwago and Andres, 1932; Minouchi and Ohta, 1934; Koller, 1937),* and the same seems to be the case in the domestic dog, where several breeds have been shown to possess 39 pairs (Ahmed, 1941). In neither of these instances, however, have more than a few of the many races been investigated cytologically, and it is possible that further work might provide some surprises. However, in view of the fact that in both man and dog all interracial crosses are fertile, except for mechanical difficulties in mating, it seems likely that the chromosome sets do not differ very much in the various races.

Where two forms that are at present regarded as falling within the same species have quite different numbers of chromosome arms it seems likely that they will eventually be regarded as specifically distinct. It must, at any rate, be regarded as highly doubtful whether such forms would interbreed successfully in the wild. S. G. Smith (1938*b*, 1941) has described two forms of the sawfly

* It is possible that the Primates are a group with a particularly constant chromosome number since both the chimpanzee and the rhesus monkey have the same chromosome number as man (Yeager, Painter and Yerkes, 1940; Painter, 1922).

Diprion polytomum, one with a haploid number of 6, the other with 7 (the chromosomes being metacentric in both instances). The first form is facultatively parthenogenetic, the second obligatorily so; it would seem better to regard them as distinct species for the present.

The European mole cricket (*Gryllotalpa gryllotalpa*) is an interesting example of a superspecies which appears to have broken up into several geographical forms with different chromosome sets. There is an extensive literature on the cytology of this insect, the more important papers being those of Payne (1916), de Winiwarter (1927, 1937), Barigozzi (1933*a*, *b*) and Steopoe (1939). Three forms are known with certainty, and others may occur, since the species has a wide distribution in Europe and the Near East, and individuals from Spain, North Africa and the eastern Mediterranean have not yet been studied cytologically.



Text-fig. 81. Spermatogonial chromosome sets in the genus *Gryllotalpa*. A = *G. gryllotalpa*, north European race with 12 chromosomes (after de Winiwarter); B = Roumanian race with 14 chromosomes (after Steopoe); C = southern Italian race with 15 chromosomes (after Payne); D = *G. borealis* with 23 chromosomes (after Payne); E = *G. africana* with 23 chromosomes (after Asana).

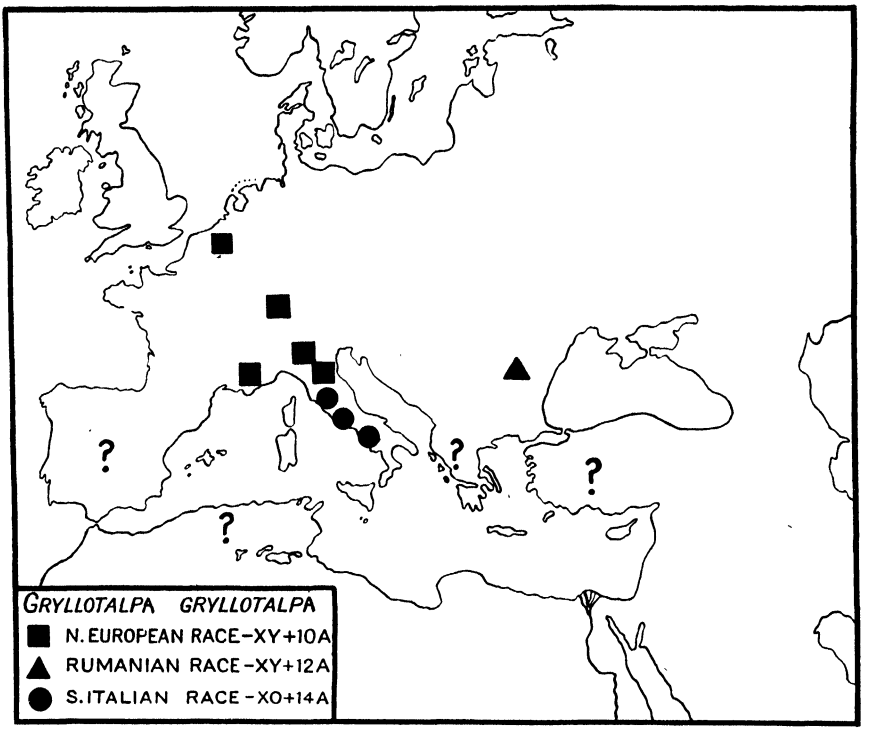
The central European form (which has been found in Belgium, Germany, Provence, Lombardy and central Italy) has five pairs of metacentric autosomes and is XY in the male. The X is metacentric, but the shape of the small Y has not been determined.

Individuals from Roumania have six pairs of metacentric autosomes and are also XY in the male (Steopoe). The situation is, however, complicated, because a small supernumerary may also be present in addition to the usual chromosome set; moreover, one of the autosomal bivalents may be 'unequal' in some individuals.

Finally, the form found in southern Italy (originally recorded from Naples, and subsequently found near Rome and Florence) has seven pairs of metacentric autosomes and lacks a Y altogether.

No constant taxonomic differences have been found between these three cytological races (Barigozzi, 1933*b*), although it is quite possible that more careful and intensive work might reveal some. Thus it seems impracticable to split the original *G. gryllotalpa* into several closely allied species, although from the cytological standpoint that would seem the obvious thing to do. It is not known whether the three 'races' can be crossed; but it is almost inconceivable on cytological grounds that they would produce fertile hybrids. It will be seen from Text-fig. 82 that the northern and the southern races are both present in central Italy, so that their distributions may actually overlap, although this is not certain.

It is not possible to tell how the chromosomal differences between the three forms have arisen. Two other species of the genus have been studied cytologically —*G. borealis* from North America (Payne, 1912*b*, 1916) and *G. africana* which occurs over most of Asia as well as in Africa (Makino, Niiyama and Asana, 1938; Asana, Makino and Niiyama, 1940). These are *XO* forms, like the southern 'race' of *G. gryllotalpa*—both have eleven pairs of metacentric autosomes and



Text-fig. 82. Distribution of the three chromosomal races of *Gryllotalpa gryllotalpa* in Europe.

a metacentric *X*. It is possible that eleven pairs of autosomes represents the primitive condition in the Gryllotalpidae, since it also occurs in the South American genus *Scapteriscus* (Dreyfus, 1942). In that case the various forms of *Gryllotalpa gryllotalpa* have probably undergone a reduction in chromosome number.

Wild populations of *G. africana* and *G. borealis* seem to show aberrations of the same kinds as the Roumanian 'race' of *G. gryllotalpa*. Thus the former may possess varying numbers of supernumeraries, while the latter may have an unequal autosomal bivalent. According to Payne's account the larger member of this unequal bivalent always passes to the same pole as the *X*. If true, this

is a very remarkable state of affairs, since, as we have seen in Chapter IV, the segregation of autosomal bivalents is almost always at random with regard to the *X*. But the situation is not really clear from Payne's work—it is not known whether *all* males carry the unequal bivalent, nor is the condition in the females known.

The fact that species of *Gryllotalpa* are liable to show supernumeraries may explain in part the rather radical changes which must have taken place during the evolution of the three different chromosome sets in the European 'supra-species'.

We have not up till now considered polyploidy as a possible factor in the evolution of chromosome numbers. In the higher plants, as is now very well known, reduplication of whole chromosome sets or one or more elements (polysomy) has been a major factor in evolution. It is quite possible that more than half the species of angiosperms are polyploid or have ultimately been derived from polyploid ancestors.

In animals, on the other hand, polyploidy seems to be much rarer, so that it has only played a very minor part in chromosomal evolution. It was pointed out by Muller (1925) that in bisexual organisms polyploidy will inevitably upset the sex-chromosome mechanism, since it automatically abolishes heterogamety. Thus a tetraploid of an originally $XY : XX$ form will have the composition $XXYY : XXXX$, and nearly all the gametes of the originally heterogametic sex will be XY (due to the two X's and the two Y's forming separate bivalents at meiosis). So that even if a tetraploid male and female meet and pair they would stand no chance of starting a tetraploid race.*

Thus on *a priori* grounds it may be expected that in animals polyploidy should be confined to the hermaphrodite groups (flatworms, oligochaetes, leeches and euthyneurous Mollusca) and to parthenogenetic forms. The evidence is, in fact, entirely in accordance with this expectation. It has frequently been assumed that *Ascaris megalocephala bivalens* is a tetraploid of *univalens*, but it is probable that this is not so (see p. 24).

Even in the hermaphrodite groups, however, the evidence for polyploidy is meagre, and it seems clear that it cannot have played anything like the major role that it has in plants (White, 1940*d*). Thus in the Pulmonata the haploid numbers of twenty-nine species range from 17 to 31, the only aberrant species being *Physa gyrina* with 6 (Mahoney, 1940). Clearly there is no evidence for polyploidy here, since *Physa* is only rather remotely related to the other species which have been studied. It has sometimes been suggested that *Helix pomatia*

* Westergaard (1940) was able to produce a stable tetraploid strain of the normally bisexual plant *Melandrium album*, and has accordingly criticized Muller's theory. He produced $XXXX$ (♀) and $XXYY$ (♂) plants by experimental means, and by crossing them an $XXXX$ (♀) : $XXXY$ (♂) strain was built up. But in this case the $XXXY$ individuals were male because the male-determining power of the Y was strong enough to override the three X's. Such a situation, if it occurs at all in animals, must be relatively rare.

shows polyploidy, but the evidence is very conflicting. The earlier authors (Ancel, 1902; Prowazek, 1902; Lee, 1911; and others) were in dispute as to whether the haploid number was 12 or 24, and at one time it was supposed that there was a var. *univalens* and a var. *bivalens*, as in *Ascaris*. The technique of these early workers was very unsatisfactory by modern standards, and Perrot and Perrot (1937) have recently shown that the true haploid number is 27. Naville (1923), however, claimed to have studied some individuals with a haploid number of 18. If this is so the 27-chromosome form might be triploid. Naville's results cannot be dismissed as worthless like those of Lee, Ancel and Prowazek, since they were carried out with care on a large amount of material. But it is clear that there are special technical difficulties in this species, and it seems highly probable that all numbers lower than 27 which have been claimed by various workers were due to faulty techniques that caused the chromosomes to clump together. Perrot (1938) has shown that two other species of the genus *Helix* (*H. aspersa* and *H. aperta*) also have the same haploid number of 27. Peacock (1940) has reported a possible case of polyploidy in the parthenogenetic mollusc *Paludestrina jenkinsi*.

In the three other large groups with hermaphrodite species there are a number of possible polyploids. Thus in the Rhabdocoela the genus *Mesostoma* contains one species with a haploid number of 2, six with 4, one with 5 and one with 8 (Valkanov, 1938; Ruebush, 1938; Husted and Ruebush, 1940). While there is no definite proof that the species with 4 and 8 chromosomes are tetraploid and octoploid, the evidence certainly points in that direction. Similarly, in the genus *Phaenocora* there are species with 3 chromosomes and others with 6 (Cognetti de Martiis, 1922). But out of the sixty-five species of Rhabdocoeles included in Text-fig. 67 only seventeen are possible polyploids and the actual number is almost certainly less than this, some species having 'multiple' numbers without being polyploid. In the large genus *Dalyellia* there is almost certainly no polyploidy, since all the eleven species which have been studied have a diploid number of 4 (Ruebush, 1938).

In the leeches there are several species with a haploid number of 8, while *Piscicola geometra* and *Hemiclepsis marginata* (Ichthyobdellidae) have a haploid number of 16 (Wendrowsky, 1928). The oligochaetes include species with the numbers 16 and 32. In neither group have a sufficient number of forms been studied to warrant a definite conclusion—although in both there is a *prima facie* case for the existence of polyploidy. But it seems that even in these hermaphrodite groups the percentage of polyploid species is low, compared with the corresponding figure for most of the families of angiosperms. This difference is probably explained, at least in part, by the fact that in hermaphrodite animals cross-fertilization is usually obligatory, while in most angiosperms self-fertilization is possible.

With one exception (*Diprion simile*—see p. 274), the only absolutely certain

instances of polyploid races and species among the higher animals occur in parthenogenetic Crustacea and insects—they will be discussed in Chapter XIII.

From time to time statements have appeared in the literature suggesting that polyploidy has occurred in the phylogeny of some group consisting entirely of bisexual species. Thus Slack (1938*a*) suggested that it had occurred in the Heteroptera, Gates (1942) has discussed the possibility of polyploidy in the evolution of the Mammalia, and Vandel (1938) considered that it had played a major role in the chromosomal evolution of animals. In view of the very strong *a priori* argument against the occurrence of polyploidy in groups with sex chromosomes one should be very careful about accepting these claims. The evidence has never been of a conclusive kind, and some of the authors who have been responsible for these statements seem to have believed that if two species had autosomal numbers, one of which was roughly double the other, then they were entitled to disregard the sex chromosomes in their count. It should be obvious that such a procedure is entirely unjustified.*

There is, of course, no particular reason why polyploid individuals should not be found in nature, as occasional aberrations. But they must be extremely rare in most groups; and in many they probably do not occur at all. In certain Urodeles, however, triploids and tetraploids are found in natural populations, although never in large numbers. Fankhauser (1938, 1939) has made a study of triploid and tetraploid individuals in the newts of the genera *Eurycea* and *Triturus*, while Böök (1940) has described a naturally occurring triploid in the European *Triturus taeniatus*. These individuals probably arose through a single egg being fertilized by several sperms, but abnormal temperatures during fertilization and early development may likewise have played a part in determining the initiation of polyploidy. Some of the triploids were male, others female, but in spite of their regular presence in many natural populations of newts and Salamanders these polyploid individuals do not seem to have given rise to any polyploid races or species in the Amphibia, so that they are probably of no evolutionary importance, as suggested by Seshachar (1941).

It might be argued that even if polyploidy of whole chromosome sets has played little or no part in the evolution of the bisexual groups of animals the reduplication of one whole chromosome at a time may have occurred. It is known that this phenomenon (polysomy) has taken place in a number of plant genera, but there is very little definite evidence for its existence in animals except in a few special cases, in most of which heterochromatic chromosomes are involved. The 'supernumeraries' which have been found in many groups usually seem to be, not whole chromosomes, but ones containing large deletions (see p. 119). The *m*-chromosomes of the coreid Hemiptera may be present in the triploid condition in some individuals of *Metapodius* (Wilson, 1910), but it

* Unfortunately, Slack's claim to have established the existence of polyploidy in the phylogeny of the Heteroptera has been quoted by other authors (e.g. Muller, 1940*a* and Huxley, 1942).

is quite possible that they are genetically inert. In any event no species of coreid is known to possess more than a single pair of *m*-chromosomes, so that even if polysomy of the *m*'s occurs occasionally it has not played a part in the evolution of the group. Similarly, the supernumerary *Y*-chromosomes in some individuals of *Metapodius* (see p. 122) must be regarded as a special case of reduplication of an inert chromosome.

In *Drosophila melanogaster* individuals trisomic for the tiny IVth chromosome (triplo-IV flies) are hardly distinguishable from normal individuals, but flies with four IVth chromosomes (tetrasomics) are inviable. Flies trisomic for the *X* ('superfemales') are very inviable. None of these chromosomal types have been found in the wild. In *D. subobscura* individuals trisomic for one of the acrocentric autosomes are viable but not much is known about them (Philip, Rendel, Spurway and Haldane, 1944). Most species of animals probably have their 'genic balance' so delicately poised that trisomy (and still more tetrasomy) will lead to a serious lowering of viability. In plants, on the other hand, genic balance is apparently not upset so easily; thus in *Datura* twelve different trisomic types are known, in each of which a different chromosome is present three times. All these trisomics are viable and phenotypically distinguishable (Blakeslee, 1934). This ability to withstand large-scale changes in the numerical proportions of the genes seems to be an important difference between the genetical systems of the plant and animal kingdoms, although exceptions may exist in both. It is possible that in some animal species where the shortest chromosomes represent a very small fraction of the total length of genetic material, polysomy of these minute chromosomes may not lead to inviability and may even have occurred in evolution. Thus in birds which have haploid numbers of over 30 each of the smallest elements probably contains less than $\frac{1}{500}$th of the total number of genes. Species such as the moths *Phigalia pedaria* and *Dasychira pudibunda*, which have undergone a spectacular increase in chromosome number, seem to constitute a special problem in chromosomal evolution, and it is just possible (although hardly probable) that they have acquired their present chromosome sets partly by reduplication of whole chromosomes rather than by structural rearrangements involving chromosome breakage.

Callan (1941*a*) studied thirty individuals of the grasshopper *Mecostethus grossus*, of which one was trisomic for the third largest chromosome—this is the only definitely established case of an animal trisomic for a large euchromatic element being found in a natural population. On the other hand, it is not certain that the somatic tissues of this individual were trisomic—the aberration may have occurred in the germ-line.

CHAPTER IX

THE EVOLUTION OF MEIOSIS AND THE CHROMOSOME CYCLE*

The general features of meiosis are extraordinarily constant throughout both the animal and vegetable kingdoms. In the vast majority of sexually reproducing organisms the same sequence of pairing, chiasma formation and segregation occur with complete regularity, such variations as are observed being concerned merely with the number of chiasmata per bivalent, their localization in particular regions, and so on. The close similarity between the meiotic processes of organisms so widely different as lilies, grasshoppers, Urodeles and rodents impressed itself very forcefully on some of the early investigators (Janssens, 1900) and has also been commented upon by modern cytologists (see Darlington and La Cour, 1942, p. 18).

In certain groups of animals, however, the usual type of meiosis has been replaced by some entirely new mechanism. Most of these aberrant variants of the normal process represent secondary simplifications, one or more of the usual sequence of stages or processes being omitted. Many of them occur in association with parthenogenesis or in groups (like the Hymenoptera) where the males are haploid. Quite a number of groups are known, however, in which the normal process of meiosis is profoundly modified, although the animals are bisexual and diploid in both sexes.

Anomalous meiotic mechanisms are usually confined to one sex, nearly always the male. Most of them involve the abolition of crossing-over, and in many of them only one or two sperms (instead of the usual four) are formed from each spermatocyte, the other products of the meiotic divisions degenerating in the same way as the polar bodies do during oogenesis. The suppression of chiasma formation in one sex necessarily lowers the recombination index of the species; it is therefore worth noting that no species is known in which it has been suppressed in both sexes.

So long as there is no evidence to the contrary, we may assume that all anomalous types of meiosis, together with such associated phenomena as the elimination of whole chromosomes during cleavage (in the Sciaridae and Cecidomyidae) or of parts of chromosomes (in *Ascaris*) were originally genetically caused. Some of the types of meiosis found in haploid males are, however, exceptions. Here the loss of one haploid set of chromosomes may in some instances have led directly to the replacement of the normal meiosis by a single equational

* Throughout this chapter (and elsewhere) we use the term *meiosis* to signify the specialized divisions (or division in the case of haploid animals) which immediately precede gamete-formation. In 'normal' meiosis a reduction from the diploid to the haploid number takes place, but in many of the 'anomalous' types no reduction occurs.

division, without any special mutation having taken place. On the other hand, the unequal cytoplasmic division which occurs during the spermatogenesis of the bee (see p. 269) must have arisen as a result of a mutation long after haploidy had become established in the order Hymenoptera.

The action of the 'sex-ratio' gene in species of *Drosophila* is a good example of an anomalous meiotic mechanism which is definitely known to be genetically determined (see p. 191). It is mutations of this type which must have given rise to most of the naturally occurring meiotic mechanisms which are unusual in type.

Not only meiosis, but all parts of the chromosome cycle, particularly the details of fertilization and cleavage, may be affected by specific genes. Thus in the silkworm, *Bombyx mori*, certain strains produce gynandromorphs which also show somatic mosaicism for various characters (Goldschmidt and Katsuki, 1927, 1928*a*, *b*, 1931; Katsuki, 1927). It was shown that this condition was determined by a single gene, whose effect was to cause the polar-body nuclei to be fertilized as well as the egg nucleus. Thus, instead of a single zygote nucleus, we have several within each egg. Since these have been fertilized by different sperm nuclei they may be of different genetical constitution. Moreover, since the female is the heterogametic sex in Lepidoptera, the polar-body nuclei will contain a *Y* if the egg nucleus contains an *X*, and vice versa, so that these strains will always produce gynandromorphs. Genetically determined mosaicism is also known in other Lepidoptera, such as *Argynnis paphia* (Goldschmidt and Fischer, 1927).

In *Drosophila simulans* the *claret* gene (a IIIrd chromosome recessive) leads to abnormalities of meiosis in the female and also to widespread irregularities during cleavage (Sturtevant, 1929*a*; Wald, 1936). It has no effect on meiosis in the male. An apparently homologous gene in *D. melanogaster* alters the colour of the eyes in the same manner, but has no cytological effects.

In social Hymenoptera colonies have sometimes been found which produced a large number of mosaic or gynandromorphic individuals. The most famous case was a hive owned by the German bee-keeper Eugster (see Morgan, 1916; Nachtsheim, 1915). Gynandromorphism in Hymenoptera is, of course, different in principle to the similar phenomenon in other organisms, the male parts resulting from an unfertilized nucleus, the female ones from a nucleus that has been fertilized.

Most of the anomalous meiotic mechanisms which have been described occur in the insects. This is probably in part due to the fact that this group has been studied more extensively by cytologists than any other, but among the Vertebrata, in which a large number of species have been studied, not a single one is known to deviate from the usual scheme of meiosis. In the other phyla of the animal kingdom there have been too few detailed investigations for us to form any idea of the prevalence of meiotic anomalies, although they undoubtedly occur in some arachnids, nematodes and rotifers.

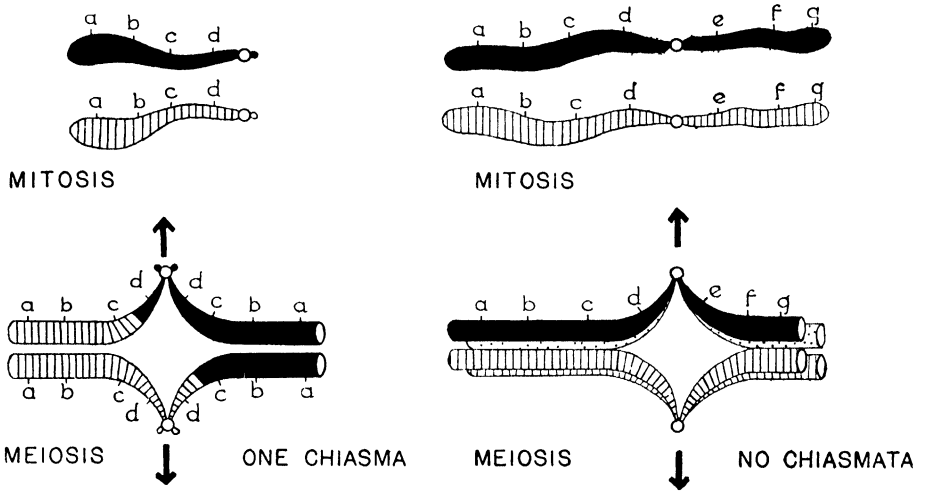
Unusual types of meiosis usually affect all the chromosomes of the set in the same way, but in a few instances only one pair behaves anomalously. Thus in the Hemiptera of the family Coreidae there is always a pair of so-called *m* chromosomes which fail to pair at zygotene in the male, and remain as univalents throughout the prophase of the first division. In some species such as *Archimerus calcarator* and *Pachylis gigas* the *m* chromosomes are exceedingly minute, while in *Protenor belfragei*, *Leptoglossus phyllopus* and *Anasa tristis* they are about the same size as the other autosomes. In all these forms their behaviour at meiosis is exactly the same: during the formation of the first division spindle the two univalents arrange themselves in the centre of the metaphase plate, one above the other, in an axial direction (Wilson, 1911). Thus at the first anaphase they regularly pass to opposite poles, although they have never formed a true bivalent. It is unfortunately not known whether the *m* chromosomes behave in the same way during oogenesis, or whether they undergo true pairing and chiasma formation in the female sex. Their method of orientation within the developing spindle is clearly a special mechanism that ensures a regular disjunction in spite of the absence of pairing. In individuals of *Metapodius* which are trisomic for the *m* chromosome the three *m*'s all arrange themselves in a row in the centre of the spindle (Wilson, 1910), and a similar orientation occurs in tetraploid spermatocytes of *Archimerus*, where a row of four *m*'s is formed (Wilson, 1932).

It is somewhat unfortunate that a number of authors (e.g. Prokofieva, 1933; Oguma, 1930) have used the term '*m* chromosome' to designate small chromosomes in other groups such as the Corixidae and Odonata whose meiosis is perfectly normal; there seems little justification for the use of the term in this broad sense.

The *m* chromosomes of the Coreidae are not the only example of autosomes which do not form bivalents at meiosis. In certain Rhabdocoeles of the genus *Mesostoma* one or more pairs of chromosomes regularly fail to pair during spermatogenesis although they form bivalents during oogenesis (Valkanov, 1938; Husted and Ruebush, 1940). The asynapsis of these chromosomes must lead to the production of a certain number of aneuploid sperms, but since all the adult worms are diploid these are presumably non-functional.

A very interesting series of different types of meiosis occurs in the Diptera. In many of the 'lower' families (suborder Nematocera) the meiosis is of the normal type. Thus in the midges and mosquitoes (Chironomidae and Culicidae) bivalents with typical chiasmata are formed in the males (Philip, 1942; Moffett, 1936). The same seems to be the case in the crane flies (Tipulidae) according to Bauer (1931), although here there are some small chromosomes of doubtful nature which remain unpaired (they may be sex chromosomes, but this is not definitely established). On the other hand, in the two nematocerous families Sciaridae and Cecidomyidae highly aberrant types of meiosis occur (see pp. 200–211).

In *Drosophila* it has long been known that there is no crossing-over in the males. Whereas in oogenesis meiosis is entirely normal (Guyénot and Naville, 1929, 1933; Naville, 1932) it has been shown by Darlington (1934) that the behaviour of the bivalents is quite different in spermatogenesis. His observations were carried out on *D. pseudoobscura*, but the general conclusions undoubtedly apply to all the species of the genus. Although the autosomes pair at zygotene in the usual way they do not pass through the usual diplotene and diakinesis stages, as had already been shown by Huettner (1930). At the stage which



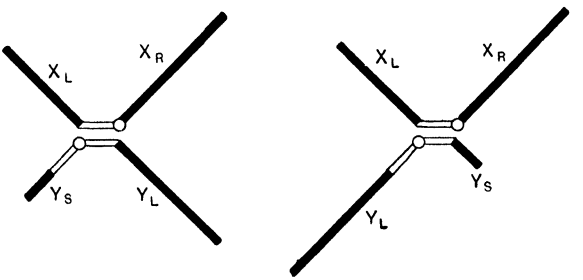
Text-fig. 83. Diagram showing the difference between an acrocentric bivalent with a single chiasma (left) and a metacentric bivalent of a Brachyceran fly such as *Drosophila* (right). The two look very similar under the microscope, although the latter has no chiasmata.

corresponds to diakinesis the two homologues of which each bivalent is composed lie parallel to one another, but they are not united by any chiasmata. In these acrocentric autosomes the minute limbs beyond the centromeres are probably held together more closely than the main chromosome bodies. When seen in polar view at the first metaphase these *Drosophila* bivalents look almost like mitotic chromosomes, although they are present in the haploid number. The same type of bivalents are found in the asilid, trypetid, muscid and tachinid flies (Stevens, 1908*b*; Metz and Nonidez, 1921, 1923, 1924; Keuneke, 1924; Ribbands, 1941; Emmart, 1935), so it is probable that this type of meiosis is found in most or all of the 'higher' Diptera (Brachycera),* although it is only in *Drosophila* that we have confirmatory genetical evidence for the absence of crossing-over in the males. It seems extremely unlikely that the *Drosophila*

* Here and elsewhere we use the term Brachycera to include all the Diptera other than Nematocera (instead of in the restricted sense which excludes the Cyclorrhapha and Pupipara).

type of meiosis is directly related in an evolutionary sense to the much more aberrant types found in the Sciaridae and Cecidomyidae. The latter almost certainly represent an entirely different line of evolution, the starting point for both lines being a normal type of meiosis such as is still found in *Chironomus* and *Culex*.

The method of pairing of the *X* and *Y* chromosomes in *Drosophila* is possibly different from that of the autosomes. Darlington (1934) believes that in species like *melanogaster* and *pseudoobscura*, with a metacentric *Y*, both limbs of the *Y* contain a short pairing segment, so that the most proximal section of the *X* can



Text-fig. 84. Pairing of the sex chromosomes in *Drosophila pseudoobscura*, according to Darlington. There are supposed to be two pairing segments in the *Y*, one on either side of the centromere, but only one in the 'left' limb of the *X*. Either of the pairing segments in the *Y* may pair with that in the *X*.

pair with either *YL* or *YS*. He also makes two further assumptions: (1) that the two pairing segments of the *Y* (on opposite sides of the centromere) are in a 'reversed' and not in a 'tandem' sequence, and (2) that a pair of 'reciprocal' chiasmata are regularly formed between the *X* and *Y*. Since the region between these hypothetical chiasmata is inert they would not be expected to produce any genetical effect. If Darlington's interpretation is correct the sex chromosomes must have retained the ancestral meiotic mechanism which has been lost in the autosomes. This seems highly unlikely on *a priori* grounds: unfortunately, there seems no sure way of testing Darlington's hypothesis by genetical methods, and, since the chiasmata cannot be directly observed, the question must remain an open one. Philip (1935) has reported crossing-over of the *bobbed* gene from *X* to *Y*, the rate of crossing-over being about 1 in 3,000. While this may be genetical evidence for chiasma formation between the sex chromosomes in the male, other interpretations are obviously possible. It is certain that the pairing between the *X* and *Y* appears to be more intimate (in the short region where it occurs) than that between the autosomes, especially at diakinesis; but this does not necessarily mean that chiasmata are present.*

* Cooper (1944) has thrown considerable doubt on Darlington's view that the *X* and *Y* are associated by chiasmata in the male *Drosophila*. He has studied the spermatogenesis of a Hippo-

As far as the autosomal bivalents are concerned, it seems likely that their constituent chromosomes are held together until metaphase (instead of falling apart as univalents) owing to the 'somatic pairing force' which is so characteristic of the Diptera, a force which is manifested at meiosis as well as in the somatic cells. It is not known whether the *X* and *Y* form chiasmata in the other families of the Brachycera, but they are certainly associated in a sex bivalent in all the species hitherto studied.

In the sheep-tick, *Melophagus ovinus* (Diptera, Pupipara), Cooper (1941) has shown that no chiasmata are formed during spermatogenesis, as in the ordinary Brachycera. The diploid number is 18, all the chromosomes being acrocentric except the *X* and *Y*. In the prophases of the spermatogonial divisions a 'somatic pairing' exists, but it only affects the minute arms beyond the centromeres. The reason for this is not quite clear, but it may be because these minute regions are unspiralized, or form only part of a complete gyre, so that a more intimate pairing of homologous parts can take place there than in the main body of the chromosome. The pairing of these minute arms is so close that they often appear to be actually fused together; thus each pair of acrocentric chromosomes looks rather like a V-shaped metacentric at the prophase of a spermatogonial mitosis. Later on, at metaphase, the chromosomes are more condensed, and the actual contact between the short arms of the homologous elements no longer exists. The *X* and *Y* do not appear to show any somatic pairing at any stage. At diakinesis there are eight autosomal bivalents (four large and four small) in each of which the homologous chromosomes are held together by the minute arms beyond the centromeres, and by nothing else. There are never any chiasmata, and the main bodies of the chromosomes are not paired, as they are in *Drosophila*. The *X* and *Y* do not form a sex bivalent in *Melophagus*, but pass as univalents to opposite poles of the spindle at the first anaphase.

The meiosis of *Melophagus* thus resembles that of *Drosophila*, but differs from it in the following respects: (1) the absence of pairing between the *X* and *Y*, (2) the restriction of somatic and meiotic pairing to the short arms of the autosomes. The whole cycle of chromosomal behaviour would be explained if it could be shown that the somatic pairing force was weaker than in *Drosophila*, so that it was only manifested in the relatively unspiralized parts of the chromosomes. This would also explain the non-pairing of the *X* and *Y*, which are metacentric in *Melophagus*, to judge from Cooper's figures.

A number of mutations are known in *Drosophila* species which affect meiosis or some other part of the chromosome cycle. It must be remembered that the abnormalities to which they give rise are superimposed upon a meiosis which is itself anomalous in the male. One of these mutations—known as Gowen's

boscid fly, *Olfersia bisulcata*, in which the *X* and *Y* form a bivalent which closely resembles that of *D. pseudoobscura*. But the *X* and *Y* only come together after the completion of condensation, i.e. just before metaphase. Thus there cannot be any chiasmata between them.

gene—prevents chromosome pairing and crossing-over in the female of *melanogaster*. It is a recessive, situated in chromosome III. The effect is confined to the female, the meiosis of males bearing the gene being normal. Naturally, Gowen's gene leads to much non-disjunction in females which are homozygous for it (Gowen, 1928, 1933).

The so-called sex-ratio condition is found in many wild populations of both the A and B races of *D. pseudoobscura* (Sturtevant and Dobzhansky, 1936*a*). In some populations it may be present in as many as 30% of the individuals (Dobzhansky, 1937*d*). Males carrying the sex-ratio 'gene' (it may really be a position-effect) produce over 90% daughters in their offspring, irrespective of the genetical constitution of the mother. A similar condition is known in *D. affinis*, *D. azteca*, *D. athabasca*, and in the European *D. obscura*, although it is not definitely known whether the mechanism is the same in every case. All these species possess metacentric *X* chromosomes, and no species with an acrocentric *X* is known to show the sex-ratio condition.

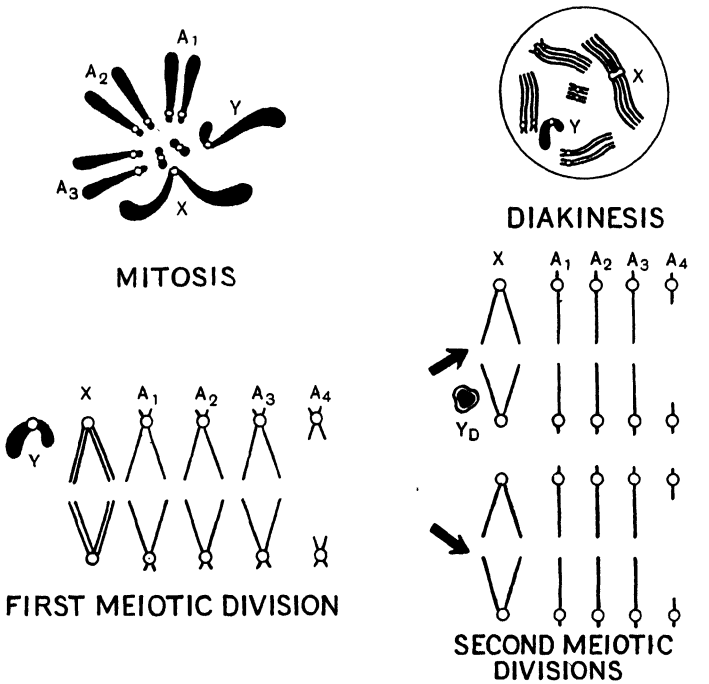
In both races of *pseudoobscura*, and in *affinis*, *athabasca* and *azteca*, the sex-ratio 'gene' is situated in the right limb of the *X*, and is associated with inversions. Thus in race A of *pseudoobscura* every sex-ratio *X* chromosome has three inversions in *X R*.

The spermatogenesis of sex-ratio males has been studied in *pseudoobscura* by Sturtevant and Dobzhansky (1936*a*); it is one of the best understood examples of a genetically determined alteration of the meiotic mechanism. The details are as follows: the *X* and *Y* fail to pair during the prophase of the first meiotic division; at the stage corresponding to diakinesis the *X* is apparently twice split, so that it consists of a bundle of four chromatids (Text-fig. 85). It divides in both meiotic divisions, so that every spermatid receives an *X*. The *Y*, on the other hand, never divides at all. It is heteropycnotic in the first division, and passes entire into one of the two daughter nuclei, so that at the second division half the cells contain a *Y* while the other half lack one. At this second division the *Y* becomes enclosed in a separate vesicle and then usually degenerates.

This is the usual sequence of events, but in some cases sperms are formed containing both an *X* and a *Y*, a *Y* alone or no sex chromosome at all. The last two classes give rise to the rare sons, which form less than 10% of the progeny of sex-ratio males. Some of these sons are *XY*, others *XO*, the latter being, of course, sterile.

It has been suggested by Darlington (in Darlington and Dobzhansky, 1942) that the sex-ratio 'gene' produces its effect by increasing the degree of nucleination of the sex chromosomes and thereby preventing them from pairing. This interpretation is quite possibly correct, but is not definitely proven (the fact that the number of 'exceptional' sons is lower in stocks kept at 16·5° C. than in ones kept at 25° C. cannot be regarded as a proof, even though it is known that in many organisms the degree of nucleination is affected by temperature).

It was pointed out by Gershenson (1928) that if the sex-ratio condition exists in a natural population it should automatically increase with each successive generation. We might thus expect to reach a situation in which the only males in the population were the 'exceptional' sons of sex-ratio fathers, the normal *X* chromosome having become extinct. It is not clear why this does not, in fact, happen.



Text-fig. 85. Diagram of meiosis in a 'sex-ratio' male of *Drosophila pseudoobscura*. A_1, A_2, A_3 and A_4 represent the four pairs of autosomes. The *X* splits in both meiotic divisions, while the *Y* is heteropycnotic and eventually degenerates (Y_D). Based on the work of Sturtevant and Dobzhansky (1936*a*).

A number of authors have suggested that chiasma formation might be absent in the particular organism that they were studying, because the structure of the bivalents at diakinesis was anomalous in one way or another. Thus Schrader (1940*a*, *b*) has shown that in the pentatomid *Rhytidolomia* the homologous chromosomes are arranged end to end in the diakinesis nuclei, usually with no visible connection between them. Pairing is probably normal, and any chiasmata which are formed must be completely terminalized before diakinesis. Cooper (1939) encountered somewhat similar difficulties of interpretation when studying the oogenesis of the mite, *Pediculopsis*, where it is also not certain whether chiasmata are present.

Another kind of technical obstacle exists in certain groups where the bivalents do not 'open out' at diplotene, so that the homologues are closely paired throughout their whole length until metaphase. This happens in the mantid, *Callimantis*, and to a lesser extent in other members of the same group (White, 1938, 1941*a*; Hughes-Schrader, 1943*a*). Here the difficulty lies not in observation but in interpretation. The similarity of the *Callimantis* bivalents to those of the Diptera Brachycera suggested that crossing-over did not occur. Since no genetical evidence is available a final decision is not possible; all that one can say is that if cross-overs occur in the male *Callimantis* they do not become cytologically visible as chiasmata.

In the moths *Bombyx* and *Galleria* it has been reported that no crossing-over occurs in the female (Sturtevant, 1915; T. L. Smith, 1938). Since very few genetic characters have been studied in these species one should not necessarily assume from this that chiasmata do not occur during oogenesis; they might be strictly localized in regions where no genes are known as yet. The earlier work of Naville (1937) and Kawaguchi (1928, 1933) on the cytology of *Bombyx* did not fully explain the genetical results, but in a recent paper Maeda (1939) has described the meiosis of both sexes and compared them. He concludes that chiasmata are not formed in the female, but it appears from an examination of his figures that a single chiasma occurs in each bivalent, near one end. This chiasma may be completely terminalized, so that the two chromosomes which form the bivalent are merely in end-to-end contact. No such strict localization occurs during spermatogenesis, so that the difference in genetical behaviour between the sexes is explained by Maeda's work, although not in the way that he has claimed.

So far we have only been considering the meiosis of monocentric chromosomes. The meiosis of *Ascaris megalocephala* has not been reinvestigated by modern workers, but it is difficult to see how chiasmata could occur in these polycentric chromosomes unless they were confined to the end-regions which are cast off during cleavage (see p. 24). If they were formed in between the centromeres one would expect that the chromosomes would be disrupted at the anaphase of the first meiotic division (unless the chiasmata were always present as reciprocal pairs). Unfortunately, the chromosomes of *A. megalocephala* are highly condensed at meiosis, so that it is not easy to interpret the structure of the bivalents from the published figures (e.g. those of Brauer, 1893 and Sturdivant, 1934). In most nematodes chiasmata are certainly formed in each bivalent (see the figures of Edwards, 1911 and Walton, 1921, 1924). If *A. megalocephala* does lack chiasmata in the central regions of its chromosomes it is probable that they are wanting in both oogenesis and spermatogenesis, since the *a priori* argument applies equally in both sexes.

In the scorpion, *Tityus bahiensis*, we have earlier (p. 117) concluded that the chromosomes are probably polycentric. It is thus of interest that the figures of

Piza (1939*a*, *b*, 1940*a*, 1941) show the metaphase bivalents in the male to be of the *Drosophila* type, with no sign of chiasmata. At the first metaphase the three bivalents are entirely included in the spindle, and as anaphase proceeds they are torn apart into their constituent halves, the ends preceding the middle part during the passage to the poles.* Whether the absence of chiasmata is general in scorpions is uncertain; but the figures of Wilson (1931), Sokolow (1913) and Sato (1936, 1940) rather suggest that the condition in other species is essentially similar: no information is available about oogenesis. If chiasmata are really absent in both sexes of the scorpions that would help to explain how polycentric chromosomes could have been evolved in one or more members of the order. The matter is worth further investigation, since up till now no organism is definitely known to have abolished crossing-over in both sexes. Such a species would, of course, only show segregation and recombination between genes situated on different chromosomes.

Some highly peculiar types of meiosis have been described in the scale insects (superfamily Coccoidea of the order Homoptera) by Schrader and Hughes-Schrader. Thomsen (1927, 1929) and Suomalainen (1940*c*) have also investigated the cytology of some parthenogenetic coccids (most members of the group are bisexual). Up to the present no scale insect has been found to have an entirely normal meiosis in the male.

The species investigated by the Schraders fall into two main groups: (1) the primitive family Monophlebidae, (2) the more specialized Eriococcidae. Those members of the family Lecaniidae which are bisexual have a chromosome cycle which is closely similar to that found in the Eriococcidae (Thomsen).

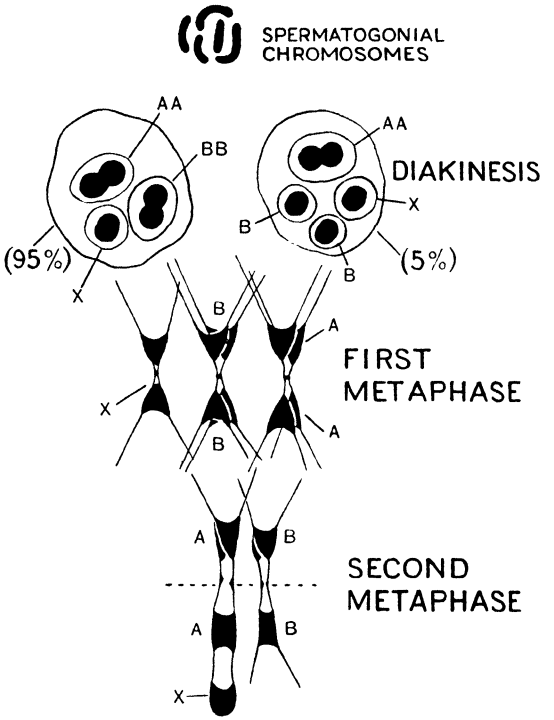
In the Monophlebidae (Margarodidae of some authors) two very distinct types of chromosome cycle occur. Since not all the tribes of this family have been studied cytologically, it is, of course, possible that further anomalous mechanisms remain to be discovered.

In the tribe Iceryini, which includes the 'fluted scales', the males are haploid (Hughes-Schrader, 1925*b*, 1926, 1927, 1930*a*, *b*; Schrader and Hughes-Schrader, 1926; Hughes-Schrader and Ris, 1941): the details of their meiosis will be discussed in a later chapter (see p. 275) in connection with the problem of sex determination. The second type of chromosome cycle is met with in the members of the tribe Llaveini (Schrader, 1931; Hughes-Schrader, 1931, 1940, 1942). In the four species *Protortonia primitiva*, *Llaveia bouvari*, *Llaveiella taenechina* and *Nautococcus schraderae* there are two pairs of autosomes and an *XO* sex-chromosome mechanism (i.e. the somatic sets of the male and female consist of 5 and 6 chromosomes, respectively). In *Llaveia* the *X* is somewhat longer than either of the other chromosomes, while in *Llaveiella* and *Nautococcus* it is the shortest one of the set. *Protortonia* is intermediate in this respect, since all the chromo-

* The later work of Brieger and Graner (1943) suggests that chiasmata may, after all, be present during the prophase of meiosis in *Tityus*; but their work is inconclusive.

somes are about the same length. Meiosis in the females of the Llaveini is quite normal, three bivalents being formed in each egg.

The spermatogenesis of the Llaveini is characterized by the fact that during the prophase of the first meiotic division the chromosomes are usually enclosed in a number of separate vesicles instead of in a single nuclear membrane. In *Protortonia* there are four vesicles: one of these contains the *X*, the other three



Text-fig. 86. Diagram showing the course of spermatogenesis in the coccid *Llaveia bouvari*. The appearance of the first metaphase bivalents is the same, regardless of whether the *B* chromosomes have been paired at diakinesis or not. After Hughes-Schrader (1931).

the autosomes. It would seem that the members of one autosomal pair are regularly included in one vesicle, while those of the other pair are in separate vesicles. There is thus no possibility of pairing or chiasma formation in one pair of autosomes, and it seems rather doubtful if any true pairing takes place between the two chromosomes in the other vesicle.

In *Llaveia* about 4% of the spermatocytes have four vesicles, as in *Protortonia*; but the remainder have only three, two of them containing pairs of autosomes, while the third contains the *X*. In *Llaveiella* three vesicles are usually formed; but in some nuclei either or both pairs of autosomes may fail to pair, and their

members may be enclosed in separate vesicles. The behaviour of the *X* in *Llaveiella* is still more extraordinary; it is normally split into two chromatids during the prophase of the first meiotic division, but in some cells these chromatids fall apart and become enclosed in entirely separate vesicles. If this happens they behave at the first division as entirely separate and independent chromosomes; each chromatid splitting and its two halves passing to opposite poles. In secondary spermatocytes which have arisen in this way there will be two *X*'s which then come together, apparently fuse, and pass undivided to one pole at the second division.

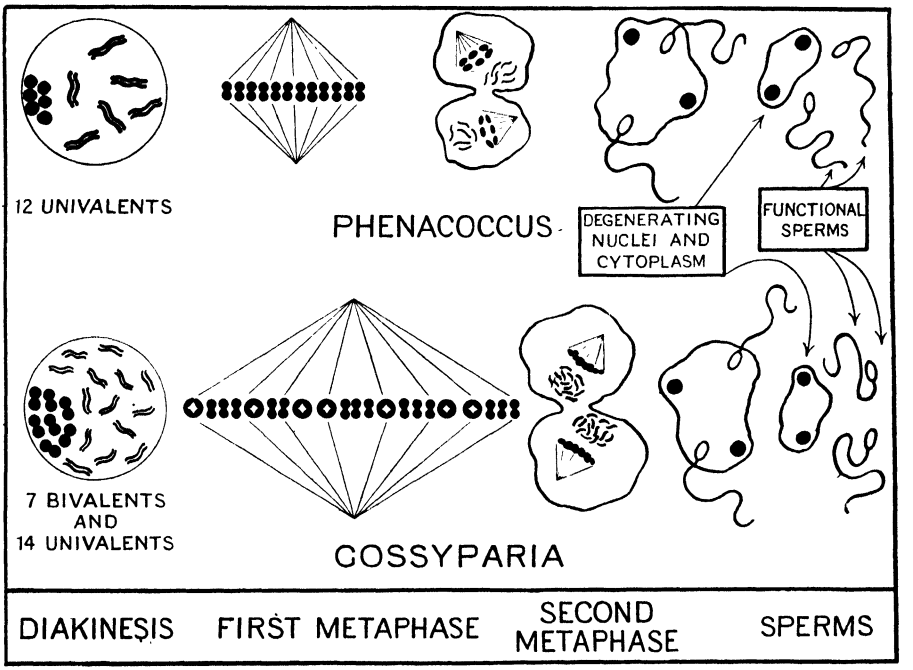
The meiotic spindles of the Llaveini are entirely unique in appearance. At the first division each chromosome, whether bivalent or univalent, forms its own spindle which consists of two great cone-shaped masses flaring out above and below the equatorial plane (Text-fig. 53). At the second division, in *Protortonia*, all the chromosomes arrange themselves in an axial direction on the spindle, so that they form a row, extending from one pole to the other. Something of the same sort seems to occur in the other genera, but the arrangement is less regular. These Llaveine spindles are of considerable interest from the point of view of the mechanism of nuclear division, but we are not concerned with this aspect here.

An entirely different kind of meiosis seems to be characteristic of the families Lecaniidae and Eriococcidae. We may take *Phenacoccus acericola* (Hughes-Schrader, 1935) as typical of this group. There are 12 chromosomes in the diploid set of both sexes, all the chromosomes being alike in size. Six bivalents are formed in the egg. In the male one haploid set of chromosomes is heteropycnotic in the somatic cells from the blastula stage onwards and during the whole of the prophase of the first meiotic division. These 6 chromosomes form a group which lies on one side of the nucleus. It is not known whether the heteropycnotic chromosomes are the maternal set or the paternal one, or whether some may be derived from one parent and some from the other. No pairing of the chromosomes takes place during spermatogenesis, so that there is no possibility of crossing-over in the male. By first metaphase the non-heteropycnotic chromosomes have become nucleinated to the same extent as the heteropycnotic ones, so that there is no visible difference between the two sets. Since no bivalents have been formed, all the chromosomes are univalent and all of them divide at the first anaphase. At the second division one set of chromosomes (presumably the same one) is again heteropycnotic. A 'half-spindle' (i.e. a cone-shaped mass of gelated protoplasm) is formed in connection with the heteropycnotic group of chromosomes, and the latter are then separated from the non-heteropycnotic group, which remain flocculent and under-nucleinated at this division.

The second meiotic division is thus 'reductional' for all parts of all the chromosomes in *Phenacoccus*. The cytoplasm is not completely divided at either

division, so that at the end of meiosis a syncytial mass is left, containing four nuclei, two of which contain heteropycnotic chromosomes, the other two non-heteropycnotic ones. Only the latter nuclei give rise to sperms, the heteropycnotic nuclei degenerating in a mass of cytoplasm which is cast off from the developing spermatids.

In three species of *Pseudococcus* (Schrader, 1921, 1923*b*, *c*) meiosis follows the same general course. There are only 10 chromosomes, 5 of which are heteropycnotic. From Schrader's original description it would appear that all four



Text-fig. 87. Diagrams of meiosis in the scale insects *Phenacoccus* and *Gossyparia*. Based on the work of Hughes-Schrader (1935) and Schrader (1929).

nuclei in the syncytial mass give rise to sperms, but in view of the later work on *Phenacoccus* it is probable that this was an error.

The chromosome cycle of *Gossyparia spuria* (Schrader, 1929) is of the same general type as that of *Phenacoccus* and *Pseudococcus*, but is even more bizarre. There are 28 chromosomes in the diploid set of both sexes, and these form 14 bivalents in the egg. During spermatogenesis 14 chromosomes are clumped together to one side of the nucleus, forming the heteropycnotic group; but these are paired in such a way as to make up 7 bodies. The other 14 chromosomes gradually become nucleinated, so that at the first metaphase there are 21 bodies on the spindle, of which 7 are presumably bivalents, the other 14 being univalent.

Thus each interkinetic nucleus receives 7 of the heteropycnotic chromosomes and 14 of the non-heteropycnotic ones, the latter having divided at the first anaphase. At the second division a 'unipolar' spindle is formed, as in *Pseudococcus* and *Phenacoccus*, and the heteropycnotic group of chromosomes is drawn away from the others. The two heteropycnotic nuclei in the syncytial mass of cytoplasm degenerate, and the two sperms are formed by the remaining nuclei.

Any attempt to interpret these extraordinary meiotic phenomena must necessarily be tentative until our knowledge of meiosis in other coccids is far more extensive than it is at present. It seems probable, however, that *Gossyparia* is a tetraploid, in which two haploid sets are heteropycnotic, the other two being non-heteropycnotic. This hypothesis would explain the peculiar pairing which takes place between the heteropycnotic chromosomes in the male (a pairing which would be unintelligible in a diploid). Thus *Phenacoccus* and *Pseudococcus* probably represent the original condition in this group, in which pairing has been entirely abolished in the male; the *Gossyparia* condition is probably derived from it by a doubling of the chromosome set, with a consequent restoration of pairing among the heteropycnotic chromosomes.

The chromosome set of the Eriococcidae and Lecaniidae is particularly difficult to understand when one considers it in relation to the problem of sex determination. One can hardly avoid the conclusion that the males are homogametic, i.e. that only one kind of sperm is produced. No sex chromosomes are detectable at any stage: since the more primitive coccids and all the other Sternorrhyncha have a sex-chromosome mechanism of the $XO : XX$ type (with the males heterogametic) it would seem probable that the original X chromosomes have been entirely lost in the specialized Eriococcidae and Lecaniidae, and that sex determination in these insects depends on some entirely new system that has replaced the old one. The sex ratios in *Pseudococcus* and *Gossyparia* do not depart significantly from equality (Schrader, 1923*c*, 1929; James, 1937, 1939). Thus the evidence seems to point towards female heterogamety—a heterogamety which possibly affects a short segment of one chromosome (or even a single gene) so that it is not detectable by cytological means.

Schrader (1923*b*) originally assumed that the heteropycnotic group of chromosomes in *Pseudococcus* represented Y chromosomes, while the non-heteropycnotic group could be looked upon as X's. According to this view there would be no autosomes at all in these scale insects. But this interpretation could only be correct if both groups of chromosomes gave rise to functional sperms. Since in *Phenacoccus* and *Gossyparia*, at any rate, the heteropycnotic groups degenerate without forming sperms, Schrader's original theory must be discarded. The heteropycnotic chromosomes cannot represent Y's since they arise anew from non-heteropycnotic ones in each male embryo. It is logical to assume that they consist either of the maternal or the paternal set, having been 'conditioned' by passage through the egg or the sperm so that in an embryo that is genetically

male they become nucleinated to a far greater extent than the other (non-heteropycnotic) set.*

Although it has not been possible to determine cytologically whether it is the maternal or the paternal chromosome set which is heteropycnotic and is lost at meiosis, the genetical work of Dickson (1941) suggests that it is the paternal set. This author studied the inheritance of resistance to hydrogen cyanide in the Californian Red Scale (*Aonidiella aurantii*), which belongs to the same group as *Pseudococcus* and presumably has the same type of chromosome cycle. He found that 'the F_2 females were intermediate between the F_1 females (i.e. their mothers) and the strain to which their paternal grandmothers belonged'. Dickson has interpreted these results as indicating that the gene or genes determining resistance to HCN are carried in the *X*-chromosome. He also assumes that scale-insects are *XY* in the male sex, which is unlikely, as we have already seen. In view of the Schraders' work on the chromosome cycles of the higher scale-insects it is clear that *all* their genes must show a kind of sex-linked inheritance, since each individual, whether male or female, is genetically descended from only three grandparents instead of four (the chromosomes of the paternal grandfather having been lost).

In attempting to interpret the evolution of meiosis in these scale insects we are hampered by the fact that no centromeres can be seen by direct observation. It is clear that in all the types of meiosis which have been so far studied in coccids there is a tendency for the first division to be equational in the males. This is certainly so for the *X* in the Llaveini, and is also so for all Llaveine univalents. Whether it also applies in the case of the 'bivalents' in *Protortonia* and *Llaveia* is uncertain. In the Eriococcidae the first division is an equational one for all the chromosomes—except possibly in *Gossyparia*, where the heteropycnotic chromosomes are associated in pairs. The nature of these pairs is not fully understood, and it cannot be decided from the evidence available whether they are true bivalents in which the chromosomes are held together by chiasmata.

In a general review of their investigations Schrader and Hughes-Schrader (1931) have put forward the view that the heteropycnosis of one chromosome set in the higher coccids represents a 'physiological inactivation' of that set. They compare this condition with the complete loss of one chromosome set in the haploid males of the Iceryini. But, as they rightly point out, there can be no question of the *Pseudococcus-Gossyparia* condition having given rise directly to the *Icerya* one, since *Icerya* is far more primitive and more closely allied to the 'basic' Llaveine group. In the absence of any genetical evidence the assumption that the heteropycnotic group of chromosomes in the higher coccids

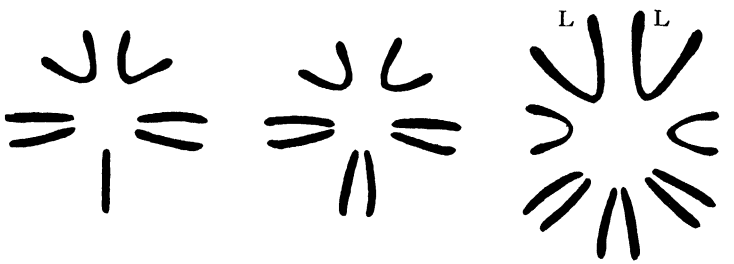
* Just what form this 'conditioning' might take is quite uncertain. But, since the raw materials from which the chromosomes are built up are ultimately derived from the cytoplasm, it is by no means inconceivable that the protein framework of the chromosomes should be permanently altered during their sojourn in the egg or the sperm.

are physiologically inactive seems premature: if they are genetically homologous to the other (non-heteropycnotic) set and only temporarily distinguishable from them on account of a difference in nucleination they cannot be inert in the ordinary sense. Possibly both sets of chromosomes contain inert segments which in the heteropycnotic set swell up to such an extent that they quite obscure the rest of the chromosome.

Vandel (1931) has rather unwisely assumed that heteropycnosis of one haploid set preceded the establishment of male haploidy in other groups where this state of affairs exists—an assumption never made by the Schraders.

The small midges of the genus *Sciara* (Diptera, suborder Nematocera) are characterized by a complicated and entirely unique chromosome cycle, which is fortunately known rather completely, both from the cytological and the genetical standpoint. Thus far fourteen species have been studied by Metz and his collaborators (Du Bois, 1932*a*, *b*, 1933; Crouse, 1939; Schmuck, 1934; Smith-Stocking, 1936; Berry, 1939, 1941; Metz, 1926–41; Metz and Moses, 1928; Metz, Moses and Hoppe, 1926; Metz and Schmuck, 1929*a*, *b*, 1931*a*, *b*; Metz and Crouse, 1939).

Sciara is a large genus belonging to the family Sciaridae, which is closely related to the fungus gnats (Mycetophilidae): it is not known whether the latter have a chromosome cycle of the normal type or if they resemble *Sciara*. There are several other genera of the Sciaridae, such as *Zygoneura*, which have not been studied cytologically as yet.

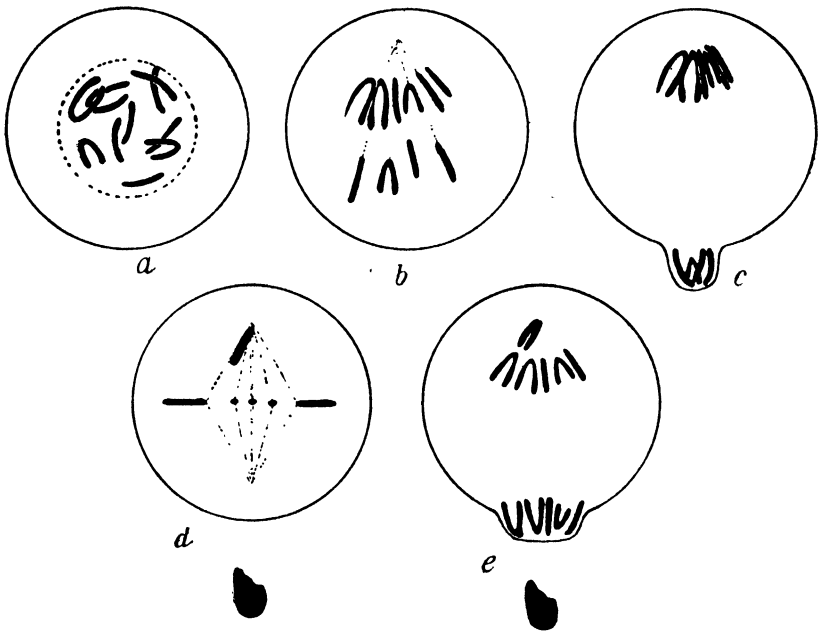


Text-fig. 88. Chromosomes of *Sciara coprophila*. *a* = male somatic set; *b* = female somatic set; *c* = spermatogonial or oogonial set. *X* chromosomes in each case at the bottom of the figure. *L* = 'limited' chromosomes. From Du Bois (1933).

Since the essential features of the chromosome cycle are similar in all the species investigated by Metz and his co-workers we may select *Sciara coprophila* (the best-known species) as the type. In this form there are 7 chromosomes in the somatic cells of the male, 8 in those of the female, one pair of chromosomes being metacentric, the other three acrocentric. The male soma is thus presumably *XO*, the female soma *XX* (the *X* being one of the acrocentrics, which are all about the same length). The spermatogonia and oogonia, however, both contain

o chromosomes (occasionally 9 or 11). This germ-line chromosome set is made ıp of the four pairs already mentioned together with a pair of large metacentrics vhich are not found at all in the soma. Both oogonia and spermatogonia are hus XX, in spite of the fact that the male soma contains only one X.

The large chromosomes which are confined to the germ cells are referred to ıs the 'limited chromosomes' ('L's' for short) by Metz. Usually a pair, they nay be present singly or in triplicate without apparently affecting the appearance



Text-fig. 89. Diagrams of meiosis in the male *Sciara coprophila*. a = a stage corresponding to liakinesis (all chromosomes unpaired); b = anaphase of first meiotic division; c = telophase (four paternal chromosomes being eliminated); d = metaphase of second meiotic division; e = telophase, showing the X splitting at the top of the spindle. From Du Bois (1933).

of the fly; on the other hand, individuals of *S. coprophila* have never been found without any limited chromosomes, although in some other species of the genus, such as *reynoldsi* and *ocellaris*, they do not occur. It is stated by Metz that the limited chromosomes vary somewhat in size, so that L's carrying deficiencies or duplications are probably present in some of the stocks that have been studied.

All these facts suggest that the limited chromosomes are probably largely inert, rather like the Y chromosome in *Drosophila*, although they possibly have some vestigial functions that are only concerned with the germ-line and not at all with the somatic tissues. At some stages in the mitotic cycle the L's are heteropycnotic, but since they are never present in somatic tissues it is not

known what they would look like in salivary nuclei. Species like *ocellaris* have probably lost their *L*'s in the course of evolution. On the other hand, in those species in which they occur the *L*'s seem never to be absent, so that one cannot properly compare them with ordinary supernumeraries such as the *B* chromosomes of maize.

The meiosis of the female *Sciara* follows the usual course: true bivalents are formed, and there is genetical evidence that crossing-over takes place (Schmuck and Metz, 1932). It is not definitely known whether the *L*'s undergo pairing and crossing-over, but if two are present they segregate from one another in the usual manner. Thus the unfertilized egg, after two meiotic divisions, contains the full haploid number of chromosomes (3 acrocentrics, 1 small metacentric and a large *L*). In those flies which have 1 or 3 *L*'s in the oogonia the eggs may contain 0, 1 or 2 *L*'s.

The spermatogenesis of *Sciara* is of a very anomalous type (Metz, Moses and Hoppe, 1926; Metz, 1933). Whereas in the tissue cells somatic pairing is very obvious, as in other Diptera, in the spermatogonia there is no obvious approximation of homologues. Each spermatogonial nucleus contains three pairs of ordinary autosomes, one pair of *X*'s and 1–3 (usually 2) *L*'s.

No pairing takes place during the meiotic prophase, so that all the chromosomes remain univalent, the *L*'s being clearly distinguishable from the others by their marked heteropycnosis. There is no regular 'equatorial plate' stage, and when the spindle of the first division forms it is a unipolar cone-shaped body, the chromosomes being all attached in an irregular manner to the base. At anaphase all the *L*'s together with one member of each of the other pairs pass to the single pole. The remaining 4 chromosomes, which seem to be less closely attached to the spindle, move in the opposite direction and are expelled from the cell in a small mass of cytoplasm which degenerates (Text-fig. 89). There is genetical evidence (Smith-Stocking, 1936) that the chromosomes which are got rid of in this way are the set derived from the father, the only paternal chromosome retained in the sperm being the *L*.

The second meiotic division is a bipolar one in which 6 chromosomes become attached to the spindle (2 *L*'s and 4 ordinary chromosomes). One of the ordinary chromosomes is not attached at the equator of the spindle but near one of the poles. This chromosome (which is, in fact, the *X*) splits into two but both of these remain in the same half of the spindle and both pass into the same spermatid. The chromosomes which pass to the other pole are cast off in a small bud of cytoplasm which degenerates like that formed at the first division. Thus only one sperm arises from each spermatocyte—it contains the limited chromosomes, two *X*'s and one member of each of the autosomes (usually 7 chromosomes altogether with slight variations due to more or less than 2 *L*'s being present). All the 'ordinary' chromosomes (autosomes and *X*'s) in the sperm are of maternal origin, so that the male *Sciara* only transmits genes derived from his

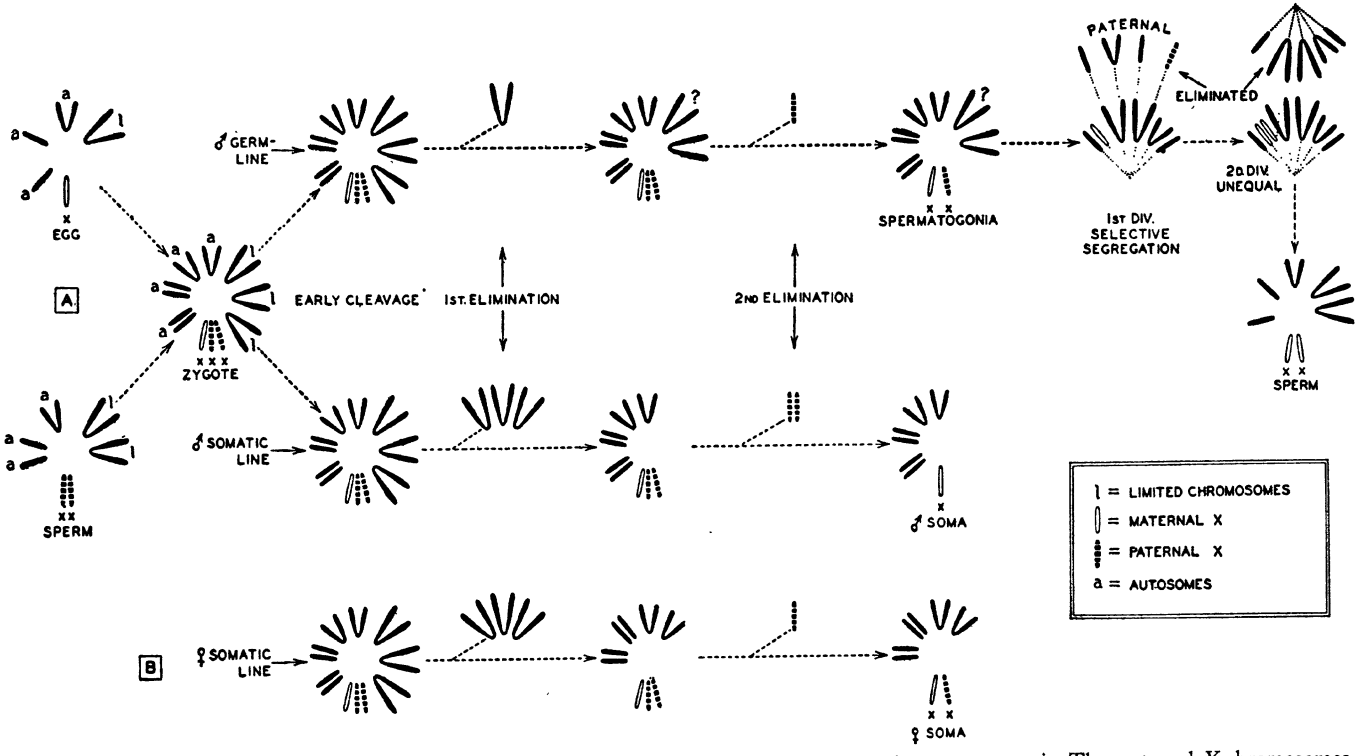
mother. Although the male soma is *XO* the males are actually homogametic, since all their sperms contain the same chromosome set.)

The meiosis of the male Sciaridae is so unique in character that it is hard to imagine how it could have arisen in the course of evolution or how it really 'works' at the present time. Failure of the chromosomes to pair and form bivalents is known in many other organisms, particularly during the oogenesis of parthenogenetic forms (see Chapter XIII), and in some instances failure of pairing is known to be caused by a single gene. Unipolar meiotic spindles are, however, decidedly uncommon: they occur in the haploid males of the beetle *Micromalthus* (see p. 278) and in some scale insects where one set of chromosomes remains incompletely nucleinated, but *Sciara* is the only case in which a unipolar meiotic spindle occurs in a diploid organism where both haploid sets are outwardly similar in appearance. It is particularly hard to imagine any physical mechanism which could cause all the maternal chromosomes to be retained while the paternal ones are eliminated in a small 'bud' of cytoplasm. Logically, one might imagine that this radical difference in behaviour, between two sets of homologous chromosomes, might result either from a difference in position within the nucleus or from a difference in chemical structure. If the former explanation were correct the mechanism would be entirely unique. There is, however, one other instance in which the maternal and paternal chromosomes behave differently, namely, the scale insects mentioned above, in which one set of chromosomes is negatively heteropycnotic. It is not altogether impossible that a so far undetected chemical difference exists between the two sets of chromosomes in *Sciara*, having been handed down through a number of cell generations from the time when they were surrounded by different cytoplasmic environments (in the egg and sperm, respectively).* But this is pure hypothesis: all one can say definitely is that the two sets of chromosomes look alike but behave differently, at the time when the spindle is formed.

The fertilized egg of *Sciara coprophila* contains three pairs of autosomes, three *X*'s and a variable number of *L*'s (usually three). One of the *X*'s has been derived from the egg pronucleus, the other two come from the sperm nucleus. During the process of cleavage a number of the chromosomes are eliminated both from the somatic cells and from the germ-line, so as to restore the chromosome sets characteristic of the adult tissues. These eliminations have been studied in detail by Du Bois (1932*a*, *b*, 1933) and Berry (1941).

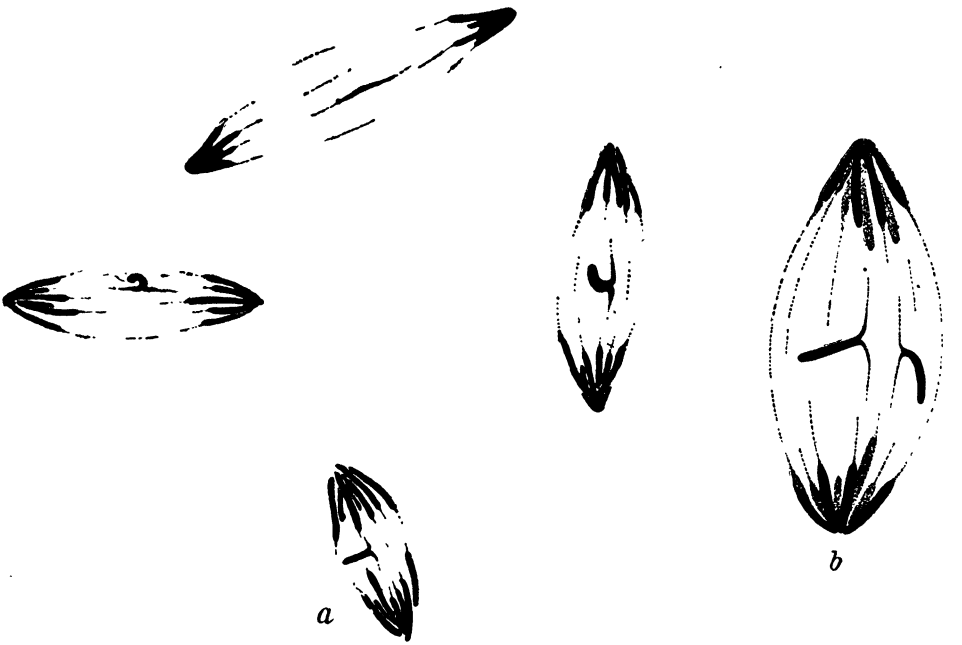
The first four cleavage divisions are ordinary mitoses. By the time the sixth cleavage occurs the separation of the germ-line from the soma has already taken place. At the fifth or the sixth cleavage the limited chromosomes are eliminated from the future somatic cells. The method of elimination is as follows: the *L*'s

* This is the explanation favoured by Metz (1938*a*), who points out that the difference between the maternal and paternal chromosomes must be reversible, since the same chromosomes which are 'paternal' in the males of one generation will be 'maternal' in the males of the next generation.



Text-fig. 90. The chromosome cycle of *Sciara coprophila* during fertilization, cleavage and spermatogenesis. The maternal *X* chromosomes which go into the sperm become, of course, the paternal *XX* at fertilization. The number of 'limited' chromosomes actually varies from one to three. Diagram A will serve equally well to represent conditions in the female, except as regards gametogenesis which is normal, and as regards the second chromosome elimination from the soma. From Metz (1938).

go through an apparently normal prophase and become attached to the spindle. At the beginning of anaphase, however, it is obvious that they are unable to split in the normal way. As the ordinary chromosomes pass to the poles the *L*'s are left in the middle part of the spindle, being apparently stretched between their daughter centromeres. Eventually the limited chromosomes degenerate completely. Their inability to divide is possibly due to some upset of their nucleic acid metabolism, analogous to that which seems to occur in the *Y* of sex-ratio males of *Drosophila*.



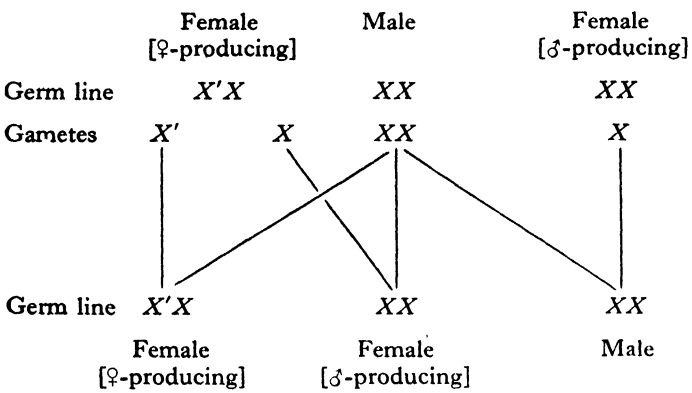
Text-fig. 91. Elimination of *X* chromosomes at the seventh cleavage division in *Sciara coprophila*. *a*=four divisions in a female embryo (only one *X* eliminated); *b*=a division in a male embryo (two *X*'s eliminated). From Du Bois (1933).

A further series of eliminations occurs during the later cleavage divisions. Thus at the seventh or the eighth mitosis the somatic nuclei, which still contain three *X* chromosomes, extrude one or two of these. In embryos which are destined to become females only one *X* is extruded, while in embryos which will become males two *X*'s are got rid of (Text-fig. 91). The genetical evidence shows that the *X*'s which are got rid of at this stage are paternal, i.e. in females one of the two sister-*X*'s brought in by the sperm is thrown out, while in males both sister-*X*'s are cast out. In the germ-line a single paternal *X* is got rid of at a slightly later stage, irrespective of the sex of the embryo. According to Berry (1941) these eliminations of *X* chromosomes take place in a totally different

manner to the eliminations of *L*'s—the *X*'s simply migrate through the nuclear membrane and then degenerate in the cytoplasm.

Apparently one or more *L*'s are eliminated from the germ-line as well, since, in spite of the fact that each sperm transmits the full number of *L*'s present in the spermatogonium, the number in the species does not increase at each generation. This elimination of the *L*'s from the germ-line has not, however, been actually observed (Metz, 1938*a*).

Having described this extraordinarily complicated series of cytological phenomena we must consider their relation to the mechanism of sex determination. Some species of *Sciara* produce unisexual progenies, others normally give



Text-fig. 92. Diagram of sex-determination in *Sciara coprophila*.

bisexual progenies, while in yet others different strains may give either unisexual or bisexual families. In all cases the sex of the offspring depends on the genetical constitution of the mother, the father being of no importance in this connection.

In species such as *S. coprophila* and *S. impatiens*, which nearly always produce unisexual families, there seem to be two kinds of females, male producers and female producers. There is no visible cytological difference between these two types and Metz has suggested that they merely differ in respect of an invisible genetic factor (possibly a single gene). The female-producing females are assumed to be heterozygous (*XX'*), the male-producing ones homozygous (*XX*). Normally male producers and female producers are present in approximately equal numbers in the population, so that a sex ratio of about 1 : 1 is maintained. The result of mating the two types of females with the single type of male is shown in Text-fig. 92.

The actual sex of the individual is apparently determined by the elimination of *X*'s during cleavage—if one *X* is eliminated the embryo becomes a female, if two are thrown out a male is produced. But it is the genetical constitution of

the mother (operating, no doubt, through the egg cytoplasm) which determines whether one or two *X*'s are lost from the somatic nuclei.

It is interesting that many of the 'unisexual' families are not, in actuality, completely so, since occasional individuals of the wrong sex are produced. Apparently these 'exceptional' individuals have the cytological constitution corresponding to their phenotype, in other words if they are males their soma is *XO*, if they are females it is *XX*. They seem to result from a failure of the genetical constitution of the mother to control the elimination of the *X*'s. It is possible that the two allelomorphs postulated by Metz (*X* and *X'*) are not the only ones, and that in actuality a series of alleles of varying potency (*X*, *X'*, *X''*, *X'''*, etc.) exists.

Since the chromosomal constitution of the germ-line is the same in both sexes of *Sciara*, what is it that causes the gonad of a female to become an ovary, that of a male to become a testis? The obvious answer would seem to be that the chromosomal constitution of the surrounding soma influences the development of the embryonic gonad in one direction or the other. This hypothesis would seem, however, to be in conflict with the findings of Du Bois (1932) on the anatomy of gynandromorphs of *S. coprophila*. These may be externally half male and half female, but their right and left gonads are always of the same sex, ovaries or testes, as the case may be. This suggests that the sex of the gonad is determined by the genetical constitution of the mother, irrespective of the sex of the soma, which is determined quite independently. In *S. ocellaris*, however, the work of Lawrence and Crouse (cited by Metz, 1938*a*) has shown that gynandromorphs may have a testis on one side and an ovary on the other. The evidence is thus somewhat conflicting.

Among the species of *Sciara* which normally produce bisexual families we may mention *S. pauciseta* and *S. prolifica*. The difference between these and a species like *coprophila* would appear to be one of degree rather than of kind: in *coprophila* the 'exceptional' individuals are very few, while in *pauciseta* and *prolifica* they may make up 50% of the offspring.*

S. ocellaris is an interesting species, since some strains produce unisexual broods, while in others the offspring of a single female are of both sexes. Crouse (1939) has shown that there is a visible cytological difference between the 'unisexual' and the 'bisexual' strains, since one autosome is acrocentric in the former, metacentric in the latter. The rearrangement responsible for this difference was probably a centric shift, since in the salivary nuclei of the hybrids between the two races the autosomes in question are paired throughout their entire length, with no sign of an inversion loop. Whether the difference in sex-determining mechanism is really a position-effect resulting from a structural rearrangement must remain an open question for the present. In the

* 'Bisexual' strains of *S. coprophila* are occasionally encountered (Reynolds, 1938).

closely related species *reynoldsi* (which, so far as is known, always produces bisexual broods) the chromosome is always metacentric.

The extraordinary complex of cytological phenomena which occur in *Sciara* can hardly be analysed from an evolutionary point of view until some other genera of Sciaridae and Mycetophilidae have been studied. The *L* chromosomes may be likened to the distal ends of the *Ascaris* chromosomes which are likewise retained in the germ-line and lost from the soma, but this does not get us very far in understanding their functions. It is, however, fairly clear that the *L*'s have no direct connection with sex determination.

The unipolar spindle during spermatogenesis is hard enough to interpret, but what are we to think of the peculiar behaviour of the *X* during the second meiotic division, which ensures that each sperm shall carry two identical *X*'s? This part of the mechanism would seem to be quite unnecessary, since one or both of these *X*'s is lost from both soma and germ-line of the future embryo. Considered as a means of producing male and female individuals in approximately equal numbers the cytogenetical system of the Sciaridae seems to be the most complicated that has arisen in the course of evolution—a highly specialized method of attaining a result which is achieved in other organisms by far simpler mechanisms.

In the gall-midges (Cecidomyidae), which also belong to the Diptera Nematocera, a variety of different types of chromosome cycle occur, which may be compared with that of *Sciara* in some respects. The cytology of *Miastor*, an aberrant cecidomyid which reproduces paedogenetically as well as by sexual means, was investigated by Kahle (1908) and Hegner (1914), whose work has been widely quoted. The later account of Kraczkiewicz (1935*a*, *b*) has added considerably to our knowledge and corrected the earlier accounts in some details.

According to Kraczkiewicz the paedogenetic larvae of *M. metraloas* have 12 chromosomes in their somatic nuclei; he considers that these represent six pairs of homologues, three long pairs and three shorter ones. The oogonial nuclei, however, contain 48 chromosomes. The latter are said to pair in bundles of four before the 'growth period' of the oocytes (i.e. at the beginning of the meiotic prophase); but it is probable this is merely the 'somatic pairing' seen in most Diptera (rather than a true meiotic pairing), since it is not maintained until metaphase, and is not followed by chiasma formation. There is a single meiotic division which is 'equational' (i.e. mitotic) in nature.

The eggs which develop parthenogenetically within the body of a paedogenetic larva thus contain 48 chromosomes; if the diploid number is 12 they are therefore octoploid. The first two cleavage divisions are ordinary mitoses, but at the third division, in all those cells which will give rise to somatic tissues only 12 chromosomes divide and pass to the poles—the remaining 36 are left at the equator and degenerate. It seems likely that this behaviour is due to an inhibition of the splitting process, as has been suggested in the case of the 'limited chromosomes'

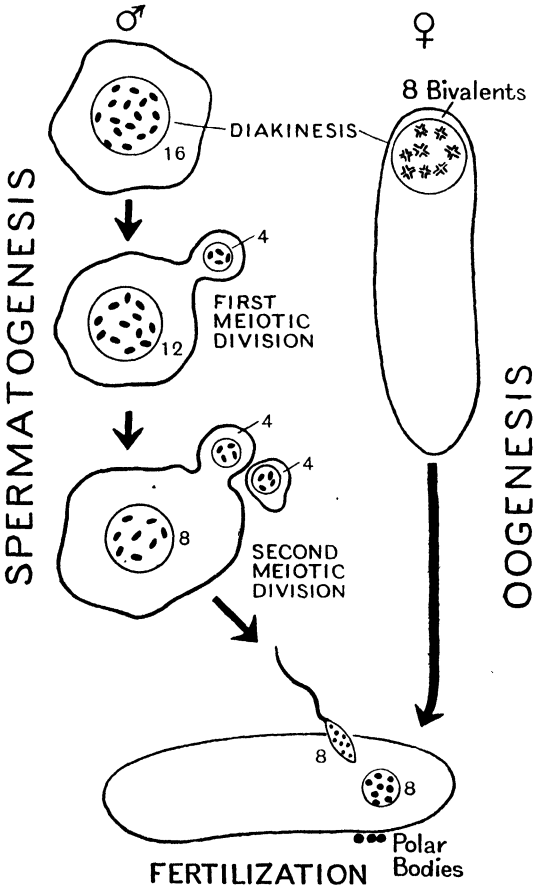
in *Sciara*. This elimination was originally described by Kahle, who wrongly believed that the ends of the chromosomes were cast off, as in *Ascaris*.

In a later paper (1937) Kraczkiewicz has described the cytology of the 'sexual' larvae of *Miastor*, which are destined to develop into adult males and females. Unfortunately his account is rather incomplete, so that it is not possible to understand the whole chromosome cycle. The female larvae apparently do not differ from the paedogenetic ones in their cytology—that is to say they have 48 chromosomes in the germ-line and 12 in the soma. The meiotic divisions in the egg were unfortunately not studied, so that it is not known whether they are 'normal' or not. The male larvae probably have 48 chromosomes in their spermatogonia (Kraczkiewicz did not succeed in counting the exact number, but estimates it at 48). In their somatic nuclei, however, the males have only 7 chromosomes, not 12. It thus appears that 5 chromosomes present in the female soma are wanting in the male—these represent two of the shorter chromosome pairs and one member of one of the long pairs. The sexual difference between the male and female soma is probably akin to that which exists in *Sciara*, and possibly arises in the same way, by elimination of 5 chromosomes at some stage in the embryology of the male. It seems difficult to avoid the conclusion that *Miastor* has a 'basic' chromosome set of six pairs, of which two at least are practically inert, so that they can be dispensed with in the male soma. The germ-line is presumably octoploid at all stages of the life history. It is extremely unfortunate that there is no connected account of meiosis in the male and female individuals: in a footnote to his 1937 paper Kraczkiewicz states that at the first meiotic division in the male 7 chromosomes pass to one pole and all the rest to the other. He thinks that the 7-chromosome cells form normal sperms after a further division, while the other cells (presumably containing 41 chromosomes) give rise to giant sperms that probably do not function. It is clear that in order to understand the chromosome cycle of *Miastor* properly much further work is required.

Another cecidomyid, *Oligarces paradoxus* (belonging to the same subfamily as *Miastor*), has been studied by Reitberger (1934, 1940). His observations show that it has the same general type of chromosome cycle, although there are some interesting differences of detail.

In the paedogenetic eggs of *Oligarces* there is a single meiotic division at which 66 univalent chromosomes can be counted. In the first three cleavage divisions there are likewise 66 chromosomes. At the third division in the embryo the three anterior cells (which will give rise to the soma) eliminate 55 chromosomes on the equatorial plate of the spindle. Thus after this division there are six nuclei containing 11 chromosomes each and two nuclei at the hind end of the embryo with the full number of 66. One of these subsequently loses 55 chromosomes, so that at the next division we have 14 somatic nuclei and 1 germ-line nucleus. Between the sixth and the eighth cleavage divisions a single

chromosome is lost from each of the somatic nuclei, which are thus eventually left with only 10 chromosomes. Reitberger suggests that these nuclei are diploid, there being 5 chromosome pairs. The germ-line would thus be 12-ploid, containing 12 haploid sets together with 6 'extra' chromosomes not found in the soma and hence analogous to the 'limited chromosomes' of *Sciara*.



Text-fig. 93. Diagram of the chromosome cycle in the cecidomyid *Phytophaga destructor* (size and appearance of nuclei purely conventional). Based on the work of Metcalfe (1935).

In the Hessian fly (*Phytophaga* or *Mayetiola destructor*), which is one of the cecidomyids that do not show paedogenesis and is a member of a different subfamily to that which includes *Miastor* and *Oligarces*, Metcalfe (1935) has shown that the spermatogonial and oogonial nuclei contain 16 chromosomes, all of which are metacentric. Oogenesis is quite normal; eight bivalents are formed

and there are two meiotic divisions. Spermatogenesis, on the other hand, is anomalous—the chromosomes do not pair and in each of the two meiotic divisions a small 'bud' of cytoplasm containing 4 chromosomes is expelled from the main cell. These buds degenerate, so that only one sperm is formed from each spermatocyte, as in *Sciara* and the louse (see p. 212). Thus at fertilization both male and female pronuclei contain 8 chromosomes and the zygote possesses the full number of 16. At the fifth cleavage division those nuclei which will pass into the somatic tissues lose 8 chromosomes which are left on the equator of the spindle, as in *Miastor* and *Oligarces*.

Thus if *Miastor* has an octoploid germ-line, *Phytophaga* probably has a tetraploid one (the alternative—namely, that it has a haploid soma—seems much less likely). The 8 chromosomes expelled in the two 'buds' probably represent two haploid sets, but it is not clear whether they are the two paternal or the two maternal ones—or a mixture of both. Neither is it known whether the 8 chromosomes lost during cleavage are paternal or maternal.

An interesting difference between *Miastor* and *Phytophaga* is that in the latter the somatic tissues of the two sexes seem to contain the same number of chromosomes, i.e. the cleavage elimination is the same in all embryos, irrespective of whether they are going to develop into males or females. Many cecidomyids produce unisexual broods (Barnes, 1931, 1936), so that it is probable that genetically distinct male-producing and female-producing females exist, as in *Sciara*.

In attempting to analyse and interpret these strange chromosome cycles we must bear in mind that all the published accounts are somewhat fragmentary. In no species of cecidomyid has a complete investigation such as that of Metz on *Sciara* been carried out as yet.

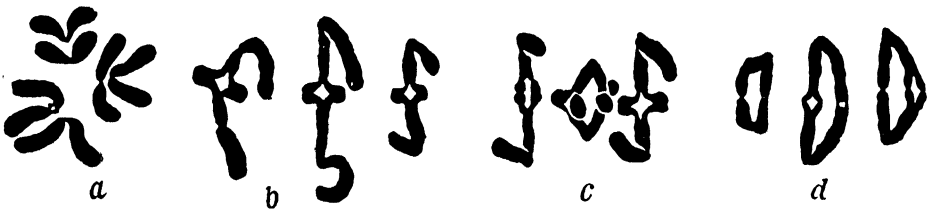
It is interesting to compare the facts about the meiosis of the Diptera with the various hypotheses that have been put forward as to the phylogenetic relationships of the various families. The *Nematocera* comprise a number of families whose exact relationship to one another has been frequently debated (Crampton, 1924; Edwards, 1925). The last-mentioned author divides these families into three main groups which have, he thinks, been separated at least since the Jurassic:

Group 1.	Mycetophilidae (including Sciaridae)	Scatopsidae
	Bibionidae	Cecidomyidae
Group 2.	Ptychopteridae	Culicidae
	Psychodidae	Chironomidae
Group 3.	Trichoceridae	Tipulidae

There are a number of families not included in this list whose exact position is somewhat doubtful. It seems worth noting that at least two families of group 1

have an anomalous meiosis, while the members of groups 2 and 3 all have (so far as is known) normal meiotic mechanisms. The unity of the higher families of Diptera (belonging to the Orthorrhapha, Cyclorrhapha and Pupipara) is shown by their all having the same type of meiosis as *Drosophila* (i.e. with bivalents but no chiasmata in the males).

In a few insects the division at which the reduction to the haploid number takes place occurs during the early part of the germ track, so that although the



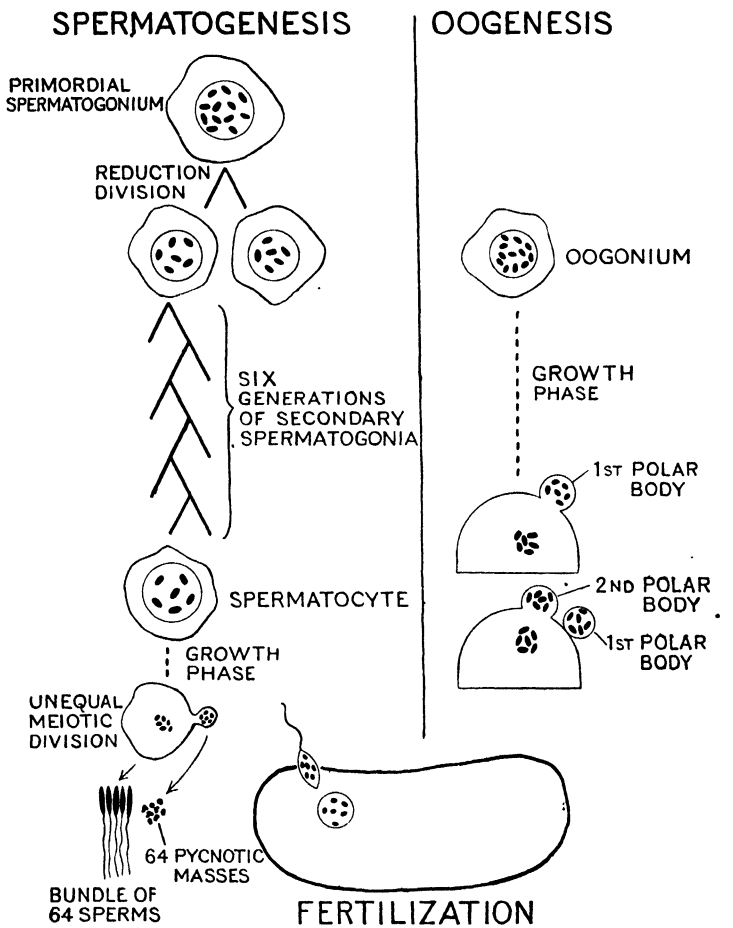
Text-fig. 94. Chromosomes and meiosis in the mosquito, *Culex pipiens*. *a* = spermatogonial metaphase; *b*, *c* and *d* = first metaphases in side view with three, four and six chiasmata respectively. From Moffett (1936).

soma and the primordial germ cells are diploid the spermatogonia and spermatocytes are haploid. This is the condition in the testicular part of the gonad in the hermaphrodites of the coccid *Icerya purchasi* (see Chapter XII). A similar state of affairs seems to exist in the louse, *Pediculus* (Doncaster and Cannon, 1919; Cannon, 1922; Hindle and Pontecorvo, 1942). Here the somatic number is 12 in both sexes, the chromosomes being very minute and all about the same size, so that no sex chromosomes can be identified with any certainty. Oogenesis has not been studied in detail, but is probably normal. In the male, however, the primordial spermatogonia undergo a reduction division, so that the secondary spermatogonia only contain six chromosomes. The details of this reduction division have not been fully worked out: apparently the chromosomes form bivalents, but it is not known whether chiasmata occur; possibly the pairing of the chromosomes is similar to that which takes place in the case of the coreid *m* chromosomes.

After this spermatogonial reduction division the haploid spermatogonia undergo six divisions by ordinary mitoses, producing cysts of 2, 4, 8, 16, 32 and 64 cells. Then follows a growth phase which converts the small spermatogonia into spermatocytes. The growth phase is followed by a single 'meiotic' division which is an unequal one as far as the cytoplasm is concerned, a small nucleated 'bud' containing 6 chromosomes being cut off from the main cell. Only the larger products of this division form sperms, the small buds degenerating. Since there is no second meiotic division each cyst gives rise to a bundle of 64 sperms and 64 small pycnotic masses.

This unique chromosome cycle (if, indeed, it has been properly interpreted)

provides a problem of nomenclature: are we to call the reductional division of the primordial spermatogonia a meiosis, and if so what are we to call the unequal division that precedes sperm formation? The latter undoubtedly represents a modified meiosis, but it is no longer reductional, since one of the early gonial



Text-fig. 95. Diagram of the chromosome cycle in the louse. Explanation in text. Based on the work of Hindle and Pontecorvo (1942).

mitoses has become transformed into a reduction division. As far as the higher animals are concerned, it would seem best to reserve the term meiosis for the two divisions (or single division in cases of haploidy) immediately preceding gamete formation, irrespective of whether a reduction takes place or not. We may call the division of the primordial spermatogonia in *Pediculus* and *Icerya*

a reduction division, which does not prejudice the question of whether chiasmata occur or not. This course leaves us free to use the term meiosis for the spermatocyte divisions in groups such as the Hymenoptera, which have haploid males (a usage which is convenient, if not strictly logical).

The sex-determining mechanism of *Pediculus* is probably also anomalous, since it has been found by various investigators that paired matings may give almost unisexual progenies (Hindle, 1919), although females mated to several males usually produce approximately equal numbers of sons and daughters (Buxton, 1940). These data are not fully explained by the peculiar chromosome cycle in the testis; they suggest that genetical differences probably exist between the males of a population, some being male producers, others female producers. This situation may be contrasted with the one that obtains in *Sciara* spp., where there are several types of females, but only one kind of male.

It is not known whether all the Anoplura have the same type of spermatogenesis as *Pediculus*, but in the biting lice (order Mallophaga) Perrot (1934) has shown that there is a single unequal division before sperm formation, so it appears probable that the *Pediculus* cycle occurs in both orders, thus showing that they are in reality closely allied, in spite of the obvious morphological differences between them.

The general significance of anomalous meiotic mechanisms is far from clear. In most groups the normal type of meiosis seems to be an entirely satisfactory method of ensuring genetical recombination and sex determination. In the Brachycera the abolition of crossing-over in the males must be looked on as one way of reducing the recombination index, equivalent in the long run to a general decrease in chiasma frequency. Owing to their low chromosome numbers and absence of chiasmata in the males the higher Diptera have lower recombination indices than any other group of comparable size. Many other types of anomalous mechanisms, such as those met with in the Sciaridae and in the higher scale insects, also have the same effect of decreasing the recombination index, but it is difficult to believe that they became established in evolution simply on this account, when a decrease in either chromosome number or chiasma frequency would have produced the same result, without any alteration in the fundamental mechanism of meiosis.

Although intermediate stages between the various 'anomalous' meiotic mechanisms and the 'normal' type must have existed at one time it seems highly unlikely that the missing links between *Sciara* and the culicid-chironomid type of meiosis or between the eriococcid and llaveine types will ever be found, since they have almost certainly been long extinct.

CHAPTER X

HYBRIDIZATION AND THE CAUSES OF HYBRID STERILITY

Experimental hybridization of animal species may have either of two aims in view. It may be carried out in such a way as to compare the genetic systems of the parent species or with the object of determining what degree of genetical isolation exists between them. Some pairs of species simply cannot be crossed, in spite of the fact that they are regarded by taxonomists as closely allied. They may refuse to copulate, or the cross may be completely sterile, so that no hybrid offspring are ever produced. In such cases the isolation mechanism is complete and absolute, so that its genetical basis can only be investigated by indirect methods, such as crossing both forms to a third one.

Where isolation is incomplete an F_1 generation can be obtained: it may consist of a few sickly embryos that never develop beyond a certain stage or of vigorous individuals that become fully fertile adults. Thus in the mosquitoes of the *Anopheles maculipennis* group there are about six forms ('subspecies' in the opinion of the earlier taxonomists but in reality quite distinct species) which are indistinguishable in the adult stage, although they have different habits and can be separated by the structure of their eggs and in some instances by larval characters (de Buck, Schoute and Swellengrebel, 1934). We may arrange these various forms in a series according to the degree of development of the hybrids between them (see Table 9). It is not, of course, certain that this series really represents the degree of phyletic relationship between the forms; in other words two species that are completely intersterile may in some instances be more closely related than others which show partial fertility when crossed. Nevertheless, investigations of this kind do throw much light upon the nature of biological isolating mechanisms, particularly when all possible combinations of crosses have been attempted (which is not the case in the *Anopheles maculipennis* group, where the same form (*atroparvus*) was used as the male parent in all the crosses).

A great deal of the work on interspecific hybridization in animals has been of an unsystematic kind, prompted by the curiosity of amateur naturalists and not directed towards the solution of any definite problem. It is likely that, in the future, experimental hybridization will be more and more developed as a technique for studying the nature of species differences. In many groups where hybridization has been considered very difficult or impossible a more carefully planned attempt to obtain hybrids would probably be successful. For many years the only interspecific hybrids known in *Drosophila* were those between *melanogaster* and *simulans*. A large number of other crosses have now been carried out in this genus, and it is clear that a great many forms which never hybridize in

nature can be induced to do so in the laboratory, either by depriving them of mates of their own species, crowding or special techniques such as artificial insemination.

TABLE 9. *Hybrids in the* Anopheles maculipennis *group*

(Data from de Buck, Schoute and Swellengrebel, 1934)

Father		Mother	F_1 hybrids
atroparvus	×	*messeae*	Eggs do not hatch, or if they do all larvae die at an early stage
atroparvus	×	*elutus* (=*sacharovi*)	Larvae hatch, but die at a late stage
atroparvus	×	*typicus* (=*maculipennis*)	Hybrid imagines healthy, but sterile (gonads very small)
atroparvus	×	*melanoon*	Hybrid imagines healthy, but males sterile; half the females are stated to have normal ovaries
atroparvus	×	*labranchiae*	Hybrid imagines healthy. Females with normal ovaries: some males with small testes

In *Drosophila* the only interspecific hybrids that have been found in the wild are those between *D. mulleri* and *D. aldrichi* (see p. 149). In birds, whose taxonomy is very well understood (see Chapter 1), there are a few instances where forms generally considered as distinct species hybridize in a small part of their range, but such a situation seems to be very far from common, although no doubt many more instances will eventually be discovered. In the Mollusca, *Cepaea nemoralis* and *C. hortensis* (which have the same chromosome number) hybridize in nature in some localities (Boettger, 1922), but in spite of this the two species remain entirely distinct, the rare hybrids being sterile. Natural hybrids in teleost fishes have been described by Hubbs and Kuronuma (1941).

There is, of course, only one way of proving that an individual caught in the wild is really a hybrid—namely, by carrying out in the laboratory the cross which is believed to have occurred in nature, and then comparing the supposed natural hybrid with those which have been produced experimentally.

Natural hybrids seem to be much commoner in plants than in animals. Thus in the European Orchidaceae many hybrids are found in the wild, some of them between forms that are usually regarded as falling in separate genera. In extreme cases we may have the development of 'hybrid swarms', i.e. populations consisting entirely of hybrid individuals with segregation of the characters of the original parent species. Very few comparable cases are known in animals, but several species of the moth *Platysamia* seem to hybridize freely in the U.S.A. (Sweadner, 1937).* In the American toads of the genus *Bufo* (*B. americanus*, *B. fowleri*, *B. woodhousii* and *B. terrestris*) hybrid populations undoubtedly occur

* Bytinski-Salz (1939) has shown that four species of this genus all have the same chromosome number (31): the male hybrids are partly fertile, while the female ones are apparently entirely sterile.

in nature (Blair, 1941) and in the fresh-water snails of the genus *Viviparus* the species *ater* and *pyramidalis* form hybrid populations in some lakes (Franz, 1928). In plants there is now a great body of evidence showing that hybridization has been a positive factor in evolution, but in animals the evidence is very meagre. We have already considered the case of *Drosophila americana*, which probably arose by hybridization between two forms belonging to the same supra-species. This kind of hybridization may have taken place quite frequently in animals, but it is of necessity not so easy to detect as hybridization on an interspecific or intergeneric scale. The latter has never been shown to have played a definite role in animal evolution, although Huxley (1942, pp. 248–54) has tabulated quite a number of instances of interspecific hybrids found in the wild.

There appears to be little correlation between the nature and extent of physiological isolation and the phenomenon of hybrid sterility. At any rate, some species which can be crossed quite freely produce entirely sterile hybrids. The horse and the donkey provide an example: the hybrids between them are vigorous, not intersexual, but quite sterile except in very rare single instances. They usually produce no viable gametes, because of a profound disturbance of meiosis in both sexes.

The whole subject of the causes of hybrid sterility is a very complex one. Each of the parent species involved in any cross probably contains within its chromosomes a large number of genes controlling the development of the gonads, the course of spermatogenesis and oogenesis, the motility of the sperm and so on. If all these genes are sufficiently alike in the two parent forms they may build up a compatible system in the hybrid, so that the latter is wholly or partially fertile. On the other hand, if there is an incompatibility between the genes or polygenic systems of the parent species we may have a general disturbance of gametogenesis, a failure of pairing among the chromosomes or an omission or modification of some essential stage or process in meiosis of the later stages of gamete formation.

In some species hybrids the gonads are very imperfectly formed, so that no meiosis can take place. This may be regarded as the result of some specific endocrine disturbance, but very little is known of the actual factors involved. Thus in the hybrids between *Drosophila melanogaster* and *D. simulans* the gonads are very small and gametogenesis is arrested before meiosis, i.e. nothing but spermatogonia and oogonia are present in the testes and ovaries of the adult flies (Kerkis, 1933).

It is unfortunate that, apart from this and other recent work on hybridization in *Drosophila*, most of the work that has been done on the cytology of animal hybrids has been carried out in groups such as the Lepidoptera, birds and fishes where the chromosomes are very unsuited for a detailed analysis on account of their small size, large number and (in many cases) uniform appearance. In the Orthoptera—which are by far the most suitable group of animals in which to

study meiosis—only two interspecific crosses have been studied cytologically: (1) *Trimerotropis citrina* × *T. maritima* (Carothers, 1939, 1941), (2) *Chorthippus bicolor* × *Ch. biguttulus* (Klingstedt, 1939). Cousin (1934, 1941) reared many thousands of offspring from the cross *Gryllus campestris* × *G. maculatus*, but no account of the cytology of these hybrids has ever appeared.

Broadly speaking, we may distinguish several types of meiosis in hybrids: (1) Complete pairing of the two sets of chromosomes. Physiology of meiosis normal. (2) Incomplete pairing. Meiosis otherwise normal. (3) Complete pairing but meiosis abnormal (spindles of unusual type, nucleination disturbed, anaphase separation incomplete or accomplished with difficulty, etc.). (4) Incomplete pairing, meiosis abnormal. (5) No pairing, meiosis otherwise normal. (6) No pairing, meiosis abnormal.

Usually it is only hybrids belonging to groups (1) and (2) which are fertile, either *inter se* or in backcrosses with the parent species, hybrids in groups (3)–(6) being nearly always sterile.

Some workers have considered failure of pairing in hybrids to be mainly due to differences in gene-sequence between the parent species. It is fairly obvious that if two species had undergone a great number of structural rearrangements since they diverged in the course of phylogeny, then the hybrid between them would be likely to show few or no bivalents at meiosis. But it is known that in *Drosophila* a large number of inversions may be present in pure species without preventing the chromosomes from pairing. It is thus probable that most failure of pairing is due to genic incompatibility upsetting the mechanism which brings the chromosomes together or the mechanism of chiasma-formation.

Dobzhansky calls sterility which is a mechanical consequence of different gene-sequences *chromosomal sterility*, reserving the term *genic sterility* for cases where the impediment to pairing is physiological and not merely mechanical. Although the distinction may be theoretically important, unless we can ascertain the exact gene-sequences of the parent species by salivary-gland analysis, it is difficult to apply it in practice. Many cases of hybrid sterility probably depend on a combination of both types of causes, one reinforcing the other; moreover, even where chromosomal pairing is completely normal meiosis may be disturbed at a later stage (our category (3)), so that no viable gametes are formed.*

As an example of the first type of species hybrids (those with a completely normal meiosis) we may take the cross between the pentatomid bugs *Euschistus variolarius* and *E. servus* studied by Foot and Strobell (1914). Here pairing of the chromosomes was apparently complete, and the hybrids were fertile, so that a second generation could be reared. In hybrids between *Cimex lectularius* and *C. columbarius* pairing of the autosomes is also complete (Darlington, 1940*a*),

* In plants there are a number of cases of hybrid sterility which seem to be purely 'chromosomal' in type, but in animals no case of chromosomal sterility is known in which genic sterility does not also seem to play a part.

so that this state of affairs may be quite usual in heteropteran species hybrids. The *Gryllus* hybrids studied by Cousin probably also belong in this category, since here again an F_2 was obtained with ease.

In all these cases the chromosome number is the same in the two parent species, and the gene-sequence is probably very similar, if not identical. Almost complete pairing can occur, however, even when the chromosome number of the parent species is different. Thus in the hybrids between the moths *Bombyx mori* (haploid number 28) and *B. mandarina* (haploid number 27) studied by Kawaguchi (1928) 26 bivalents and an association of three chromosomes are formed at meiosis (the latter being due to the pairing of two *mori* chromosomes with one of *mandarina*). Associations of more than two chromosomes are also seen at meiosis in the hybrids between the moths *Orgyia antiqua* (haploid number 14) and *O. thyellina* (haploid number 11) studied by Cretschmar (1928).

The situation where wide differences in parental chromosome numbers do not prevent complete pairing seems to be rather characteristic of lepidopteran hybrids. Thus *Dicraneura vinula vinula* has a haploid number of 21, while *D. vinula delavoiei* has 31 chromosomes, but in spite of this in the hybrid between them 21 bodies are frequently found at the first metaphase, 10 of these being made up of two *delavoiei* chromosomes paired with one *vinula* chromosome (Federley, 1939). On the other hand, in the hybrid between *Cerura* (*Dicraneura*) *bifida* (haploid number 49) and *C.* (*D.*) *furcula* (haploid number 29) 52–70 bodies are seen at the first metaphase, so that here pairing is incomplete, although some chromosomes obviously do manage to associate. A similar situation exists in the hybrids between the moths *Saturnia pavonia* (haploid number 29) and *S. pyri* (haploid number 30) investigated by Pariser (1927). In the F_1 hybrids there are about 8–14 bivalents. These hybrids produce sperms which contain slightly less than the diploid set of chromosomes; when backcrossed to either of the parental species they give rise to subtriploid individuals which are intersexual.

A large number of interspecific and even intergeneric crosses have been studied in the sphingid moths (Federley, 1915, 1916, 1928, 1929; Bytinski-Salz, 1934; Bytinski-Salz and Günther, 1930). In the genera *Celerio* and *Pergesa* the extent to which the chromosomes of the F_1 hybrids pair at meiosis seems to be directly correlated with the degree of relationship between the parent species, as judged by ordinary taxonomic criteria. Thus all hybrids between *C. euphorbiae*, *C. galii*, *C. hippophaes* and *C. vespertilio* show complete pairing at first metaphase, and so do hybrids between *P. elpenor* and *P. porcellus*. In hybrids between species of *Pergesa* and species of *Celerio*, however, there is very little pairing (only 4 or 5 bivalents being formed out of a potential 29). *Celerio lineata* seems to be more distantly related to the other species of the genus than they are to one another, since in the hybrids between it and *euphorbiae*, *galii*, *hippophaes* and *vespertilio* pairing is incomplete, although rather less so than in the intergeneric hybrids. In none of these Lepidopteran hybrids do we find the gross abnormalities of

meiosis which occur in many *Drosophila* hybrids. Apparently the genetic control of the physiology of meiosis is less delicately poised than in *Drosophila*, so that it is not so easily upset by the presence of the haploid sets of two different species within the same nucleus.

All the above data refer, of course, to the male hybrids. In the female hybrids of *Celerio* and *Pergesa* the histology of the ovaries is normal in the offspring of interspecific crosses, but in the female hybrids of intergeneric crosses the ovarioles do not contain any fully developed eggs (in many of these sphingid species crosses the female pupae never hatch—see p. 225). In some hawk-moths such as *Smerinthus ocellatus* hybrids between two subspecies of the same species may show incomplete pairing (Federley, 1914, 1915), so that the degree of taxonomic relationship which is associated with incomplete pairing obviously varies from one genus to another.

By way of contrast with the sphingid hybrids we may consider the crosses carried out by Federley in the moths of the genus *Pygaera* (Federley, 1913, 1931). Whereas female hybrids between *P. curtula* (29 chromosomes) and *P. pigra* (23 chromosomes) show almost complete pairing at meiosis, in the spermatogenesis of the hybrid males there is little or no pairing at the first metaphase. The univalent chromosomes split at both meiotic divisions, so that the spermatids usually contain the diploid chromosome number. There has been some discussion as to whether the failure of pairing in these *Pygaera* hybrids is 'genic' or 'chromosomal'. Dobzhansky (1937*d*) suggests that some of the data indicate that a true chromosomal sterility is involved. Thus Federley was able to show that in triploid *Pygaera* hybrids containing two chromosome sets from one species and one from the other the two homologous sets formed bivalents, the third set being left unpaired. This is a different condition to that met with in triploid hybrids between *D. melanogaster* and *D. simulans*, where the two *melanogaster* sets in a $2m + 1s$ hybrid do not pair (Schultz and Dobzhansky, 1933). The fact that pairing is almost complete in female *Pygaera* hybrids strongly suggests, however, that failure of pairing in the male hybrids is physiological (i.e. genic in origin). The pairing which occurs in triploid *Pygaera* hybrids cannot really be regarded as an argument in favour of 'chromosomal' sterility, since the genic equilibrium is obviously different in a diploid and in a triploid hybrid.

As an example of the third type of species hybrid (those in which pairing is complete, but meiosis is physiologically abnormal) we may take the hybrids between the grasshoppers *Chorthippus biguttulus* and *Ch. bicolor* studied by Klingstedt (1939). These species are difficult to distinguish, but there can be no doubt that they are taxonomically distinct. Where the distributions of the two forms overlap they sometimes hybridize in nature, and one of the hybrid individuals studied by Klingstedt was caught in the wild.

In the spermatogenesis of the hybrid males all the chromosomes usually pair, and the chiasma frequency is not much below normal. At the first metaphase

the bivalents are much thinner than usual and their orientation is irregular. Sometimes one large ring bivalent surrounds the whole spindle, so that the axis of the latter passes through the loop. It seems likely that the spindle itself is abnormal, although Klingstedt did not pay particular attention to this aspect of the problem. Anaphase separation seems to take place with great difficulty, and many chromosomes break or fail to separate. It is not quite clear how far this is due to abnormalities of the spindle or to disturbances in the nucleination and splitting of the chromosomes.

This cross teaches us a number of things about the nature of the parent species involved in it. Both of them have in addition to five pairs of acrocentrics three pairs of large metacentric chromosomes. Since these latter always form three bivalents in the hybrid (usually with chiasmata in both arms) the arrangement of the chromosome limbs must be the same in both species (and not, for example, *AB*, *CD*, *EF* in one and *AB*, *CE*, *DF* in the other). Some chromosome 'bridges' were observed in the hybrids at the first anaphase, but it is uncertain whether they were due to crossing-over in inversions or to the difficulty which the chromosomes experience in separating from one another. One 'unequal bivalent' composed of a large and a small acrocentric was observed in the natural hybrid.

Although Klingstedt's experiment was not carried beyond the first generation, it seems likely that the hybrids would have been entirely sterile, in spite of the complete pairing of the chromosomes.

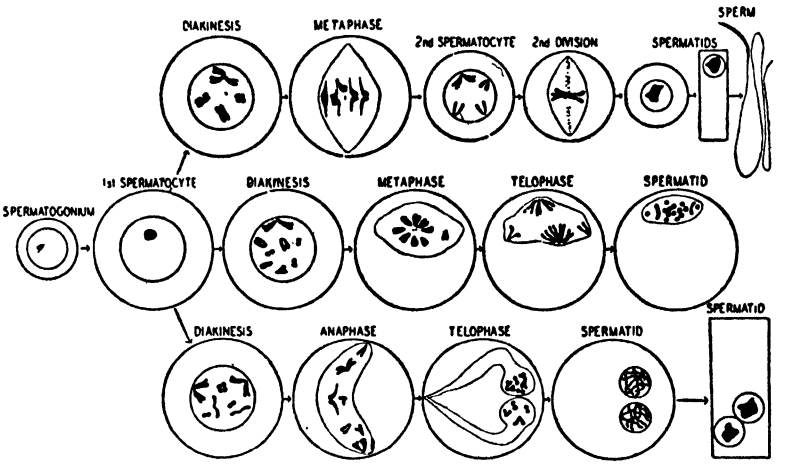
As a further example of hybrids belonging to categories (3) and (4) we may take those between the A and B races of *D. pseudoobscura*, which have been studied in considerable detail by Dobzhansky and Boche (1933) and Dobzhansky (1934). It had earlier been shown by Lancefield (1929) that the hybrid males from the cross A ♀ × B ♂ have testes of normal size, whereas in A ♂ × B ♀ hybrids the testes are very much reduced in size. In either case, however, the hybrid males are entirely sterile. Corresponding to the difference in testis size, the cytology of the reciprocal hybrids is quite different. The matter is, however, even more complicated than this, since within each race it is possible to distinguish 'strong' and 'weak' strains which give different-sized testes when crossed ('strong' strains giving small testes, 'weak' ones producing testes of normal or only slightly subnormal size).

In A ♀ × B ♂ hybrids the early stages of spermatogenesis are normal. In some cases all the chromosomes pair to form bivalents during the meiotic prophase, while in other cases only some of them, or none at all, do so. In general, hybrids between 'strong' races show few or no bivalents, hybrids between weak strains having a higher frequency of pairing.

At the anaphase of the first meiotic division in A ♀ × B ♂ hybrids the spindle elongates to an extraordinary extent, so that it becomes bent round within the cell into a horseshoe shape. No division of the cell body occurs, so that both

telophase nuclei become included within a single cell. The second meiotic division never occurs at all, so that giant vermiform diploid spermatids are formed, which never develop into functional sperms.

The spermatogenesis of the A ♂ × B ♀ hybrids follows an entirely different course. There are very few spermatogonia and spermatocytes, and the number of spermatogonial divisions is often reduced. The greater part of the mature testis is filled with cellular debris produced by the degeneration of the spermatids.



Text-fig. 96. *Drosophila pseudoobscura.* Diagrams of normal spermatogenesis (top row), spermatogenesis in A ♂ × B ♀ hybrids (middle row) and A ♀ × B ♂ hybrids (bottom row). From Dobzhansky (1934).

The chromosomes do not usually pair at meiosis and the anaphase of the first meiotic division is abnormal, although there is no marked elongation of the spindle as in the A ♀ × B ♂ hybrids. No cell division occurs, and there is no second meiotic division, but in strong A ♂ × B ♀ hybrids a number of supernumerary mitoses may occur after meiosis, leading to the production of multinucleate spermatids.

In neither type of hybrid are viable sperms produced, thus explaining the complete sterility of the F_1 males. The genic incompatibility which gives rise to hybrid sterility in *D. pseudoobscura* is probably fairly complex, so that different degrees of incompatibility occur, according to the 'strength' of the strains used in the cross.

The female hybrids between the A and B races are slightly fertile when backcrossed to the parent forms. This fact enabled Dobzhansky (1936*b*, 1937*d*) to obtain individuals containing various combinations of the parental chromosomes. These types varied in fertility, and it was shown that the sterility of the male hybrids depended on numerous genes situated in all the chromosomes except the minute Vth one. The cytoplasm, however, plays some role in determining

the size of the testes in the hybrid males, since two males containing the same chromosome set may differ in the size of the testis, according to the history of the cytoplasm in which the chromosomes lie (i.e. whether the egg was laid by an F_1 female or a pure A or B fly). The *Y* plays no part in the determination of testis size.

The hybrids between *simulans* and *melanogaster* are entirely sterile, so that it has not been possible to analyse the causes of their sterility in the same way. Nevertheless, Muller and Pontecorvo (1940*a*, *b*, 1941) found an ingenious way of overcoming this difficulty. They crossed triploid *melanogaster* females (which produced eggs with some extra chromosomes) with *simulans* males that had had some of their chromosomes incapacitated by a heavy dose of X-rays. In this way they were able to obtain offspring with various combinations of *melanogaster* and *simulans* chromosomes, and to prove that the sterility effect, like that of the A × B hybrids in *pseudoobscura*, depends on numerous genes scattered over all the chromosomes. Males which possess a *simulans Y* but in which all the other chromosomes are derived from *melanogaster* are sterile, just like *XO* males. Individuals having all their chromosomes from *melanogaster* except the two IVth chromosomes were fairly viable, fertile if female but sterile if male (the male sterility in this case probably depends on a single gene in the IVth chromosome).

The hybrids between *Drosophila pseudoobscura* and *D. miranda* have been studied cytologically by Kaufmann (1940). Whereas the male hybrids have very small testes in which no sperms are formed the female hybrids produce numerous eggs in which some kind of meiosis goes on (it is stated that there are no striking irregularities of meiosis, but it is uncertain how far pairing and chiasma formation are normal). At any rate such eggs may, after polar-body formation, be fertilized by sperms of either parent species and cleavage may proceed as far as the 16-celled stage. Kaufmann points out that a chance distribution of the 10 chromosomes at meiosis should give some pronuclei containing only *pseudoobscura* and some with only *miranda* chromosomes, and that consequently some zygotes will have a normal *pseudoobscura* or *miranda* set (but he seems to have left crossing-over out of account). Kaufmann consequently believes that the hybridity of the cytoplasm is in part responsible for the death of the backcross zygotes during cleavage.

In *Drosophila* hybridization is only possible between very closely related species, so that one can subdivide the genes into a large number of units within which hybridization is possible under laboratory conditions (although the hybrids may be sterile) but between which hybridization is entirely impossible. Such a situation probably exists in a large number of insect genera. In some groups, however, intergeneric crosses can be carried out without any great difficulty. Huxley (1942, p. 294) mentions the pheasants, the ducks and the Canidae as groups in which intergeneric hybrids can easily be obtained, and to this list we may add the geometrid moths and some families, at any rate, of

teleost fishes (Hubbs and Kuronuma, 1941). In these forms the 'crossable groups' are wider than the genera recognized by systematists, whereas in *Drosophila* and probably in most insect orders each genus comprises several 'crossable groups'. As Huxley points out, in some forms barriers to crossing have evolved faster than extensive morphological differences, while in others the situation is reversed—a fact that merely emphasizes once again that the 'pattern' of evolution varies from group to group (see Chapter XIV for a further discussion of this point). In the viviparous fishes of the family Poeciliidae hybridization can be carried out without great difficulty under laboratory conditions, and the fertility of the hybrids is such that by repeated crossing Hubbs (1941) was able to obtain individuals in which as many as five species had been combined.

In a great many interspecific crosses the sexuality of the hybrids is undisturbed and the sex ratio is normal; that is to say, the F_1 consists of males and females in approximately equal numbers. This is what we should expect if the sex-determining mechanism of the parent species is similar quantitatively as well as qualitatively. In a great many crosses, however, one sex may be present in reduced numbers or altogether absent. In some other cases intersexes appear in the hybrid generation. Thus in the cross between the mallard and the Muscovy ducks (*Anas platyrhyncha* and *Cairina moschata*) the progeny of the mating *Cairina* ♀ × *Anas* ♂ are sterile males and females, while those of the reciprocal mating are sterile males and intersexes which outwardly resemble males but actually represent much modified females with rudimentary ovaries (Sokolovskaja, 1935; Crew and Koller, 1936). In this case the sex ratio does not seem to be disturbed, so that males and intersexes are produced in approximately equal numbers.

A somewhat analogous case in *Drosophila* has been described by Wharton (1942). *D. melanopalpa* females crossed to *D. repleta* males from Guatemala gave rise to offspring which ranged from normal males through all grades of intersexuality to normal females. The reciprocal cross was sterile, and crosses between *melanopalpa* and various other strains of *repleta* gave rise to normal male and female hybrids with no intersexes.

In the work of Keilin and Nuttall (1919) on hybrids between the head and body lice of man intersexes appeared in the F_2 and subsequent generations, but since Pontecorvo (unpublished) has found intersexes in pure cultures of body lice it is not certain that hybridization was responsible for the appearance of intersexes in Keilin and Nuttall's experiments.

One of the most complete studies of intersexuality in hybrids has been carried out in interracial crosses of the gypsy moth (*Lymantria dispar*) by Goldschmidt (1931*a*, 1932, 1934). Here the sex-determining mechanism seems to be in a very active state of evolution, since the species has broken up into a number of different geographical races whose sex chromosomes differ very greatly in 'potency' (see p. 236 for a further discussion).

Haldane (1922), after reviewing the known cases of interspecific hybridization, enunciated the rule that when one sex in the offspring of a cross is absent, rare or sterile, that sex is the heterogametic one (i.e. the female in birds and Lepidoptera, the male in most other groups). We have already noted a number of examples of 'Haldane's rule' in the genus *Drosophila*. In the Lepidoptera a great many instances are also known. Thus in the hawk moths the cross *Pergesa elpenor* ♀ × *P. porcellus* ♂ gives caterpillars of both sexes, but the females die in the pupal stage. The same seems to be true of the cross *Celerio euphorbiae* ♀ × *C. galii* ♂, although the reciprocal mating gives hybrids of both sexes (Federley, 1929). In the *elpenor* × *porcellus* cross the *X* of the former and the *Y* of the latter seem to combine to give a lethal effect in the pupal stage. Similar results were obtained by Federley (1931) in some of his *Pygaera* crosses. Thus in the cross between *P. curtula* ♂ by *P. anachoreta* ♀ the combination *XcYa* is semi-lethal and similarly in the cross between *anachoreta* and *pigra* the combination *XpYa* leads to the death of most of the female larvae.

Two explanations seem to exist for Haldane's rule. These are not alternatives, since they have both been proved to exist in concrete instances, and it is not impossible that in some cases both may co-exist in a single species cross. In the first place the *Y* of one species may be lethal or lead to sterility in the presence of the *X*, autosomes or cytoplasm of the other. This explanation will not, of course, apply to *XO* : *XX* organisms. In the second place the *X* of species A may, when present by itself, without that of species B, interact with the autosomes or cytoplasm of B in such a way as to lead to lethality, poor viability or reduced fertility.

'Haldane's rule' seems to be widely applicable in *Drosophila** and the Lepidoptera; several examples of it have also been found in tsetse fly crosses by Vanderplank (unpublished). As far as the vertebrates are concerned, the evidence is rather meagre. In birds, particularly, it is difficult to estimate the significance of the sex ratios obtained in interspecific crosses, since intersexuality and sex reversal are not uncommon, and a large number of embryos of undetermined sex usually die before hatching (see Hertwig, 1936). Nevertheless, the data of Thomas and Huxley (1927) suggest that in a number of pheasant species crosses examples of 'Haldane's rule' occur, and, in general, it seems clear that if one sex is deficient in bird species crosses it is nearly always the female. The deficiency of hen birds may, however, be due in some instances to some of them having undergone sex reversal (although Painter and Cole (1943) have shown that this is not so in the pigeon-ring dove cross, where the deficiency is due to differential mortality).

* One definite exception to Haldane's rule occurs in the *mulleri* group of *Drosophila*. When females of *D. m. mulleri* are crossed with males of certain strains of *D. aldrichi* the progeny are nearly all males, the female zygotes being mostly killed by a gene in the *aldrichi X* chromosome which acts as a semi-lethal in the hybrid, although it has no such effect in the pure species (Patterson, 1942*a*).

In mammals the sex ratio usually does not deviate far from equality in the species crosses that have been studied. Even here, however, there do not seem to be any clear exceptions to Haldane's rule (i.e. instances where the homogametic sex is lacking in the F_1).

It is unfortunate that very little reliable work has been carried out on the cytology of mammalian hybrids. In the F_1 of the cross between *Mus musculus* and *M. bactrianus* meiosis is probably normal, since the mice are fully fertile. The situation in the wolf-dog hybrids studied by Iljin (1941) seems to be essentially similar, since here also all the hybrids were fertile. In the mule sterility is almost complete, although a few fertile mule-mares have been recorded in the literature (the male mule is apparently always sterile). It is therefore probable that meiosis in the female is highly abnormal but not so drastically upset as to render impossible the production of an occasional ovum with a normal complement of chromosomes.

Among the mammalian crosses in which the F_1 males are sterile although the females are fertile we may mention that between the guinea-pig, *Cavia cobaya* and *C. rufescens*, and various crosses between ordinary cattle (*Bos taurus*) and species of *Bibos* and *Bison* (details in Hertwig, 1936).

In some instances the absence of one sex in the F_1 of an interspecific cross may be due, not to differential mortality, but to a complete sex reversal. Thus Federley (1933) found that the cross *Smerinthus populi* ♀ × *S. ocellatus* ♂ gave only male offspring. He was able to eliminate the possibility of a selective mortality, since all the larvae which died were dissected or sectioned and found to be male. Here it would appear that the *ocellatus X* chromosome is sufficiently 'strong' to overcome the female-determining genes of the *populi Y* or autosomes. Thus both X^pX^o and X^oY^p individuals are male. This situation seems to be a decidedly unusual one, although it may occur elsewhere in groups such as the cyprinodont fishes, amphibia and birds, in which complete sex reversal can be effected by an alteration in the endocrine balance of the organism.

Although we have hitherto dismissed hybridization as an effective agent in animal evolution, it is possible that even very rare acts of hybridization may play a certain part, by injecting from time to time a set of foreign chromosomes into the total 'stock' of genes possessed by a species. This type of genetic process has been called 'introgressive hybridization', and although its significance is difficult to estimate it should not be dismissed. Even if the F_1 hybrids have a fairly low viability and fertility a certain number of the foreign chromosomes or chromosome regions, broken up by repeated crossing-over, may manage to survive, thus increasing the 'reservoir' of genetic variability in the population.

It may be objected that if introgressive hybridization were at all widespread in nature there should be more evidence for it. It must be remembered, however, that the foreign genes will very soon become 'diluted', and that after repeated backcrossing their effects in the population will hardly be noticeable on a casual

examination. Thus Bytinski-Salz found that after only two generations of back-crossing the hybrid *Celerio euphorbiae* × *galii* to one or other of its parents he obtained 7 : 1 hybrids (i.e. moths with seven-eighths of their genes from one species and one-eighth from the other) which were indistinguishable from the original species (Federley, 1932).

It seems unlikely that introgressive hybridization has been of much importance in speciation, but even a very occasional act of hybridization may keep a population less homozygous than it would otherwise be, and may play a role very similar to mutation in this respect. Muller (1942) has even considered that 'leakage' of genes from one species to another may be sufficiently beneficial to be 'encouraged' by selection. In general, however, hybridization will be deleterious, reducing the fertility of the population if it occurs at all freely. Thus most mutations and genetic combinations which render an imperfect isolation mechanism more effective will have a positive selective value.

According to the modern selectionist viewpoint genetical isolation mechanisms should be weaker between forms that are geographically isolated than between those whose distribution areas are contiguous or overlap. To put the matter in a slightly different way: if two forms are geographically isolated selection will not have an opportunity to spread mutations promoting and increasing the efficiency of the isolation mechanism, and any increases in its efficiency will be merely a by-product of the general process of genetical divergence. Unfortunately this rather theoretical conclusion has only been tested by experiment in one instance. Dobzhansky and Koller (1939) found that *Drosophila pseudoobscura* showed an 'aversion' to pairing with *D. miranda*, and that this was particularly strong in strains of *pseudoobscura* collected in localities near the areas where *miranda* occurs (although there were some exceptions, such as a strain of *pseudoobscura* from Oaxaca in southern Mexico which showed a very strong degree of sexual isolation from *miranda*, although isolated geographically from the latter species by several hundred miles (other Mexican strains show a much lower degree of isolation from *miranda*). We may designate the situation just described as a *negative cline of crossability* in contrast to the positive cline which occurs in the series *D. subfunebris–D. m. limpiensis–D. m. macrospina* from California to Florida (see p. 148). The existence of both types of cline within a single genus shows the need for caution in interpreting the origin of isolating mechanisms.

If we regard genetical isolation mechanisms as built up mainly by selection we might suppose that forms inhabiting different oceanic islands or isolated mountain tops, even though distinct species by morphological criteria, might in many instances be more or less fully interfertile (or at any rate easier to hybridize than forms whose areas of distribution overlap). Whether this situation exists in fact cannot be determined until adequate experimental work has been carried out on suitable material.

CHAPTER XI

THE EVOLUTION OF THE SEX-DETERMINING MECHANISM

Several large groups of the Metazoa, such as the flatworms, oligochaetes, leeches and euthyneurous Mollusca, consist almost entirely of hermaphrodite forms. Others, such as the echinoderms, insects and vertebrates, are almost invariably bisexual. Exceptional species or genera occur in nearly all these groups, however —proving that bisexuality has arisen from hermaphroditism (and vice versa) many times in the course of evolution. Thus the flatworms of the genus *Schistosomum* (*Bilharzia*) are bisexual, while in the nereidiform polychaetes (a typically bisexual group) *Lycaestis* is hermaphrodite. In the insects only two undoubted instances of functional hermaphroditism are known, the coccid *Icerya purchasi* (see p. 275) and the flies of the family Termitoxeniidae (see p. 246).

The occasional occurrence in normally bisexual species of teratological hermaphroditism (whether genetic in origin or not) proves that all genetic systems are capable, under appropriate circumstances, of giving rise to either male or female tissues. In some groups sex appears to be very stable, at any rate in the adult stage, while in others it can more easily be changed by appropriate experimental methods. In some Mollusca, teleosts and Amphibia sex reversal is common and may occur in the normal ontogeny of some species.

Although it is reasonable to look for traces of sex chromosomes in hermaphroditic species which are closely allied to bisexual forms (and which may hence be presumed to have recently acquired unisexuality), it is quite unreasonable to expect animals such as snails, earthworms or flukes (which have doubtless been hermaphroditic for a vast period of geological history) to possess any special sex chromosomes. Clearly, in these forms the testicular and ovarian tissues of the adult (whether enclosed in separate organs or in a common gland) are produced by histological differentiation. In a snail or a leech oogonia and spermatogonia possess the same chromosome set and differ from one another in the same kind of way as say liver cells and kidney cells of the same individual. Various authors (e.g. Perrot, 1930) who have claimed at one time or another to have discovered sex chromosomes in such groups were certainly mistaken, either in their observations or in their interpretation. Careful studies (such as those of Witschi (1935) on the cirripede *Lepas*) have shown that in groups of hermaphrodite species no special sex chromosomes exist.

Even in bisexual species it is by no means certain that the sex of the individual is always under genetical control. Thus in forms like the worms *Bonellia viridis*

and *B. fuliginosa* (Baltzer, 1914, 1926, 1928; Seiler, 1927*b*; Herbst, 1928–9), the slipper-limpet, *Crepidula plana* (Gould, 1917), and the cirripede *Scalpellum scalpellum* (Callan, 1941*c*), chemical stimuli from the environment undoubtedly play a major role in determining the sex of the developing young; but even in these cases it is not certain that genetic sex-determining factors are entirely absent (Goldschmidt, 1931*b*).

In a few bisexual species of animals a method of sex determination exists which is almost certainly not chromosomal, although its basis is unknown. Thus in the small marine worm *Dinophilus* the females produce two kinds of eggs, large and small. The former develop into females, the latter into males (Shearer, 1912; Nachtsheim, 1914; de Beauchamp, 1910). The difference between the two kinds of eggs is present long before meiosis, so that it can hardly be genetic in origin. No sex chromosomes are known to exist, so that sex determination in *Dinophilus* apparently depends upon the quantity of egg cytoplasm available for the development of the embryo. Possibly at some stage in the development of the *Dinophilus* ovary a division occurs in which the cytoplasm is unequally divided between two oogonial nuclei.

Apart from exceptions such as these, most bisexual animals undoubtedly possess a genetical sex-determining mechanism of one kind or another. In many groups, however, the sex chromosomes have not been definitely identified, either because the attempt has not yet been made, or because they are not visibly different from one another or from the other chromosomes.

Usually the genetical sex mechanism consists of a pair of chromosomes which may be regarded as having become specialized in the course of their evolution in accordance with their peculiar function. In one sex the members of the pair are identical and homologous throughout their whole length (*X* chromosomes), while in the other they are not homologous, or only partly so (*X* and *Y* chromosomes). The sex which is *XX* is said to be *homogametic*, since it produces only one kind of gametes, while the one which is *XY* is said to be *heterogametic*, producing two kinds of gametes in equal numbers. Thus the *X* chromosome is represented in both sexes, while the *Y* is present in one only. In a number of species the *Y* is absent altogether (having presumably been lost in the course of evolution); in these cases the diploid number in the heterogametic sex is an odd one. We can thus distinguish between an $XY : XX$ type of mechanism and an $XO : XX$ one, the *O* indicating merely the absence of a *Y*. In addition to these simple types there are a number of more complex sex-determining systems, in which more than one pair of chromosomes is involved, so that there are several kinds of *X*'s or *Y*'s. Even in these instances, however, one sex is always heterogametic, the other homogametic, so that the general principle of the mechanism is the same.

In most groups of animals it is the male sex which is heterogametic, so that there are two kinds of sperms, but only one kind of egg. In the Lepidoptera,

Trichoptera, reptiles* and birds and in some fishes and Amphibia, however, the situation is reversed (Klingstedt, 1931; Makino and Kichijo, 1934; Seiler, 1920; Sokolow and Trofimow, 1933; Oguma, 1934, 1937*a*, *b*, 1938). In these groups the *X* chromosomes must be preponderantly male-determining, instead of female-determining, as they are in animals with male heterogamety (some authors use the terminology *ZW* : *ZZ* in the case of female heterogamety, to indicate that the functions of the sex chromosomes are reversed). It is worth noting that the Trichoptera and Lepidoptera are universally regarded as very closely allied orders, while it is generally believed that the birds are descended from Mesozoic reptiles—so it would seem that female heterogamety must have arisen once in the phylogeny of the insects and once in that of the amniota, being on both occasions transmitted to a whole branch of the evolutionary tree.† In a few other groups, such as the Opilionids, Phalangids and scorpions (Sokolow, 1913, 1929*a*, *b*; Wilson, 1931; Sato, 1936, 1940; Piza, 1939*a*, *b*; Tomohiro, 1940), careful work on the chromosomes of the males has failed to demonstrate any heterogamety in that sex. While it would be premature to conclude that these groups must necessarily possess female heterogamety there is clearly reason to suspect its existence.

In general it may be said that the *X* and *Y* chromosomes are subject to all the usual 'laws' of chromosomal evolution, and also to a number of special principles which depend on the fact that the *Y* is always present in the haploid condition and is confined to one sex, while the *X* is haploid in one sex and diploid in the other. This peculiar situation imposes certain special restrictions upon the evolution of the *X* and *Y*, since many types of structural change will, if they involve the sex chromosomes, upset the genetic equilibrium upon which sex determination depends.

If the *X* and *Y* have arisen from a pair of autosomes by a process of evolutionary divergence we should expect that in the more primitive types of sex mechanism they should differ very slightly, while in the more advanced types the differences should be much greater. As an example of a species with a very 'primitive' type of sex-chromosome mechanism we may take the fish *Lebistes*. Here the genetical evidence indicates that the male is heterogametic, but the *X* and *Y* are not distinguishable from one another cytologically (Vaupel, 1929), and a considerable amount of crossing-over takes place between them (Winge,

* The statement that reptiles show female heterogamety rests upon the observations of Oguma, who examined embryonic mitoses of *Lacerta vivipara* and the chelonian *Amyda japonica*, In both species Oguma claims that the female somatic number is one less than that of the male, thus suggesting the presence of an *XO* : *XX* mechanism; but since the somatic chromosome numbers are relatively high (35 and 63 respectively), it would seem desirable that this work should be independently confirmed before a definite conclusion is drawn. It is at any rate certain that there is no obvious male heterogamety in reptiles, so that female heterogamety is not unlikely. Matthey (1943) in a brief abstract has cast some doubt on the existence of cytologically distinguishable sex chromosomes in reptiles.

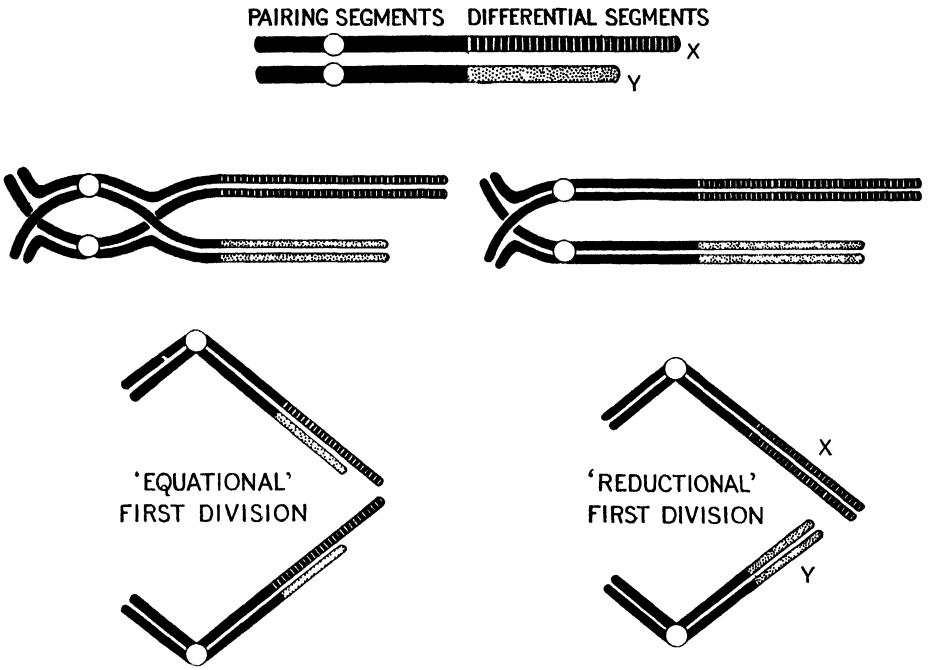
† It is not known whether the male or the female is heterogametic in the Monotremes.

1923, 1932). In this species it would seem that the *X* and *Y* are homologous for most of their length, the differential region—upon the existence of which sex determination depends—being quite short (possibly it is actually a single gene). Winge was able, by selection, to obtain a stock of *Lebistes*, all the individuals of which were *XX*, but in which an autosomal pair of genes had come to control sex determination. This stock showed female heterogamety, the newly arisen mechanism giving femaleness when heterozygous. This experiment of Winge's illustrates the extreme instability of the sex mechanism in these fishes, and enables one to understand how an evolutionary change-over from male to female heterogamety could occur in a group where the sex-chromosome mechanism is still of a very primitive type. That changes of this kind have actually occurred in the evolution of the teleost fishes is shown by the work of Bellamy (1936), who found that in the related genus *Platypoecilus* one species had male heterogamety, while in another the female was the heterogametic sex. It seems probable that in most fishes and Amphibia the *X* and *Y* chromosomes are as little differentiated from autosomes as they are in *Lebistes*; it is only when we come to the higher Vertebrata (birds, mammals and possibly reptiles) that definite sex chromosomes can be studied cytologically. No sex chromosomes seem to be recognizable in the males of the elasmobranch fishes (Matthey, 1937; Makino, 1937) or in various other teleosts (Makino, 1934*a*; Prokofieva, 1934), while the work of Makino (1932*b*) and Saez, Rojas and de Robertis (1935, 1936) suggests that earlier accounts of morphologically distinct *X* and *Y* chromosomes in the Anura (e.g. those of Witschi, 1924, 1933) were probably erroneous.

In the Urodeles, although no sex chromosomes can be distinguished cytologically, the work of Humphrey (1942) demonstrates that in the axolotl the female is the heterogametic sex. He performed the interesting experiment of mating a female which had been experimentally changed into a male with a normal female. The offspring consisted of 74% females and 26% males. Humphrey explains this result by supposing that the females have the constitution *XY* so that a mating of *XY* (sex-reversed female) by *XY* (normal female) gives 1 *XX*: 2 *XY*: 1 *YY* (i.e. one quarter males if *YY* individuals are viable and female). The existence of *YY* females in the F_1 (indistinguishable in appearance from normal *XY* females) was confirmed by rearing a second generation (six out of 16 F_1 females gave only female offspring). The fact that *YY* axolotls are both viable and female suggests that sex determination does not depend on an *X* : autosome balance as in *Drosophila* but on the presence or absence of a *Y* as in the plant *Melandrium*. Whether the *X* and *Y* in the axolotl differ in a single gene or in a short differential region is not yet known.

In the more advanced kinds of *X* and *Y* chromosomes the differential segments are often long and conspicuous. Thus, from the *Lebistes* stage onwards, the evolution of the sex chromosomes may be looked upon as a progressive increase in the length of the differential segment at the expense of the homologous one.

At meiosis in the heterogametic sex the homologous region, when present, behaves as a *pairing segment*, so that the X and Y come to constitute a sex bivalent in which the two chromosomes are held together by chiasmata. The behaviour of this bivalent is not essentially different from that of the unequal



Text-fig. 97. Diagrams of 'equational' and 'reductional' XY sex bivalents in a mammal such as the rat.

autosomal bivalents described in a previous chapter (see p. 107). The unequal (differential) regions segregate from one another at either the first or the second meiotic division, according to the position of the chiasma or chiasmata. Each gamete thus receives an X-differential segment or a Y-differential segment. Where the heterogametic sex is XO the X behaves like other univalents, dividing in one division (usually the second) but not in the other, so that half the gametes receive an X while the other half lack one. An important difference between the differential segments of the X and Y is that the former can cross-over in the homogametic sex whereas the latter can never undergo crossing-over.

It will be realized that it is only the presence of a region which is common to both X and Y that enables a sex bivalent to be formed. The pairing segment thus performs an important mechanical function, ensuring that the differential segments are distributed correctly in the meiotic divisions. In certain groups

such as the Heteroptera and the Neuroptera, however, the segregation of the sex chromosomes appears to be controlled by special mechanisms of a different type, and in these groups the *X* and *Y* seem to lack pairing segments altogether, although this does not necessarily mean that they contain no homologous regions.

It should be pointed out that the degree of specialization of the *X* and *Y* chromosomes, and the extent of their differential segments do not seem to bear any direct relationship to the degree of development of secondary sexual characters. Sexual dimorphism is, in fact, rather pronounced in *Lebistes*, with its very primitive sex-chromosome mechanism.

Where the *X* and *Y* chromosomes differ in size the *Y* is nearly always the smaller. Its differential segment is probably always inert, and hence tends to become reduced through successive deletions of short regions. The differential segment of the *X* will not undergo this reduction in length, since it is this region which controls the whole process of sex determination.

In most of the more 'advanced' types of sex mechanism the *X* and *Y* are partially or entirely heterochromatic. Thus in *Drosophila melanogaster* the *Y* is wholly composed of heterochromatin, while the *X* has its proximal 2/5 heterochromatic (there are also smaller intercalary heterochromatic segments in the distal part of the *X*). In the *XO* Orthoptera the *X* always seems to be heterochromatic throughout its entire length, although there may be regional differences in the degree of heteropycnosis (Text-fig. 5). In the course of their evolution the 'advanced' kinds of sex chromosomes have, in all probability, gradually lost their original genetic functions, becoming more and more inert, except so far as sex determination is concerned. Thus no sex-linked mutants were found by Nabours (1929) in the Tettigidae or by Sansome and La Cour (1935) in the grasshopper *Chorthippus*. In the early days of animal cytology there was some controversy as to whether the *X* and *Y* were to be regarded as true chromosomes or not (Mohr, 1915). Although this question has long been settled in the affirmative we must admit that in some groups the sex chromosomes probably play little part in the genetical control of the morphogenetic processes except to switch them on to the male or the female track. It happens that two of the animals which have been studied most intensively from the genetic point of view (*Drosophila* and the fowl) both possess a long active (and euchromatic) differential segment in the *X*. But it is probable that they are somewhat unusual in this respect—indeed, if all heterochromatic regions are inert many groups of animals possessing highly evolved sex chromosomes must lack 'sex-linked' genes almost completely. In rodents, on which a large amount of genetical work has been carried out, not a single sex-linked gene has been discovered up till now with certainty, though one has been postulated as a controller of tumour-transplantability, although it is known that there is a large, although heterochromatic, differential segment in the *X* of many species. The existence of a large group of sex-linked genes must be regarded as a special kind of genetical

adaptation—they are in a particular relationship to the rest of the gene-complex, since they produce the same effect in both sexes although represented twice in the female and only once in the male.

TABLE 10. *Behaviour of the XY bivalent at meiosis in the Mammalia*

Species	Reductional %	Equational %	Author
Man	80–90	10–20	Koller, 1937
Rat	90	10	Koller and Darlington, 1934
Golden hamster	81·6	18·4	Koller, 1938
Grey squirrel	100	—	Koller, 1936*b*
Apodemus sylvaticus	8	92	Koller, 1941*a*
	20	80	Matthey, 1938
A. hebridensis	—	100	Koller, 1941*a*
A. agrarius	—	100	Matthey, 1938
Arvicola scherman	50	50	Matthey, 1938
Mole	100	—	Koller, 1936*c*
Ferret	68	32	Koller, 1936*c*
Sheep	30	70	Ahmed, 1940
Cat	100	—	Koller, 1941*b*

A considerable amount of discussion has taken place as to the exact way in which the differential regions influence the determination of sex. Except for the axolotl, no animal is known in which the *Y* plays any considerable part in the process (although this is the position in some dioecious plants such as *Melandrium*). In *Drosophila*, as we have already seen, the *Y* exerts an influence upon the sperm, but it cannot be regarded as a sex-determiner in the ordinary sense. It is, of course, not impossible that in some animals the *Y* may play a much more important role.

Theoretically, sex might be determined (1) by the absolute number of *X* chromosomes (or, rather, *X*-differential segments) in the zygote, (2) by the ratio between the number of *X*'s and the number of autosomes, or (3) by some kind of algebraic difference between the number of *X*'s and the number of autosomes. In *Drosophila*, at any rate, the second possibility seems to be the nearest to the truth. The work of Bridges (1925*a*, 1932) has shown very clearly that the autosomes are preponderantly male-determining, the *X* female-determining, and that the sex of the zygote depends upon the ratio between the two. Bridges found that artificially produced triploid flies which possessed three sets of autosomes but only two *X*'s were intersexual. Since normal females have two *X*'s the extra set of autosomes must have shifted the balance in the male direction. It is known that true diploid, triploid and tetraploid flies (having the constitutions $2A2X$, $3A3X$ and $4A4X$, whose *A* represents a haploid set of autosomes) are all females; no haploid *Drosophila* ($1A1X$) has ever been produced, but haploid patches of tissue in otherwise diploid flies are female in type (Bridges, 1925*b*, 1930; McKnight, 1937). The ratios $1A:1X$, $2A:2X$, $3A:3X$, $4A:4X$ are of

course all the same while the algebraic differences ($1A-1X$, $2A-2X$, etc.) are different. Flies of the composition $2A3X$ and $3A1X$ have also been produced experimentally. Theoretically, these should be 'super-females' and 'super-males'. In fact they are sterile flies which are relatively inviable but resemble normal females and males fairly closely. It would seem, therefore, as if maleness and femaleness represent two alternative conditions which may be attained but not surpassed. Unfortunately no data on the effects of different $X:A$ ratios exist for other animals. In the Urodeles where, apart from the axolotl, it is not known which sex is heterogametic, Fankhauser (1937) obtained a haploid newt that was apparently female, while triploids may be of either sex (Fankhauser, 1938; Böök, 1940).

A number of mutations are known in *Drosophila* which affect the development of the reproductive system, but it is doubtful how far the wild-type allelomorphs of these should be regarded as sex genes in the ordinary sense. In *Drosophila virilis* (Lebedeff, 1938), *D. simulans* (Sturtevant, 1921*a*) and *D. pseudoobscura* (Dobzhansky and Spassky, 1941) autosomal genes are known which produce intersexual types. In *D. virilis* $2X3A$ individuals are males or females according to whether the IIIrd chromosome gene *ix* is homozygous or heterozygous.

These facts might seem to suggest that perhaps the normal sex determination in *Drosophila* depends on a single gene pair or at any rate on the action of relatively few genes. This is not the case, however. Various authors (Dobzhansky and Schultz, 1931, 1934; Patterson, Stone and Bedichek, 1937; Bedichek-Pipkin, 1940) have studied $2X3A$ intersexes in which certain regions of the X were present only once or in triplicate (due to deficiencies or duplications). They found that all regions of the X were female-determining, so that any extra fragment shifted the intersexuality away from maleness, the extent of the shift being roughly proportional to its length. This result suggests two alternative possibilities: (1) that the number of sex genes in the X is fairly large and that they are distributed along its whole length, no single one of them being much more powerful than the others, or (2) that the female-determining powers of the X depend on some general quality of its protein framework rather than on any specific genes at all. As changes in gene-order within the X do not influence sex, this hypothesis seems rather improbable.

As far as the autosomes are concerned, it seems probable that chromosomes II and III, at any rate, contain male-determining genes. But it must be admitted that, apart from the data in Table 11, there is no very definite evidence for the existence of such genes, and certainly no information is available as to their number or distribution in the autosomes.

In the gypsy moth, *Lymantria dispar*, Goldschmidt (1931*a*, *b*, 1932, 1934) has carried out a large number of interracial crosses with a view to elucidating the genetical mechanism of sex determination. *Lymantria* is, of course, heterogametic in the female sex, so that the X is a male-determining chromosome. The

genetical evidence suggests that the female-determining factors are carried either in the *Y* or in the cytoplasm.

The importance of *Lymantria* lies in the fact that the potency of the sex genes in the *X* differs in the numerous geographical races into which the species can be subdivided. Since sexual dimorphism is very pronounced in *Lymantria* the material was obviously well suited for an analysis of sex determination.

Goldschmidt designates an individual as 'weak' if its *X* bears sex genes of low potency, 'strong' moths being those in which the *X* is very actively male-determining. It is not clear whether the *X* contains a single gene exhibiting multiple allelomorphism or a system of polygenes, as in *Drosophila*.

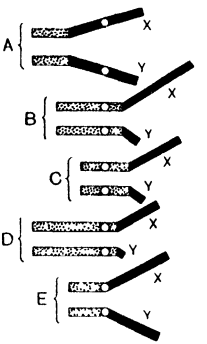
The species is distributed over the whole of the Palaearctic region from Europe to Japan. Most of the European races and those from the island of Hokkaido are 'weak', while those from the southern island of Japan are 'medium' or 'strong'. In pure-bred races the male- and female-determining factors are in equilibrium, so that no intersexes are produced, but in interracial crosses the balance may be upset. Thus when 'weak' females of one race are crossed with 'strong' males of another the F_1 generation consists of males and intersexes, the latter being *XY* individuals whose *X* is too strong for the female-determining factors they have inherited from their mother. Conversely, crosses between strong females and weak males give rise to *XX* intersexes in the F_2 generation. All degrees of intersexuality may be obtained by using parents of the appropriate 'strength'. Individuals which are only slightly intersexual are fertile, but the more completely intermediate ones are sterile.

Goldschmidt was able to distinguish as many as eight different races from different parts of Japan which could be arranged in a series, according to the 'strength' of the *X*. The difference between the end-members of the series was so great that when females of the weakest race were crossed with males of the strongest one the offspring were all completely male in appearance, although half of them were *XY* and half *XX*. The 'weakest' subspecies, *hokkaidoensis*, is so clearly cut off from the other races that it might almost be considered a distinct species.

The significance of the *Lymantria* work for the general theory of sex determination has been frequently discussed. Its significance from the evolutionary point of view is, however, by no means clear. Why, after all, should the strength of sex-determining genes be in an active state of evolution in a particular species? It is possible that the whole gene-complex of *Lymantria* has differentiated into a number of geographical races, and that the sex genes should be regarded merely as part of a much larger system of balanced relationships which must evolve in harmony with the whole if they are to continue to produce effective and fertile individuals of both sexes. Goldschmidt himself regards the sex genes of *Lymantria* as controlling the *rate* of sexual differentiation, but his views have been severely criticized by Newby (1942).

In the species of the genus *Drosophila* nearly the whole of the *X* forms a differential segment, the pairing segment being a very short region adjacent to the centromere. Thus in this genus metacentric *X*'s and *Y*'s contain two differential segments separated by a pairing segment, while acrocentric ones only have a single differential segment. The behaviour of the *XY* bivalent at meiosis has already been discussed (p. 189).

In mammals the pairing segments of the sex chromosomes are usually much longer than in *Drosophila*, so that the interpretation of the meiotic behaviour is easier. The *X* always has a relatively long differential segment, but that of the *Y* is often very short, so that in some species it is not certain whether it occurs at all. In the marsupials (Koller, 1936*a*) the centromeres of the *X* and *Y* appear to lie in the differential segments, while in the Eutheria, on the other hand (Koller and Darlington, 1934; Koller, 1936*c*, *d*, 1937, 1938, 1941*a*) they lie in the pairing segments or so near the point of junction between the pairing and differential regions that one cannot be sure which they lie in (Text-fig. 98). In man the differential segment of the *Y* may be absent altogether—more probably it is merely very small. In the grey squirrel, on the other hand, the *Y* has a very long differential region. In the marsupial *Trichosurus*, Koller (1936*a*) has claimed that there are two differential segments in both *X* and *Y*, separated by the pairing segment—but this would appear to require confirmation. He likewise (1941*b*) claims that in the cat there are two terminal pairing segments: if true, this is a point of difference from all other eutherian mammals hitherto investigated.



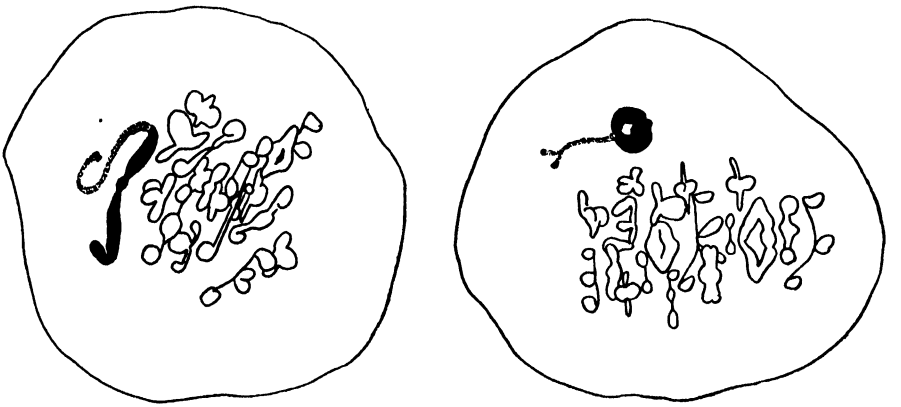
Text-fig. 98. Diagrams of the sex-chromosome pair in various mammals. Based mainly on the work of Koller (1936*b*, *c*, 1937, 1938, 1941*b*). Pairing regions stippled, differential ones black. A = marsupials; B = man, rat; C = ferret; D = golden hamster; E = squirrel, *Sciurus carolinensis*.

Very frequently the differential segments of mammalian sex chromosomes are heteropycnotic at meiosis (Text-fig. 99), thus suggesting that they may be largely inert. This conclusion is supported by the failure of geneticists to find any sex-linked genes in rodents. In man, on the other hand, a number of sex-linked genes (such as those for haemophilia and colour-blindness) are known to exist—they must lie in the differential segment of the *X*.*

The pairing segments in mammals seem to be usually euchromatic, and there is evidence that in man they contain a number of active genes (Haldane, 1936).

* Snyder (1941) mentions four hereditary conditions in man which he suggests may have been due to mutations in the differential region of the *Y*. But since three of these have only arisen once (i.e. only one pedigree is known) they may very likely have been due to translocations in which the *Y* was involved. Alternatively, they may have been due to dominant mutations in the pairing segment of the *Y*, situated so that crossing-over only rarely occurred between them and the differential segment.

On the other hand, Pontecorvo (1943) is of the opinion that in some mammals the pairing segments are heterochromatic, although their cycle of heteropycnosis is not the same as that of the differential regions. The genetical behaviour of a gene located in the pairing segment will depend on the amount of crossing-over which takes place between it and the differential region. Such genes may be described as partially sex-linked, to distinguish them from the totally sex-linked



a *b*

Text-fig. 99. First metaphases in the golden hamster, *Cricetus auratus*. *a* = a cell with a 'reductional' *XY* bivalent; *b* = a cell with an 'equational' sex bivalent. From Koller (1938).

genes which lie in the differential segment of the *X*. Haldane has shown that a number of human genes exhibit partial sex-linkage, and may consequently be assumed to lie in the pairing segment, which is common to both *X* and *Y*. *Achromatopsia* (recessive) lies less than 10 cross-over units from the differential segment and consequently shows a fairly high degree of sex-linkage; *retinitis pigmentosa* is situated about 30 units away and shows much more incomplete sex-linkage. It is possible that a number of other genes at present regarded as autosomal actually lie in the pairing segment of the *X* and *Y*, but are situated more than 50 units away from the differential segments.

The number of chiasmata formed in the pairing segment in mammals is usually one or two. In man, the rat, the golden hamster (*Cricetus auratus*) and the ferret (all of which have the centromeres in the pairing region), a chiasma is sometimes formed between the centromeres and the differential regions. If this happens we get an 'equational' sex bivalent, and the differential segments do not segregate from one another until the second division. If no chiasma is formed in this situation a 'reductional' sex bivalent is formed, and the differential regions segregate at the first division (Text-fig. 97). Failure to realize that two different types of *XY* bivalent may exist in different cells of the same individual has led to a great deal of confusion in the literature on mammalian sex chromosomes.

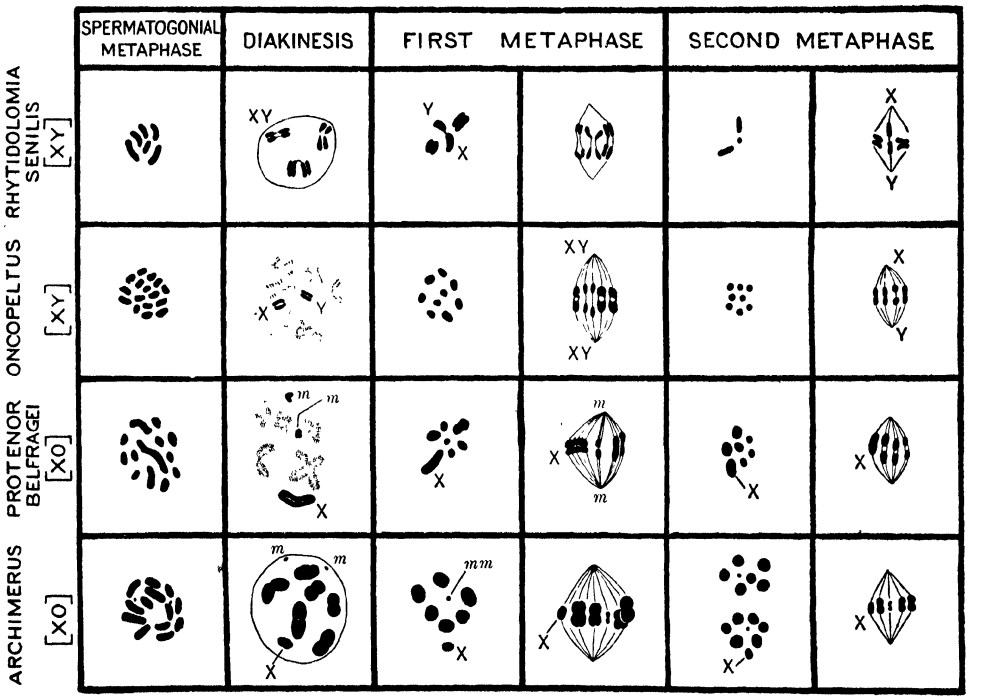
Oguma (1937*c*, *d*) has claimed that some mammals (including man) are *XO* in the male sex, but his opinion is not shared by other workers in this field. Matthey has recently (1938) disputed Koller and Darlington's account of the sex chromosomes in the rat; he believes that both *X* and *Y* are acrocentric in this animal—but his evidence does not seem very convincing. In spite of these disagreements it is fairly clear that all the eutherian mammals have the same general type of sex-chromosome mechanism. The differences between allied species seem to reside mainly in the relative lengths of the pairing and differential segments, and in the position of the centromere. Thus in the field-mouse, *Apodemus sylvaticus*, the sex bivalent is reductional in about 8% of the cells, while in the related species *A. hebridensis* and *A. agrarius* it is said to be always equational (Koller, 1941*a*; Matthey, 1938). The centromere is presumably near the junction of the pairing and differential regions in the first species, farther away from the differential regions in the others. It is not clear, however, whether a homosomal or a heterosomal rearrangement has caused the difference.

In Table 10 the data of various authorities on the relative frequencies of 'reductional' and 'equational' sex bivalents in several species of mammals are gathered together. It will be noted that in the mole and the grey squirrel no 'equational' bivalents are formed; Koller has interpreted this as indicating that in these species the centromere lies at the junction of the pairing and differential segments, so that no chiasma can be formed between the centromere and the differential region. In the sheep (Ahmed, 1940) the pairing segment of the *X* and *Y* is relatively very long, since as many as three chiasmata may be formed in it.

In the more primitive *XY* : *XX* mechanisms which we have been discussing a pairing segment is always present, and the segregation of the differential regions to opposite poles at meiosis depends on chiasma formation in this segment. This appears to be the case in all the Mammalia, the Diptera and in a number of other groups. In several orders of insects, however, no chiasmata are ever formed between the *X* and *Y* chromosomes. This is notably so in the Heteroptera and in the Neuropteroid groups (Planipennia, Rhaphidioidea and Sialoidea); and the same is possibly also true of the Dermaptera (Callan, 1941*b*).

All the species of Neuroptera which have been studied cytologically have an *XY* : *XX* sex-chromosome mechanism (except *Ascalaphus libelluloides*, which we shall consider later). A large number of species, belonging to all three subgroups, have been investigated by Naville and de Beaumont (1933, 1936), Itoh (1933*a*, *b*), Katayama (1939*a*), Kichijo (1934), Asana and Kichijo (1936), Klingstedt (1934, 1937*b*) and Oguma and Asana (1932), so that it is quite possible that no *XO* : *XX* species occur in this group. The general course of meiosis seems to be the same in all the Neuroptera. The *X* and *Y* chromosomes do not appear to undergo any pairing process during the prophase of meiosis; when the spindle forms, at first metaphase, they become associated with it, one near one pole,

one near the other. At anaphase they pass to opposite poles. This type of behaviour has been called distance pairing, but the word 'pairing' seems rather inappropriate to describe the process, since the *X* and *Y* never come near one another. The very regular behaviour of the sex chromosomes during the period



Text-fig. 100. Main stages of meiosis in four representative members of the order Heteroptera. In all except *Archimerus* the segregation of the sex chromosomes takes place at the second division, all the second metaphases being of the same type. In *Archimerus* there are two types of second metaphases, with and without an *X* chromosome. *Protenor* and *Archimerus* belong to the family Coreidae, and have *m* chromosomes (large in *Protenor*, very small in *Archimerus*). The *X* and *Y* form a bivalent in *Rhytidolomia*, but not in *Oncopeltus*. Figures from Wilson (1905*b*, 1912) and Schrader (1940*a*), but redrawn and modified.

of spindle formation is clearly a specialized and adaptive character which is peculiar to this group of insects. It ensures that the *X* and *Y* must pass to opposite poles, even though no sex bivalent is formed.* In the females it has been shown by Naville and de Beaumont (1933) that the two *X*'s form a true bivalent, being united by a chiasma (Text-fig. 101).

* Klingstedt (1937*b*) claims that in *Sisyra* (and possibly also in the Sialoidea) there is no distance pairing between the *X* and *Y*. His figures certainly suggest that the two chromosomes are much closer together at metaphase than in other Neuroptera, but it is not clear whether they form a true bivalent or not.

In the Heteroptera both *XY* and *XO* species occur, and in a number of families (particularly the Reduviidae, Cimicidae and Nepidae) there are complex mechanisms involving several kinds of *X*'s. As in the Neuroptera there are no pairing segments, so that the *X* and *Y* cannot form a true sex bivalent. The other peculiar feature of these heteropteran sex chromosomes is that they segregate from one another at the second instead of at the first meiotic division, as in most other groups (a few species which are exceptions to this rule will be discussed later). In some Heteroptera no pairing of the *X* and *Y* takes place during the prophase of meiosis; in others a temporary pairing occurs, but it evidently does not involve chiasma formation, since the two chromosomes nearly always separate after diakinesis, so that they form two entirely independent univalents at the first metaphase. Only in some pentatomids, such as *Rhytidolomia senilis* (Wilson, 1913; Schrader, 1940*a*, *b*), does the association between the *X* and *Y* persist throughout the first metaphase; but in this case an autosome may have been translocated to the *XY* pair so that it now forms a euchromatic pairing segment (see p. 175). In all Heteroptera the sex chromosomes are heteropycnotic throughout the prophase of meiosis, and they frequently have large nucleoli associated with them. At the anaphase of the first division a half of each sex chromosome passes to either pole. Thus all the second spermatocytes contain the same chromosome number, a haploid set of autosomes together with an *X* and a *Y*. In the second division the *X* and *Y* arrange themselves in an axial direction on the spindle, one above the other when the spindle is viewed from the side. They are closely associated at this stage, but there are, of course, no chiasmata between them: they may be said to form a 'pseudo-bivalent'. When the anaphase separation occurs the two chromosomes of the pseudo-bivalent pass to opposite poles.

The course of events in the *XO* species of Heteroptera is fundamentally similar: the single *X* chromosome divides in the first division and segregates to one pole in the second. The details have been studied in a number of genera (*Anasa*, *Protenor*, *Alydus*, *Pyrrhocoris*) by Wilson (1905*a*, *b*, 1906, 1907, 1909*a*, *b* and *c*, 1912). A few *XO* : *XX* species of Coreidae such as *Archimerus calcarator* (Wilson, 1905*a*, *b*, 1909*a*) and *Pachylis gigas* (Schrader, 1932) seem, however, to have reverted to the 'usual' type of behaviour in which the *X* passes undivided to one pole in the first division.

The Heteroptera are one of those groups in which it has not yet been possible to see centromeres, and in view of the work of Hughes-Schrader and Ris (1941) one may even doubt whether individualized centromeres exist in this group at all. The behaviour of the sex chromosomes at meiosis in the male Heteroptera implies that if centromeres are present they divide in the first division but not in the second one (whereas those of the autosomes do the reverse). It is, of course, possible that the anomalous behaviour of the *X* and *Y* depends solely on the fact that these chromosomes are univalents in the first division.

In the Coreidae, however, the *m* chromosomes (see p. 187) are unpaired at diakinesis and come together at prometaphase to form a pseudo-bivalent; but they subsequently behave like the other autosomes and not like the *X* and *Y*. It would seem, therefore, that there is a real difference between the division mechanism of the autosomes and that of the sex chromosomes in the Heteroptera. Meiosis has not been thoroughly studied in the females, but it is probable that the two *X* chromosomes form a true bivalent and that they divide at the same time as the autosomes.

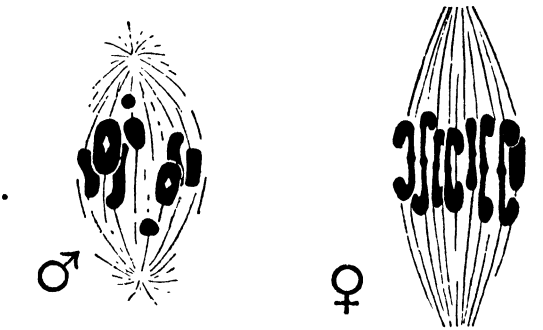
We have already mentioned several species of Heteroptera in which the behaviour of the sex chromosomes has reverted to the normal type. An even more interesting instance of reversion has occurred in an undetermined species (or subspecies) of *Lethocerus* (family Belostomatidae) from Michigan (Chickering, 1932; Chickering and Bacorn, 1933). Whereas *L. americanus* has three pairs of autosomes, together with a small *X* and *Y* which behave in the usual heteropteran manner at meiosis, the undetermined species has only two pairs of chromosomes, there being no trace of the *X* and *Y*. At meiosis two true bivalents are formed, the chromosomes being held together by chiasmata. Chickering and Bacorn suppose that the *X* and *Y* have been incorporated in one of the autosomal pairs, the other pair representing two of the pairs seen in *L. americanus* fused together. If this is so it presumably resulted from two successive translocations, one involving the *X*, the other the *Y*. The only possible alternative to this interpretation would be that the *X* and *Y* had really been lost from the chromosome set, the function of sex determination having been taken over by one of the autosomes.

In the Homoptera nearly all the species of the suborder Auchenorhyncha are *XO* in the males (Boring, 1907, 1913*a*; Boring and Fogler, 1915); the *X* behaves at meiosis in a 'normal' way, dividing in the second division. Some of the species of *Aphrophora* and *Enchenopa* are *XY* (Misra, 1937*a*; Kornhauser, 1914), but it is not clear if these are instances of recent reversion from *XO* systems or not. The *X* and *Y* pair in the first division and segregate from one another at the first anaphase in the usual way. In the suborder Sternorhyncha the bisexual species of aphids and scale insects all seem to be *XO* in the males, with the exception of those forms which have haploid males (see p. 275) and some of the more specialized coccids which appear to have lost their sex chromosomes altogether (see p. 198). In the three genera of coccids which are known to be *XO* (*Llaveia*, *Llaveiella* and *Protortonia*) the *X* divides in the first division, i.e. it behaves 'anomalously' (see p. 196). This is the reverse of what happens in the aphids, where the *X* passes undivided to one pole at the first division.

In the dragonflies (Odonata) all the species which have been studied up till now are *XO* : *XX* (E. A. Smith, 1916; Oksala, 1939; Oguma, 1930; Oguma and Asana, 1932; Asana and Makino, 1935; Kichijo, 1939; Makalowskaia, 1940).

As in the Heteroptera the X behaves in the 'anomalous' manner in the meiosis of the male, dividing in the first division, but not in the second.

It would seem, therefore, that the 'anomalous' type of behaviour has arisen independently in the sex chromosomes of several orders of Insects. In the Coleoptera it is only known in the fireflies of the genus *Photinus* (Stevens, 1909). Outside the Insecta this type of behaviour is not known at all.



Text-fig. 101. First metaphases in the two sexes of the neuropteran *Macronemurus appendiculatus*. X and Y chromosomes lying unpaired on opposite sides of the equatorial plane in the male. In the female (which seems to have a lower chiasma-frequency) the two X's form a bivalent which cannot be distinguished from the autosomal ones. From Naville and de Beaumont (1933).

In the earwigs (Dermaptera) some of the species are $XY : XX$, while others have a complex sex-determining mechanism; in the common European species *Forficula auricularia* both mechanisms are present, in different individuals of the same natural populations (see p. 260). According to Callan (1941*b*) no chiasmata are formed between the sex chromosomes: a pseudo-bivalent (or pseudo-trivalent) is formed at the first division and the segregation is of the 'normal' type, i.e. the centromeres of the sex chromosomes divide at the second division and not at the first. It is possible that such a mechanism (absence of chiasma formation, formation of a pseudo-bivalent, normal segregation) exists in other orders of insects; but the sex chromosomes of the Coleoptera, Plecoptera and Ephemeroptera have not been studied critically by modern workers; the figures of Nowlin (1906), Stevens (1905*a*, 1906*a*, 1908*b*, 1909), Brauer, 1928, Minouchi (1935), Nakahara (1919), and Katayama (1939*b*) merely show that in those species of these orders which do possess a Y chromosome (many Coleoptera are XO) a sex bivalent is formed—it is not possible to be sure that a true pairing segment exists.*

* The nature of the sex-determining mechanism in other orders of insects is still rather uncertain. One species of psocid is known to be XO in the male (Boring, 1913*b*). In the Mecoptera only the genus *Panorpa* has been studied—four species are all XO (Naville and de Beaumont, 1934). The strepsipteron *Achroschismus* was studied in detail by Hughes-Schrader (1925*a*) who established the existence of an XY pair in the male—her figures do not enable one

We may thus conclude that in at least four orders of insects (Neuroptera, Heteroptera, Odonata and Dermaptera), and possibly in others as well, special sex-chromosome mechanisms have been evolved at some remote period from the more primitive mechanism where there is a pairing segment, common to both *X* and *Y*, in which chiasmata can be formed. It is interesting to note that all these four orders are relatively ancient ones which are known or inferred to have existed since Palaeozoic times. The Diptera, on the other hand, are a more modern group, not known to have been in existence before the Jurassic; yet they have much more primitive sex-chromosome mechanisms.

TABLE 11. *Sex determination in* Drosophila melanogaster

No. of *X* chromosomes and sets of autosomes present		Ratio *X* : *A*	Type
3 *X*	2 *A*	1·5	Super-female
4 *X*	3 *A*	1·25	,,
4 *X*	4 *A*	1·0	Tetraploid female
3 *X*	3 *A*	1·0	Triploid female
2 *X*	2 *A*	1·0	Diploid female
3 *X*	4 *A*	0·75	Intersex
2 *X*	3 *A*	0·67	,,
1 *X*	2 *A*	0·5	Diploid male
1 *X*	3 *A*	0·33	Super-male

It is very difficult at present to place the different types of sex chromosomes met with in the Diptera into an evolutionary series. In the Nematocera (the more primitive section of the order, in which the antennae are long and filamentous) the very existence of sex chromosomes has never been definitely established except in *Sciara*, whose sex-determining mechanism is so unusual that its *X* is almost certainly a new formation, unrelated to the sex chromosomes of other Diptera. Thus in the mosquitoes (family Culicidae) the various species of *Culex* and *Anopheles* all have three pairs of long metacentric chromosomes (Stevens, 1911; Whiting, 1917; Moffett, 1936). Possibly one of these contains a differential segment which is very difficult to demonstrate cytologically. (Stevens thought that she had detected such a segment in *Anopheles*, but Whiting was unable to find one in *Culex*.) In a more recent investigation Moffett showed that in *C. pipiens* three bivalents are formed at meiosis in the male, and that all of these may be ring-shaped in some cells (unlike the bivalents of *Drosophila* and the 'higher' Diptera, they show definite chiasmata). The fact that chiasmata

to decide as to the nature of the sex bivalent which is formed. No cytological work appears to have been carried out on the minor orders Embioptera and Zoraptera, while in the termites Stevens (1905*a*) was unable to find any sex chromosomes. The position in the Mallophaga and Anoplura has already been discussed (see pp. 212–214). In the flea, *Leptopsylla musculi*, Karnkowska (1932) has shown that the somatic number in the male is 22, but she was not able to find any sex chromosomes.

may be present near all the chromosome ends suggests that if any differential segments are present at all they must occupy an interstitial position in one of the chromosomes, with a pairing segment on either side.

Most of the true midges (family Chironomidae) have three pairs of metacentric chromosomes and a short acrocentric IVth chromosome pair which usually bears the main nucleolus. Although the salivaries of a large number of species have been studied by Bauer (1935, 1936*b*) and Philip (1942) no differential segments have been discovered, and it is apparently not possible to detect any differences between the salivary chromosome sets of male and female larvae. Nor has a study of meiosis in the male revealed any morphological differences between the chromosomes such as would establish the existence of an *XY* pair. Four bivalents are found, the chiasmata being quite clear, as in *Culex*. The mode of sex determination in the Chironomidae is thus entirely obscure—if differential segments are present at all they must be exceedingly minute, possibly extending over only 1–2 bands in the salivaries. The fact that various types of gynandromorphs (bilateral, anterior-posterior, etc.) have been found in several species of Culicidae and Chironomidae proves that some kind of genetical sex-determining mechanism exists, even though it cannot be detected cytologically.

In another member of the Nematocera, the crane-fly *Tipula paludosa*, Bauer (1931) has shown that the normal chromosome set consists of three large pairs of metacentrics and a pair of smaller chromosomes which may be present in triplicate or quadruplicate in some individuals. The larger chromosomes form bivalents in the male, but the smaller ones do not undergo regular pairing. Whether these small elements represent sex chromosomes is quite uncertain; they seem to be largely heterochromatic but are presumably not quite inert, since less than two are never found. The organism must be adapted to withstand their presence in the trisomic and tetrasomic number. In some respects they seem to resemble the 'limited' chromosomes of *Sciara* (see p. 201).

Most of the higher Diptera (Brachycera) possess definite *X* and *Y* chromosomes (Stevens, 1908*b*; Metz, 1914, 1916*a*, *b*; Metz and Nonidez, 1921, 1923, 1924; Keuneke, 1924; Cooper, 1941). Their size varies considerably; in some species one of them (presumably the *Y*) is heterochromatic while the other is mainly euchromatic. Except in *Melophagus* a sex bivalent is formed in all cases, but the nature of the connection between *X* and *Y* is not very clear: most probably there is always a pairing segment which holds the sex chromosomes together without a chiasma (in the aberrant fly *Melophagus* studied by Cooper a pairing segment is either absent or ineffective—see p. 190). Until more work has been done on the cytology of the higher Diptera the past evolutionary history of the *Drosophila* *XY* pair must remain obscure; neither have we any evidence whether it is typical or aberrant for the group as a whole. In some Tachinidae both the *X* and the *Y* seem to be mainly heterochromatic, so that possibly the presence of a long active differential segment in the *X* is not universal in the Brachycera.

Apart from *Drosophila mercatorum*, *D. orbospiracula* and *D. annulimana* (see Chap. VII), only two other higher Diptera are known to have become *XO*, the *Y* having been lost. The species in question are the asilid *Dasyllis grossa* (Metz, 1922) and the trypetid *Tephritis arnicae* (Keuneke, 1924). In the latter the *X* apparently divides in the first division instead of in the second.

A few of the Brachycera seem to have altogether forsaken the chromosomal method of sex determination for some new mechanism. Thus in the tachinid *Chrysomyia rufifacies* the females seem to produce unisexual broods (Roy and Siddons, 1939), while in some at least of the family Termitoxeniidae (aberrant flies that inhabit termite nests) hermaphroditism seems to occur (Wasmann, 1900–1; Assmuth, 1923; Mergelsberg, 1935; Reichensperger, 1936). Unfortunately these interesting cases have not yet been investigated cytologically.

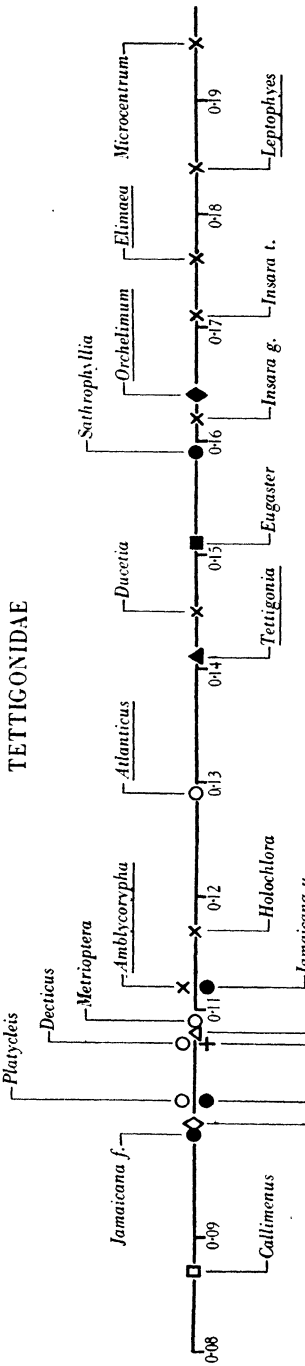
We have so far considered the evolution of the sex chromosomes as if it were a process entirely independent from that of the autosomes. It can safely be assumed that where a pairing segment is present translocations between it and the autosomes will occasionally occur, and that they will be subject to the usual laws applying in the case of translocations between two different autosomes. This is almost certainly what has happened in the Mammalia. In some instances, however, the pairing region has special properties which would probably cause a translocation between it and an autosome to lead to an unworkable arrangement. If the pairing segment is interstitial it will probably be more effectively isolated than if it is terminal in position.

It is nevertheless clear that at some stage in the ancestry of the *obscura* group of *Drosophila* a centric fusion occurred between an acrocentric *X* and an autosomal chromosome arm (see p. 131). But we have already pointed out that centric fusions must be considered as a special category of structural rearrangements, whose effects are in many ways different from those of ordinary translocations.

As far as the differential segments are concerned, it is probable that in most groups of animals they are fairly effectively isolated from the autosomes; that is to say, transferences of material between the differential segments and the autosomes must be much rarer than translocations between one autosome and another (they may not have occurred at all in some groups). The reason for this is as follows: since the differential region of the *X* is haploid in the heterogametic sex any autosomal region translocated to it will become haploid in that sex, thereby upsetting the genic balance of the organism. Conversely, any part of the *X*-differential segment, when translocated to an autosome, will suddenly become diploid in both sexes, whereas it had previously been haploid in one. Reciprocal translocations will, of course, produce both kinds of unbalance simultaneously. Stone and Griffen (1940) studied a number of such translocations between the *X* and various autosomes in *Drosophila*. They found that all of them were less viable or less fertile than normal stocks. It is nevertheless clear that occasional transferences of this type have taken place in the evolution of the

genus *Drosophila*. Thus in *D. ananassae* (see p. 130) a region derived from the inert segment of the *X* has been transferred to the dot chromosome. Here the genic unbalance which resulted was presumably not serious, since the region was almost or entirely inert. Translocations involving the differential segment of the *Y* are obviously in a special category, since any autosomal region transferred to this situation will, unless it is also present elsewhere in the chromosome set, be confined to one sex and will always be haploid. For this reason the differential segment of the *Y* must be considered to be in a state of even greater isolation than that of the *X*.

It is probable that the principle of evolutionary isolation applies fairly strictly in those groups where the sex chromosomes are heterochromatic throughout almost their entire length (Orthoptera, Heteroptera). In the Orthoptera Saltatoria where the *X* chromosomes are heterochromatic from end to end, transferences of material between them and the autosomes should be easily detectable if they occurred (White, 1941*b*). The fact that they have not been seen is strong evidence in favour of the *a priori* view that if they did occur they would be inviable. In many Orthoptera there are heterochromatic segments in the autosomes, but there is no reason to believe that these regions originated in the sex chromosome. In the Acrididae,



Text-fig. 102. Values of X/A (ratio of length of X chromosome to total length of all the autosomes in a spermatogonial metaphase) in 23 species of tettigoniids. Species with metacentric X's underlined. From White (1941*b*). × = subfamily Phaneropterinae; ● = Pseudophyllinae; ○ = Decticinae; □ = Bradyporinae; ■ = Hetrodinae; ◇ = Mecopodinae; ◆ = Conocephalinae; △ = Copiphorinae; + = Listroscelinae; ▲ = Tettigoninae.

in particular, the heterochromatic autosomal regions behave quite differently from the *X* heterochromatin during the spermatogonial divisions (White, 1940*a*, 1941*b*).

In the long-horned grasshoppers (Tettigoniidae) and in some groups of praying mantids the *X* may vary quite considerably in length, even within the limits of a single subfamily. The Phaneropterinae (Tettigoniidae) and the Empusinae (Mantoidea) provide some very striking instances of this state of affairs (White, 1941*b*). This kind of variation is almost certainly due to the occurrence of homosomal duplications and deficiencies in the *X*. Such duplications and deficiencies of short segments, happening from time to time in the course of evolution, may be expected to alter the genic balance upon which sex determination depends; they will be preserved if they shift it to a more advantageous equilibrium position.

Another effect of this type of structural change will probably be to alter quantitatively the nucleic acid metabolism of the organism, especially when the regions concerned are heterochromatic (see the work of Caspersson and Schultz (1938), in which it was shown that the presence of an extra *Y* in a female *Drosophila* increased the quantity of cytoplasmic nucleotides in the oocyte). In a number of species of insects segments of the *X* including the centromere appear to have been reduplicated, the regions in question forming independent chromosomes which increase the chromosome number of the species and give rise to 'multiple' sex mechanisms (see p. 252). Physiologically, there is not much difference between duplicated regions of the *X* which are included in the original chromosome and those which form new chromosomes.

In two subfamilies of the Tettigoniidae (Decticinae and Phaneropterinae) both acrocentric and metacentric *X* chromosomes occur. In the Decticinae the *X* is acrocentric in the genera *Metrioptera*, *Gampsocleis*, *Decticus* and *Pholidoptera*, but metacentric in *Atlanticus* (Text-fig. 76). In the Phaneropterinae the genera *Phaneroptera*, *Ducetia*, *Holochlora*, *Insara* and *Microcentrum* have acrocentric *X*'s, while *Amblycorypha*, *Leptophyes*, *Isotima* and *Elimaea* have metacentric ones. Careful measurements have shown that the metacentric *X*'s of these four genera are, on the whole, no longer (relative to the autosomes) than the acrocentric *X*'s of the remaining genera (Text-fig. 117). We have no means of ascertaining which condition was the original one in the Phaneropterinae and Decticinae, but the change from one shape to the other probably resulted from a homosomal rearrangement involving a shift in the position of the centromere, as has happened in the short-horned grasshoppers of the genera *Circotettix* and *Trimerotropis* (see p. 109). Since the genera of Phaneropterinae with metacentric *X*'s are not taxonomically close to one another, it is probable that changes of this sort have taken place repeatedly in the phylogeny of the subfamily.

It is worth pointing out that in some groups of Orthoptera no changes in the shape of the *X* chromosome are known to have occurred. Thus all the Tettigidae

(grouse locusts) which have been studied cytologically possess acrocentric *X*'s (Robertson, 1916; Harman, 1915, 1920; Misra, 1937*b*); and in the *XO* genera of mantids, although the length of the *X* varies very greatly, it is always metacentric (White, 1941*a*; Hughes-Schrader, 1943*b*).

Variation in the length of the *Y* has been noted in a number of groups. It may occur between species, or within the limits of a single species. Thus in *Drosophila pseudoobscura* as many as seven different types of *Y* have been found, all of which occur in nature (Dobzhansky, 1937*c*). All of them are metacentric; they differ in absolute length, and in the relative proportions of the two arms. These different types of *Y* seem to be adapted to the autosomes of the strains in which they occur, but some of them are lethal in interracial hybrids (Sturtevant, 1937*b*).

D. pseudoobscura is possibly an extreme example of variability in the length of the *Y*, but it is probable that if sufficiently careful measurements were made many other species would be found to vary in the same manner, although perhaps not to the same extent. In the neuropteran *Chrysopa vulgaris* Naville and de Beaumont (1933) have shown that the sex chromosome which they assumed to be the *Y* varied in size from individual to individual. In several of the families of Heteroptera (Coreidae, Lygaeidae, Pentatomidae, etc.) the *Y* may vary greatly in size from genus to genus, being sometimes as large as the *X*, sometimes much smaller or even absent altogether (Wilson, 1905*a*, *b*, 1906, 1907, 1911). In *Metapodius femoratus* (Coreidae) males from certain localities lack the *Y* which is usually found; they seem to be quite normal in all other respects (Wilson, 1910).

It is rather remarkable how frequently the *Y* persists in spite of being entirely heterochromatic. This is the case in all the Neuroptera and in certain families of the Heteroptera, such as the Pentatomidae. One can imagine several kinds of function for a heterochromatic *Y*, and it is probable that in the groups in question one or more of these is sufficiently important to prevent it becoming lost in the course of evolution. In the first place it may serve a purely mechanical function, facilitating the regular segregation of the *X* at meiosis. Secondly, the *Y* may still retain some vestigial genetic properties, as it appears to do in *Drosophila* (Neuhaus, 1939). Thirdly, it may play a part in the general nucleic acid metabolism of the organism. It is interesting to note that in the reduviid bugs with several *X* chromosomes ($X_1X_2X_3$ ... etc.) the *Y* is frequently much larger than in the *XY* species (Text-fig. 108). This may be an adaptation which ensures an approximately equal production of nucleic acid in both sexes. In the Orthoptera Saltatoria, however, the amount of heterochromatin must differ very greatly in the two sexes, and it is even possible (although perhaps unlikely) that this difference is in itself responsible for sex determination. But in the bed-bug (see p. 258) the number of *X* chromosomes varies very greatly without giving rise to intersexes. This suggests (1) that this insect is adapted to withstand very

great variations in the total amount of heterochromatin, and (2) that most of the supernumerary *X*'s are inert, both in the general sense and with regard to sex determination. In *D. melanogaster* and *D. pseudoobscura* *XYYY* males are sterile (Schultz, 1941 *a*), but it is not clear whether this effect is due to an excess of heterochromatin or to some other cause (in *D. virilis* *XYYY* males are said to be fertile—the *Y* is acrocentric in this species, so that the increase in the amount of heterochromatin is proportionately less than in *melanogaster*).

When considering the evolutionary isolation of the sex chromosomes we mentioned that whole-arm transfers occasionally occurred between them and the autosomes. Some of these are particularly interesting, since they have changed the whole character of the sex-chromosome mechanism. Although *XO* mechanisms have arisen from *XY* ones by loss of the *Y* chromosome, there is no doubt that the reverse process also takes place occasionally. Thus some of the *XY* mechanisms which we can observe at the present day are of immense antiquity, while others have arisen relatively recently by 'reversion'.

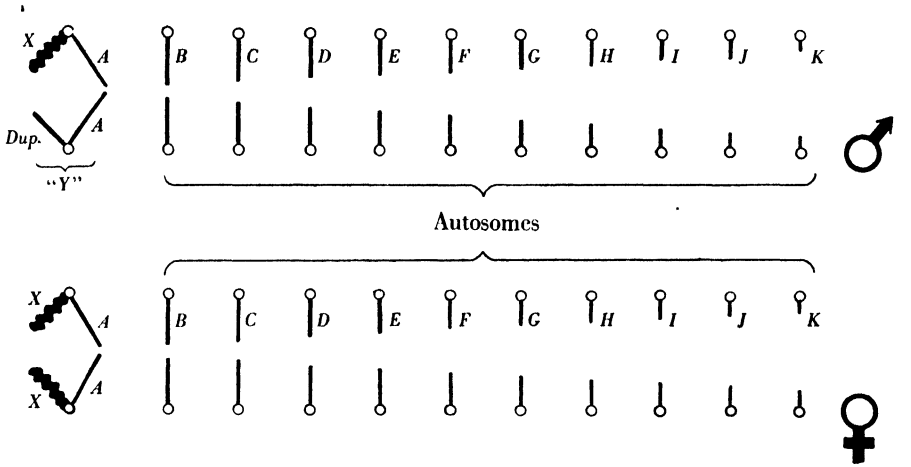
The most usual method of reversion seems to be as follows: if in an *XO* species a centric fusion takes place between an acrocentric autosome and an acrocentric *X* then the homologous 'unfused' autosome will become, in effect, a *Y*—that is to say, it will be a chromosome confined to the male line which pairs with one limb of the *X* at meiosis. Such a newly arisen *Y* may be called a neo-*Y* to distinguish it from one that has been confined to the male sex during the whole history of the group in question.* Most neo-*Y*'s will presumably be genetically active, and will not at first contain a differential segment, although such a segment will probably develop in course of time.

In two genera of Acrididae, *Hesperotettix* (subfamily Catantopinae) and *Mermiria* (subfamily Truxalinae), some of the species were shown by McClung (1917) to have become *XY* by the above method.† Two species of *Hesperotettix*, *H. brevipennis* and *H. festivus*, still retain the original *XO* condition, while *H. pratense* and *H. speciosus* are *XY*. It would seem that the autosome which has become involved in the sex mechanism is possibly not the same one in these two species, since it is one of the larger ones in *H. speciosus* and a medium-sized one in *H. pratense*. The *X*'s of these *XY* species are, of course, metacentric, one limb (representing the original *X*) being heteropycnotic at meiosis while the other reveals its autosomal origin by the fact that it is non-heteropycnotic.

* Helwig (1941) has objected to the designation of a 'former autosome' as a neo-*Y* when it has become confined to the male line, without indicating at what stage he would consider such a chromosome to have ceased to be an autosome.

† It has several times been stated that de Sinéty (1901) discovered this *XY* condition in two genera of phasmids, *Leptynia* and *Menexenus*. But Cappe de Baillon and de Vichet (1940) re-examined his material of *Leptynia* and showed that the bivalent he studied was an unequal pair of autosomes rather than an *X* and a neo-*Y*. Favrelle (1936) has shown that another species of *Menexenus* is *XO* in the male.

In *H. viridis* different individuals may be either *XO* or *XY*, indicating that the translocation responsible for changing the character of the sex mechanism has occurred, but has not spread throughout the whole of the species. Some of the autosomes of *H. viridis* have also 'fused' with one another to form metacentrics. The individuals studied by McClung varied in the number of such



Text-fig. 103. Diagrams of the male and female chromosome sets in the grasshopper *Mermiria bivittata*. The fusion of the original *X* with one member of a pair of autosomes has led to an *XY* system, in which the *Y* is a 'neo-*Y*' containing a duplicated region (*Dup.*). Further explanation in text. Based on the work of McClung (1917).

metacentrics; the number of chromosome arms was always 23 in the males, however, except in one individual where a supernumerary chromosome was present.

Mermiria bivittata has apparently become *XY* in the same manner as the species of *Hesperotettix*; but the situation is a little more complicated, since the neo-*Y* is a metacentric chromosome, i.e. it has a second limb. It is not clear where this limb has come from: it seems to constitute a differential segment in the *Y* and may have been derived by a duplication or translocation of some sort—apparently there are two races of *Mermiria bivittata* which differ in the length of this 'second limb' of the neo-*Y*. *M. intertexta* and *Hypochlora alba* also possess neo-*Y*'s (King and Beams, 1938), but no details of the cytology of these species has been published; according to Helwig (1941) a number of similar cases are known in other genera of grasshoppers.

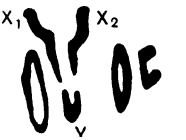
It is probable that 'reversion' of an *XO* to an *XY* mechanism can occur in various other ways that do not involve centric fusion, but no clear case has been worked out as yet. Apart from the grasshoppers mentioned above the only *XY* species of Orthoptera Saltatoria are the following: *Gryllotalpa gryllotalpa*, north

European and Roumanian races (see p. 179); *Oecanthus longicauda* (Makino, 1932*a*); *Schizodactylus monstrosus* (McClung and Asana, 1933). In none of these three species is the nature of the XY mechanism clear from the published accounts. Two other species of *Gryllotalpa* (*G. borealis* and *G. africana*) and the South Italian race of *G. gryllotalpa* are $XO : XX$ forms, so it is not impossible that the Y of the northern and Roumanian races is a neo-Y. In *Oecanthus* the American species *Oe. nigricornis* is $XO : XX$ (Johnson, 1931) so that here again the Y of *Oe. longicauda* may be a recent acquisition, although there is no proof of this at present. It is not clear from the published accounts whether chiasmata are formed between the X and Y in the three species mentioned above. It would appear, however, that the Y's of all three are heterochromatic so that they are probably not of autosomal origin, as in the grasshoppers *Hesperotettix* and *Mermiria*. Theoretically a supernumerary X fragment might become a neo-Y through becoming confined to the male line: but no instance of such a conversion is known, unless these three XY Saltatoria are to be interpreted in this sense. *Schizodactylus* is a very isolated genus, often put in a separate family of the Ensifera, while in the case of *Gryllotalpa* we have already seen (p. 181) that a great many structural rearrangements must have taken place in the phylogeny of the genus.

We have already referred several times to the existence of sex-chromosome mechanisms in which more than one kind of X or one kind of Y is present. Such systems may be classified as X_1X_2Y, $X_1X_2X_3Y$, X_1X_2O, $X\,Y_1Y_2$, etc., according to the number of non-homologous (or only partly homologous) X's and Y's. Naturally, the only way to understand the origin of these complex mechanisms is to compare them with the simpler conditions met with in related species or genera. This has been possible in the cases of *Drosophila americana* and *D. miranda* (see Chapter VII), and the same principles can be applied in other instances.

The easiest cases to interpret are those where a multiple mechanism has arisen from the XY or XO condition by the inclusion of an autosome pair in the sex-chromosome mechanism. Such a situation exists in one section of the Mantoidea (praying mantids). The genera *Mantis*, *Tenodera*, *Paratenodera*, *Hierodula*, *Sphodromantis*, *Stagmomantis* and *Choeradodis* all have an X_1X_2Y mechanism, whereas the other mantid genera so far studied (*Miomantis*, *Acontiothespis*, *Ameles*, *Iris*, *Empusa*, *Gongylus*, *Callimantis*, *Liturgousa* and *Angela*) are XO in the males (Oguma, 1921; King, 1931; Asana, 1934; White, 1938, 1940*b*, 1941*a*; Hughes-Schrader, 1943*a*, *b*). Since no XY species are known it seems likely that the conversion from the XO condition to the X_1X_2Y one took place directly, without an intermediate XY stage. All the other known facts are in favour of this hypothesis. Since the seven X_1X_2Y genera are taxonomically closely related (although *Choeradodis* has usually been placed in a separate subfamily, on rather inadequate grounds) it is virtually certain that they have

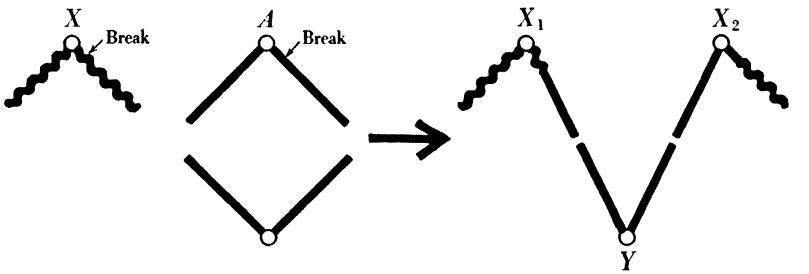
all arisen from a single ancestral species which, from XO, became X_1X_2Y. Such a transformation probably resulted from a reciprocal translocation between the X and an autosome, both chromosomes being metacentric and the breakage points being situated very close to the centromeres (Text-fig. 105).



Text-fig. 104. The X_1X_2Y sex trivalent and three autosomal bivalents in the mantid, *Sphodromantis viridis*.

The three sex chromosomes in the males of the X_1X_2Y species form a trivalent at meiosis. The females are $X_1X_1X_2X_2$, and although no direct observations have been made on their meiosis, it seems probable that the four sex chromosomes form two bivalents.

If we call the six-chromosome arms of the male sex trivalent X_1L, X_1R, YL, YR, X_2L and X_2R, then the distal ends of X_1R and X_2L pair with the distal ends of YL and YR respectively. X_1L and X_2R remain free and unpaired; they clearly represent the two limbs of the original X chromosome. The Y is presumably a 'neo-Y' like those of *Hesperotettix* and *Mermiria*, i.e. an autosome which as a result of a mutual translocation in its homologue has become confined to the male line.



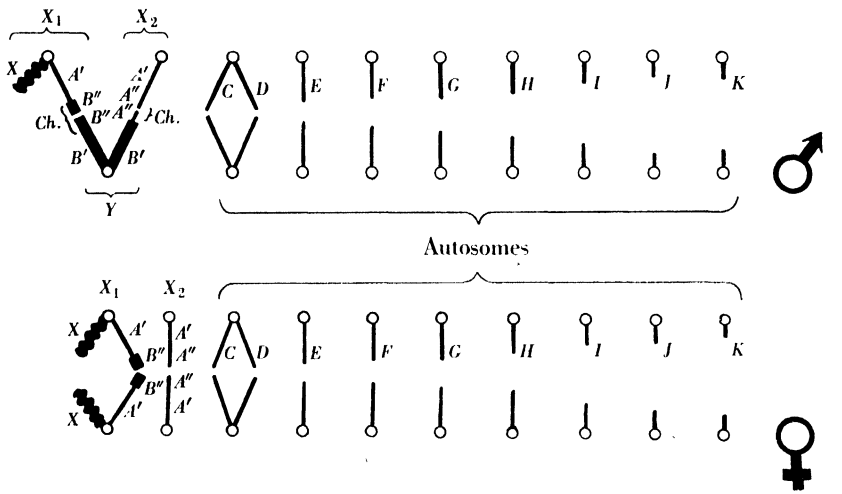
Text-fig. 105. Diagram of the presumed mode of origin of the X_1X_2Y mechanism in mantids by a mutual translocation in an XO species. From White (1941*a*).

The relative lengths of the chromosome arms of X_1 and X_2 are very similar in *Tenodera aridifolia*, *Paratenodera sinensis* and two species of *Sphodromantis* (and also in *Stagmomantis* and *Choeradodis*, to judge from the published figures). This suggests that no major structural changes (other than paracentric inversions) have taken place since the origin of the X_1X_2Y system. The Y, on the other hand, varies considerably in size and shape; in *Tenodera aridifolia* and *Sphodromantis viridis*, its two arms are equal in length. In *Tenodera sinensis* and in *Sphodromantis gastrica* they are markedly unequal, while in a species of *Hierodula* (Asana, 1934) the Y is apparently very small. This element has thus undergone a number of structural changes, some of which have involved gain or loss of material from the chromosome.

With two exceptions all the X_1X_2Y species which have been studied have 12 pairs of autosomes (diploid number 27 in the male). The exceptions are

Sphodromantis viridis which has only 10 pairs of autosomes (diploid number 23 in the male) and *Choeradodis rhombicollis*, which has 14 pairs of autosomes (Hughes-Schrader, 1943*b*). It is thus probable that *Sphodromantis viridis* has lost two pairs of autosomes since the origin of the X_1X_2Y system while *Choeradodis rhombicollis* has gained two (although it is impossible to say definitely that the translocation took place in a 27-chromosome species).

The genera of mantids in which the X_1X_2Y mechanism has been found include at least 200 species; we have every reason to believe that the whole group which we may call the Mantinae *sensu stricto* forms a natural taxonomic unit, descended from a single species in which the translocation originally took place. This group is now distributed all over the Old World, and one large genus (*Stagmomantis*) is Central American. *Choeradodis* has a curious distribution, being found in Southern Asia as well as in Central America. Judging from the number of



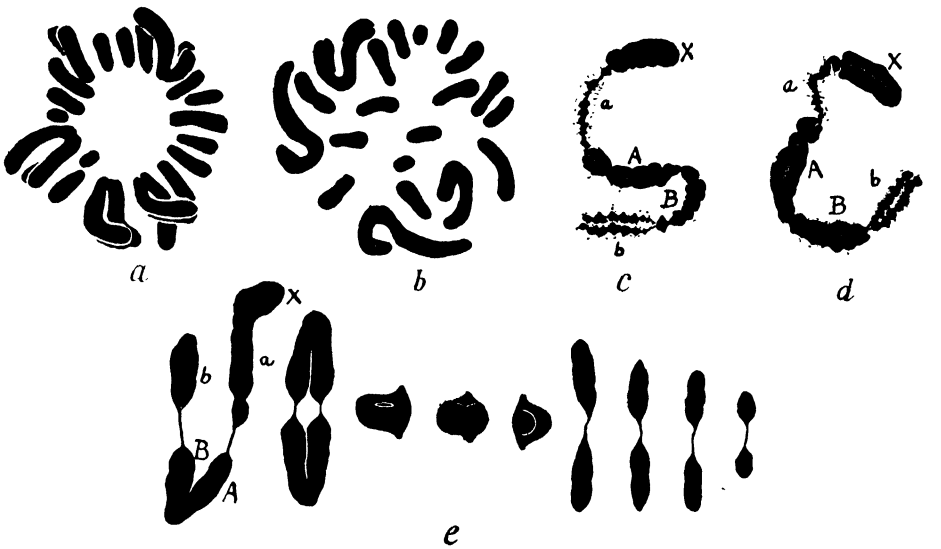
Text-fig. 106. Diagram of the male and female chromosome sets of the grasshopper *Paratylotropidia brunneri*. *Ch.* = regions in which chiasmata are formed in the sex-trivalent. From White (1940).

genera and species included in the X_1X_2Y group the translocation probably took place at least as long ago as the Miocene and possibly earlier. The large number of X_1X_2Y species in Africa and Asia suggests that it took place somewhere in the Old World. In all probability the American continent was subsequently invaded by X_1X_2Y mantids on two separate occasions (by the ancestors of *Choeradodis* and *Stagmomantis* respectively).

A second example of an X_1X_2Y mechanism whose origin can be inferred with a fair degree of probability occurs in the Acrididae (King and Beams, 1938). The species in question, *Paratylotropidia brunneri*, is a very rare grasshopper belonging

to the group Melanopli of the subfamily Catantopinae. It occurs in a number of isolated localities in Dakota, Texas, Arkansas, Oklahoma and Iowa, its distribution being of a type which suggests that the species is a 'relict' one. There is one other species of the genus, which has been found only once, in North Carolina.

The diploid chromosome sets of the male and female *P. brunneri* are shown in Text-fig. 106. It will be seen that there are 19 chromosomes in the male and 20 in the female. The number of chromosome arms is, however, the same as in



Text-fig. 107. Chromosomes of *Paratylotropidia brunneri*. *a*=spermatogonial metaphase (19 chromosomes); *b*=female somatic metaphase (20 chromosomes); *c*=sex-trivalent at diplotene; *d*=the same at diakinesis; *e*=entire chromosome set at first metaphase viewed from the side. From King and Beams (1938).

the usual grasshopper set (23 in the male, 24 in the female). Both sexes have four metacentric chromosomes. Two of these represent a pair of autosomes; the other two are the two X_1's in the female, the X_1 and Y in the male. During meiosis in the male a sex trivalent is formed which resembles the mantid one but consists of two metacentric chromosomes (X_1 and Y) and one acrocentric one (X_2). The three chromosomes of the trivalent arrange themselves on the spindle in such a way that X_1 and X_2 go to one pole and the Y to the other.

It was recognized by King and Beams that the five chromosome arms of the trivalent must have been derived from an originally acrocentric X and two pairs of acrocentric autosomes. They considered that X_1R was homologous to XL and X_2 to YR. If this were so it would signify that the X_1X_2Y system had

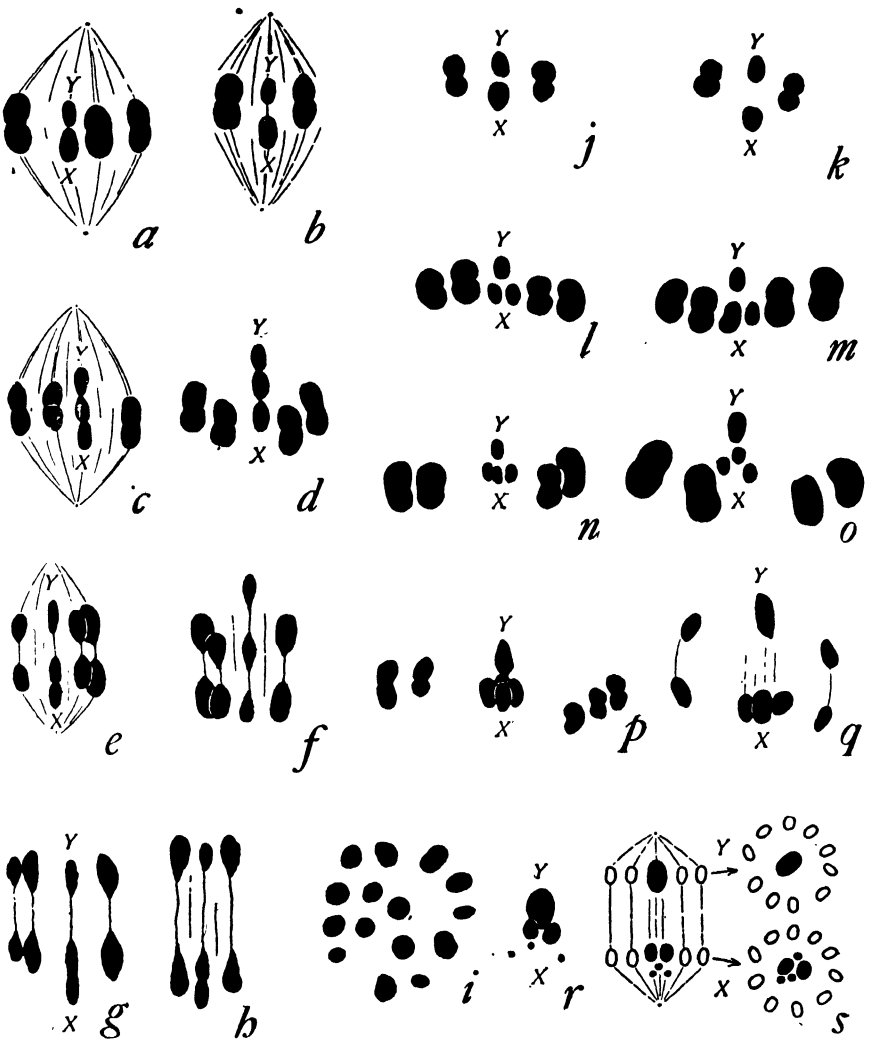
arisen by two 'centric fusions', one between the X and an autosome, which we can call 'A', and the other between the homologue of A and a second autosome, 'B'. Thus X_1 would be composed of X and A, Y of A and B, while X_2 would be the unaltered B chromosome.

An alternative hypothesis as to the origin of the *Paratylotropidia* X_1X_2Y system has been put forward (White, 1940*b*) according to which three rather than two translocations were involved, one a centric fusion between X and A, the second a mutual one between the tip of X_1R and the tip of a B chromosome, the third a centric fusion between the two B chromosomes. This would leave the two ends of the Y homologous to the distal ends of X_1R and X_2 (with which they pair at meiosis); and it would account for the regional differences in heteropycnosis which cannot be satisfactorily explained on King and Beams' original interpretation, unless one assumes that they have arisen since the origin of the sex trivalent (an assumption which seems unlikely, but which may nevertheless be true).

Whatever theory one adopts, the *Paratylotropidia* sex-chromosome mechanism is of interest since, although it is superficially similar to the mantid one, it has arisen in a different manner, from acrocentrics instead of from metacentrics, and by several translocations instead of by a single one.

It is interesting to compare the complex sex-chromosome mechanisms of these Orthoptera with those of *Drosophila miranda* and *D. americana* (see Chapter VII), since the latter have arisen from $XY : XX$ systems, the former from $XO : XX$ ones. They are similar in principle, however, since in all these cases the complexity of the sex mechanism has arisen by an addition of autosomal chromosomes as a result of translocation.

The multiple sex-chromosome mechanisms which have been described in a number of species of Heteroptera seem to be of an entirely different kind from those of the Orthoptera and *Drosophila* species. It will be seen from Table 13 that the Heteroptera with multiple mechanism belong to several different families, but the facts are closely similar in all of these. It will be remembered that the sex chromosomes of the order Heteroptera are characterized by total heteropycnosis and by the fact that the X and Y divide in the first meiotic division and form a pseudo-bivalent at the second one. These peculiarities of structure and behaviour are shown by all the sex chromosomes in the species with complete mechanisms. Thus in the $X_1X_2X_3X_4Y$ species such as *Nepa cinerea* all the X's are heteropycnotic, they behave 'anomalously', and a 'pseudo-quinquevalent' is formed at the second division. These facts suggest most strongly that X_2, X_3, ..., etc., are not of autosomal origin but have originated by fragmentation of the original X or by reduplication of parts of it. This hypothesis is greatly strengthened by the fact that the number of autosomes is not lower in species with multiple mechanisms than in related species with simpler mechanisms (compare *Sinea rileyi* with other species of the genus).



Text-fig. 108. The sex chromosomes of various Heteroptera. *a* and *b* = *Thyanta custator* (an *XY* species), second metaphases in side view; *c* and *d* = corresponding views of *Thyanta calceata* (an X_1X_2Y species); *e–h* = anaphases of the same; *i* = polar view of first metaphase in the same; *j*, *k* = *Diplocodus exsanguis* (*XY*), second metaphase in side view; *l* = similar view of *Rocconota annulicornis* (X_1X_2Y); *m* = similar view of *Conorhinus sanguisugus* (X_1X_2Y); *n* = *Sinea diadema* ($X_1X_2X_3Y$); *o* = *Prionidus cristatus* ($X_1X_2X_3Y$); *p*, *q* = metaphase and anaphase of second division in *Gelastocoris oculatus*; *r* = the sex chromosomes of *Acholla multispinosa* ($X_1X_2X_3X_4X_5Y$) at the second division; *s* = diagram of the distribution of the sex-chromosomes in the second division of *Acholla*. From Wilson (1911).

The segregation of all the X's in such a species as *Nepa cinerea* to the same pole at the second division clearly depends on the existence of a Y (Darlington, 1940*a*). Normally all the X's arrange themselves in a group opposed to the Y, so that at anaphase they separate from it and are all moved in the same direction as the spindle elongates. Whether the X's of these species form multivalents or bivalents in oogenesis is not known.

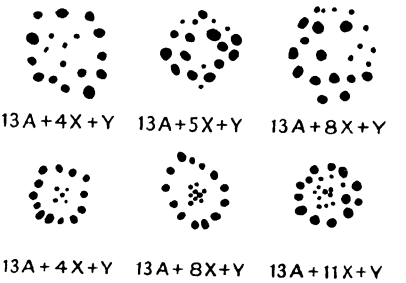
One of the most interesting series of species with multiple mechanisms is found in the family Reduviidae (assassin bugs). A large number of American species of this group were studied by Payne (1909, 1910, 1912*a*). A few of them, such as *Diplocodus exsanguis* and *Reduvius personatus*, are XY in the males; others, such as *Fitchia spinulosa*, *Rocconata annulicornis* and *Conorhinus sanguisugus*, are X_1X_2Y. *Prionidus cristatus* and four species of the genus *Sinea* are $X_1X_2X_3Y$, *Pnirontis modesta* is $X_1X_2X_3X_4Y$, while *Acholla multispinosa* and *Sinea rileyi* are $X_1X_2X_3X_4X_5Y$. In *Fitchia* and *Rocconata* X_1 and X_2 are almost exactly the same size, while in *Conorhinus* one of them is larger than the other. In *Acholla* two of the X's are about the same size while the other three are quite minute (Text-fig. 108). The Y of this species is enormous, both relative to the X's and in comparison with the autosomes. It has probably undergone homosomal duplications of material like those that have been inferred in the case of the X in some Orthoptera. It would appear that the sex-chromosome mechanism of the reduviids is in a very active state of evolution; the X's and Y are structurally isolated from the autosomes, but have undergone extensive duplications or fragmentation in the phylogeny of the group.

Much less is known about the sex chromosomes of the water scorpions (family Nepidae), but the two species which have been studied (*Nepa cinerea* and *Ranatra linearis*) are both $X_1X_2X_3X_4Y$ (Steopoe, 1925, 1927, 1931). In *Ranatra* the X's are quite small, the Y somewhat larger.

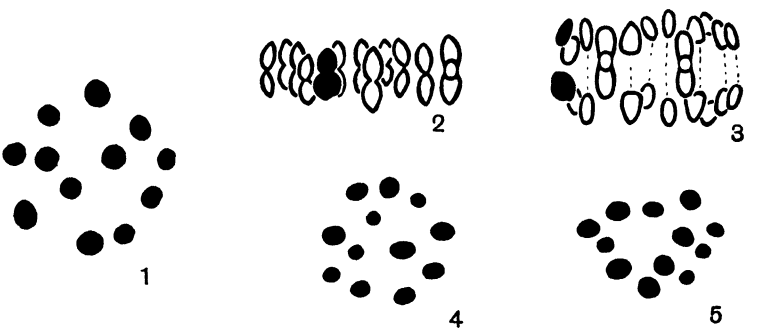
Up till now we have been considering 'multiple' mechanisms which are constant in all the individuals of a particular species. In the bed bug (*Cimex lectularius*), however, the number of X's varies very greatly from individual to individual (Slack, 1939*a*, *b*; Darlington, 1940*a*). The related species *C. rotundatus*, *C. columbarius* and *C. stadleri* are X_1X_2Y, but in *lectularius* a large number of supplementary X's of various sizes are usually present, so that the total number of X's in the male individuals varies from 2 to 15. The females have not been studied so extensively, but it is known that they may possess from 6 to 14 X's in the diploid set. It is probable that of all these X chromosomes only the first two play an essential part in sex determination. The others are probably semi-inert; it is unlikely that they are completely functionless, since in that case one would expect them to have been lost from the species instead of accumulating until in some populations there is an average of nine X's in the males. The variation in number of X's which exists between the individuals of a population is due to the frequent occurrence of non-disjunction of the X's at meiosis. Even

in insects with 14 or 15 X's, however, the orientation of the sex chromosomes on the spindle at the second division is usually quite regular, all the X's forming a group opposed to the single Y.

The bed bug is the only member of the Heteroptera in which the number of X's is known to vary.* In certain species of the genus *Metapodius* (Coreidae), however, the number of Y chromosomes is far from constant (Wilson, 1907, 1909*a*, 1910). In some individuals of *M. femoratus* the Y may be entirely absent; in the majority it is present, either alone or accompanied by a number of supernumerary chromosomes whose behaviour suggests that they are, in part at any rate, homologous to the original Y. The facts that XO individuals are viable does not necessarily prove that they are fertile; but Montgomery (1906) apparently found a population all the males of which lacked a Y (unfortunately it is not absolutely certain that they belonged to this species). The existence of individuals with three or four supernumerary Y's suggests that they may possibly be of some slight advantage to the species, either by affecting its nucleic acid metabolism or



Text-fig. 109. First metaphases (top row) and second metaphases (bottom row) in the bed bug, *Cimex lectularius*, showing different numbers of X chromosomes (there are always 13 autosomal bivalents in this species). In the first metaphases the arrangement of the chromosomes is apparently haphazard, while in the second metaphases the sex chromosomes form a group in the centre of the spindle, surrounded by a ring of autosomes. The Y cannot be identified with certainty.

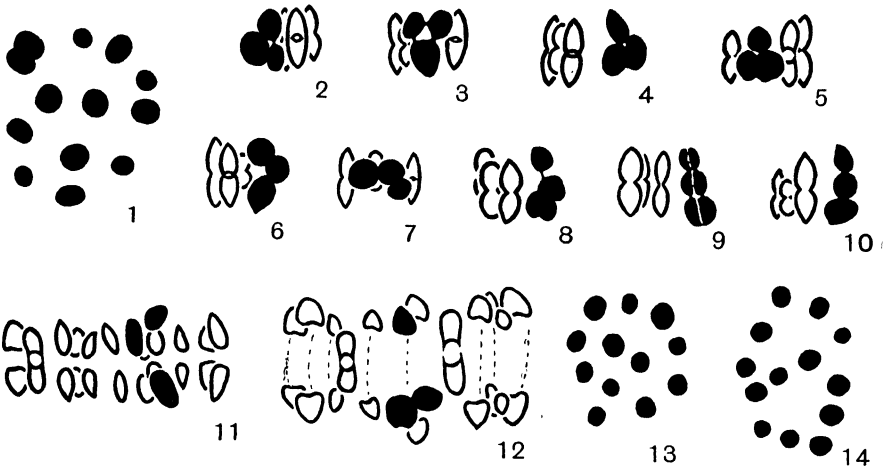


Text-fig. 110. Meiosis in a 24-chromosome male of *Forficula auricularia*. 1 and 2 = first metaphases in polar and side view (X and Y chromosomes black in 2); 3 = first anaphase; 4, 5 = second metaphases. From Callan (1941*b*).

* In the Neuropteran *Ascalaphus libelluloides* there exists a situation in some ways comparable to that found in the bed bug. Naville and de Beaumont (1933) found that the number of sex chromosomes varied very considerably in both sexes of this species. It appears probable, but not certain, that both X's and Y's may be represented by one or more elements. Other species of the genus have a simple $XY : XX$ mechanism of the usual neuropteran type (Naville and de Beaumont, 1936).

through some effect on fertility or viability. The situation in *M. terminalis* and *granulosus* is essentially the same as in *femoratus*; but no *XO* males are known to occur in these species.

Turning now from the Heteroptera to other orders of insects we find that complex sex mechanisms occur in various members of the Dermaptera and Coleoptera. A particularly interesting case exists in the common European earwig, *Forficula auricularia* (W. P. Morgan, 1928; Callan, 1941*b*). Here two kinds of males exist (XY and X_1X_2Y); most natural populations contain both



Text-fig. 111. Meiosis in a 25-chromosome male of *Forficula auricularia*. 1 = first metaphase in polar view; 2–10 = the same in side view, showing various modes of association between the two X's and the Y; 11, 12 = first anaphases; 13, 14 = second metaphases showing 12 and 13 chromosomes respectively. From Callan (1941*b*).

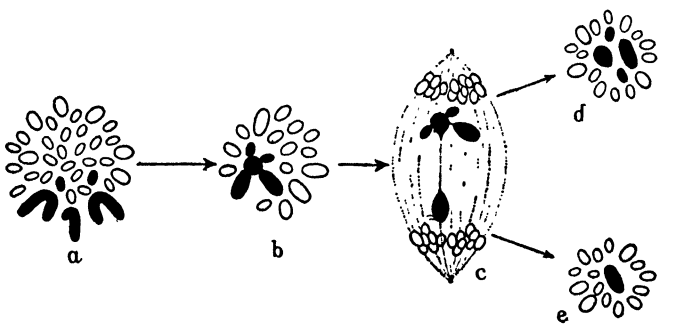
types, the X_1X_2Y males being in a minority (see Table 12). Some earwig colonies, however, seem to contain only the XY type of male. The exact relationship between the two sex mechanisms that co-exist in this species is not known; but it seems certain that neither X_1 nor X_2 is precisely identical with the X of the XY individuals. Callan has suggested that the X_1X_2Y type of male arose by the inclusion of an autosome in the sex mechanism, as has happened in the mantids and *Paratylotropidia*. This interpretation seems highly improbable, since all three sex chromosomes show total heteropycnosis, and their behaviour at meiosis suggests that they have no true pairing segments. It is more probable that both X_1 and X_2 are homologous to parts of the single X of the XY individuals. The fact that both types of males frequently co-exist in colonies of *Forficula auricularia* suggests that one type may be unstable, so that it gives rise to the other from time to time. No external morphological differences can be detected between XY and X_1X_2Y males, and the sex ratios of natural populations do not

deviate far from equality. It is probable that there are several types of females (XX and $X_1X_1X_2X_2$ and possibly intermediates as well) in 'mixed' colonies of *F. auricularia*.

TABLE 12. Forficula auricularia: *proportions of* XY *and* X_1X_2Y *males in different localities*

	XY	X_1X_2Y	% XY	Author
Switzerland	50%	50%	50	W. P. Morgan, 1928
Merton (South London)	60	0	100	Callan, 1941*b*
Marcham, Berkshire	71	7	91	
Gillingham, Kent	52	13	80	
Wallington, Surrey	15	5	75	

Other species of earwigs may be either XY (e.g. *Forficula scudderi* (Misra, 1937*c*), *Labia minor* (W. P. Morgan, 1928) and two species of *Labidura* (W. P. Morgan, 1928; Asana and Makino, 1934)) or X_1X_2Y (e.g. three species of *Anisolabis* (W. P. Morgan, 1928; Sugiyama, 1933; Schrader, 1941*c*)). Only in *Forficula auricularia*, however, do the two types exist in the same species. *Anisolabis* is not closely related to *Forficula* (being in fact a member of a different suborder), so that there is no reason to believe that the X_1X_2Y mechanisms of these genera have had a common origin.



Text-fig. 112. Behaviour of the sex chromosomes in the beetle *Blaps lusitanica*. *a* = spermatogonial metaphase; *b*, *c* = first meiotic division; *d*, *e* = second meiotic divisions ($X_1X_2X_3X_4$ and Y classes). Sex chromosomes black, autosomes in outline. From Wilson (1925).

In the Coleoptera the most noteworthy example of a complex sex mechanism is in the tenebrionid *Blaps lusitanica* (Nonidez, 1915, 1920). A sex quinquevalent is formed in the spermatogenesis of this species, but it is uncertain whether it is $X_1X_2X_3X_4Y$ or $X\,Y_1Y_2Y_3Y_4$. Two kinds of sperms are formed, one with 16 chromosomes, the other with 19; but it is not known how many chromosomes the female has. Obviously one cannot determine the origin of this complex

mechanism from the data at present available, although a related species (*B. walthi*) seems to be *XO* (Nonidez, 1915). A rather peculiar sex-determining mechanism which seems to resemble that of *Blaps lusitanica* in some respects exists in the ostracod *Heterocypris incongruens* (Bauer, 1940). Two races of this Crustacean exist, one of which consists exclusively of parthenogenetic females with 20 chromosomes, while the other is bisexual. In the latter race the males have 15 chromosomes, the females 20. During oogenesis 10 bivalents are formed, but at meiosis in the male there are only five normal bivalents: the remaining five chromosomes form a compact mass (? pseudoquinquevalent) which is attached to one of the bivalents (the nature of this attachment is not clear, but it does not seem to be by means of chiasmata). At the first meiotic division the group of five chromosomes passes entire to one pole, so that two kinds of sperms are formed, with 5 and 10 chromosomes respectively.

The most obvious intepretation would seem to be that the males are $X_1X_2X_3X_4X_5O$, the females being $X_1X_1X_2X_2X_3X_3X_4X_4X_5X_5$, but the position is not entirely clear and Bauer seems to regard the bivalent to which the group of 5 is attached as an XY pair.

It will be seen from Table 13 that a considerable number of animal species belonging to various groups have complex sex mechanisms which can be described by the general formula X_nO. It is not easy to interpret either the origin or the mode of functioning of any of these cases. One of the chief difficulties is to imagine any mechanical reason why the several X's should travel to the same pole at meiosis in the absence of a Y.

In the stone fly, *Perla marginata*, there are two X's in the male and four in the female (Junker, 1923). During the prophase of the first meiotic division in the male X_1 and X_2 (which are unequal in size) lie close together, but do not form a bivalent, since they separate later and form univalents at metaphase. At first anaphase they pass to the same pole, so that two kinds of sperms are formed, one with 10 chromosomes, the other with 12 (there are ten pairs of autosomes in this species). It appears that both X_1 and X_2 are heteropycnotic during the prophase, but it is not known what degree of homology (if any) exists between them. Any attempt to speculate as to the evolutionary origin of this mechanism would be premature. It is interesting to note that two other species of stone flies (*Perla immarginata* and *Acroneuria jezoensis*) are XY in the males (Nakahara, 1919; Itoh, 1933*c*), but it is not easy to see how either condition could have arisen directly from the other.

Similar $X_1X_2 : X_1X_1X_2X_2$ mechanisms have been described for the coreid bug, *Syromastes marginatus*, by Wilson (1909*a*, *b*) and for the 'silver fish', *Thermobia domestica*, by Perrot (1933). Goldsmith (1919) has also reported the same type of mechanism in several species of tiger beetles (Cicindelidae).

The above X_1X_2 mechanisms exist, for the most part, in single species whose relatives are XY or XO. In the spiders, however, the whole group seems to

be characterized by a sex mechanism of this type (Painter, 1914; Hard, 1939). It is assumed that the females have four *X* chromosomes, but this point has not been verified by direct observation. At the first meiotic division in the male the two negatively heteropycnotic *X*'s lie close to one another, side by side, and pass undivided to one pole at anaphase.* Since this mechanism has been found in eleven families of spiders, belonging to both of the two main suborders (Mygalomorphae and Araneomorphae) it quite possibly occurs in all members of the group. As the spiders go back in geological history as far as the Devonian, their sex-chromosome mechanism must be of great antiquity—unlike the other 'multiple mechanisms' which we have been considering, which are mostly of recent origin. It would therefore be useless to speculate as to how the spider mechanism arose. It is not clear from the published accounts whether the two *X*'s in the males are homologous or not. Quite possibly they are, since they seem to be always the same length. If so we have a unique sex mechanism which may be represented as follows: XX (♂) : $XXXX$ (♀). In any case an investigation of the chromosomes in the females would be of interest. Whatever the exact nature of the mechanism in spiders it is clearly a very stable one from the evolutionary point of view. The autosomes vary in number from 9 pairs in *Anyphaena saltibunda* to 21 pairs in *Dugesiella henzi* (Painter, 1914). The sex determining mechanism in other arachnids is not known, since sex chromosomes have never been conclusively demonstrated (see p. 230).

A few other X_nO mechanisms may be briefly mentioned. The aphid *Euceraphis betulae* is $X_1X_2X_3X_4O$ in the male, the related species being XO (Shinji, 1931). All the *X*'s go to the same pole at the first meiotic division and, as in other aphids (see p. 300), the second spermatocytes which lack sex chromosomes degenerate, so that only one kind of sperm is formed.

In the nematodes (Goodrich, 1914, 1916; Walton, 1916, 1924) a number of species have X_nO mechanisms. *Belascaris triquetra* and *Ganguleterakis spinosa* are X_1X_2O, *Ascaris lumbricoides* is apparently $X_1X_2X_3X_4X_5O$, *Toxascaris canis* is $X_1X_2X_3X_4X_5X_6O$, while *Contracaecum incurvum* has as many as eight *X*'s. It does not appear possible to analyse the origin of these mechanisms at present, but it is obvious that the more complex ones have arisen from simpler types. The nematodes may be compared with the reduviids in this respect. In both groups highly complex mechanism have arisen; but in the former the starting point was an XO mechanism, in the latter an XY one.

In conclusion it may legitimately be asked: What is the general biological significance of the evolution of the sex chromosomes? Do new kinds of sex mechanisms become established in phylogeny because they are more effective as sex-determining agencies—or is their survival more or less accidental? Any attempt to answer these questions except in a most general way would be

* According to Sokolska (1925) the sex-chromosome mechanism of *Tegenaria domestica* is of a different type. But her account is confused and probably incorrect.

TABLE 13. *The known cases of multiple sex-chromosome mechanisms*

Group and species	Sex chromosomes in heterogametic sex	Author
PLATYHELMINTHES		
Schistosomum (*Bilharzia*) *haematobium**	X_1X_2O (?)	Lindner, 1914
NEMATODA		
Ascaris incurva (*Contracaecum incurvum*)	$X_1X_2X_3X_4X_5X_6X_7X_8Y$	Goodrich, 1914, 1916
Ascaris lumbricoides	$X_1X_2X_3X_4X_5O$	Walton, 1924
Belascaris triquetra	X_1X_2O	,, ,,
Ganguleterakis spinosa	X_1X_2O	,, ,,
CRUSTACEA		
OSTRACODA		
Heterocypris incongruens	$X_1X_2X_3X_4X_5O$	Bauer, 1940
ARACHNIDA		
Agelena naevia	X_1X_2O	Painter, 1914
Amaurobius sylvestris	X_1X_2O	,, ,,
Anyphaena saltibunda	X_1X_2O	,, ,,
Callipes imbecilla	X_1X_2O	,, ,,
Dolomedes fontanus	X_1X_2O	,, ,,
Dugesiella henzi	X_1X_2O	,, ,,
Epeira scolopetaria	X_1X_2O	,, ,,
E. sericata	X_1X_2O	,, ,,
Lycosa communis	X_1X_2O	,, ,,
Maevia vittata	X_1X_2O	,, ,,
Oxyopes salticus	X_1X_2O	,, ,,
Schizocosa crassipes	X_1X_2O	Hard, 1939
Xysticus triguttatus	X_1X_2O	Painter, 1914
INSECTA		
THYSANURA		
Thermobia domestica	X_1X_2O	Perrot, 1933
PLECOPTERA		
Perla marginata	X_1X_2O	Junker, 1923
MANTOIDEA		
Mantis religiosa	X_1X_2Y	King, 1931
Tenodera spp.	X_1X_2Y	King, 1931; Oguma, 1921; White, 1941*a*
Sphodromantis spp.	X_1X_2Y	White, 1941*a*
Hierodula sp.	X_1X_2Y	Asana, 1934
Stagmomantis carolina	X_1X_2Y	King, 1931
Choeradodis rhombicollis	X_1X_2Y	Hughes-Schrader, 1943*b*
SALTATORIA		
Paratylotropidia brunneri	X_1X_2Y	King and Beams, 1938
DERMAPTERA		
Anisolabis spp.	X_1X_2Y	Morgan, 1928; Sugiyama, 1933; Schrader, 1941*c*
Forficula auricularia (some individuals)	X_1X_2Y	Morgan, 1928; Callan, 1941*b*
HETEROPTERA		
Lygaeidae		
Lygaeus equestris (some individuals)	$X\,Y\,Y$	von Pfaler, 1937
Eremocoris erraticus	X_1X_2Y	,, ,,
Coreidae		
Syromastes marginatus	X_1X_2O	Wilson, 1909

TABLE 13 (*cont.*)

INSECTA (*cont.*)		
Pentatomidae		
Thyanta calceata	X_1X_2Y	Wilson, 1909
Galgulidae		
Galgulus (*Gelastocoris*) *oculatus*	$X_1X_2X_3X_4Y$	Payne, 1908
Nepidae		
Nepa cinerea	$X_1X_2X_3X_4Y$	Steopoe, 1925, 1931
Ranatra linearis	$X_1X_2X_3X_4Y$	Steopoe, 1927
Reduviidae		
Acholla multispinosa	$X_1X_2X_3X_4X_5Y$	Payne, 1909, 1910
Conorhinus sanguisugus	X_1X_2Y	Payne, 1909, 1912*a*
Diplocodus exsanguis	X_1X_2Y	Payne, 1909
Fitchia spinulosa	X_1X_2Y	Payne, 1909
Pnirontis modesta	$X_1X_2X_3X_4Y$	Payne, 1912*a*
Prionidus cristatus	$X_1X_2X_3Y$	Payne, 1909; Montgomery, 1901, 1906
Pselliodes cinctus	$X_1X_2X_3Y$	Payne, 1912*a*; Goldsmith, 1916
Rocconata annulicornis	X_1X_2Y	Payne, 1909
Sinea diadema	$X_1X_2X_3Y$	Payne, 1909; Montgomery, 1901, 1906
S. complexa	$X_1X_2X_3Y$	Payne, 1912*a*
S. confusa	$X_1X_2X_3Y$	,, ,,
S. spinipes	$X_1X_2X_3Y$	,, ,,
S. rileyi	$X_1X_2X_3X_4X_5Y$	,, ,,
Cimicidae		
Cimex rotundatus	X_1X_2Y	Slack, 1939*a*, *b*
C. stadleri	X_1X_2Y	,, ,,
C. columbarius	X_1X_2Y	Darlington, 1940*a*
C. lectularius	3–16 X's and a Y number of X's variable	Slack, 1939*a*, *b*; Darlington, 1940*a*
HOMOPTERA		
Aphididae		
Euceraphis betulae	$X_1X_2X_3X_4O$	Shinji, 1931
Stomaphis yanois	X_1X_2O	Honda, 1921
Phylloxera caryaecaulis	X_1X_2O	Morgan, 1906, 1908, 1909*a*, *b*, 1912, 1915
Ph. fallax	X_1X_2O	
NEUROPTERA		
Ascalaphus libelluloides	Number of X's and Y's variable	Naville and de Beaumont, 1933
LEPIDOPTERA		
Phragmatobia fuliginosa (3 races)	XY, XY_1Y_2, $X_1X_2Y_1Y_2$	Seiler, 1925
DIPTERA		
Drosophila miranda	X_1X_2Y	Dobzhansky, 1935; Dobzhansky and Tan, 1936*a*, *b*; McKnight, 1939; Koller, 1939
Drosophila americana	$X\ Y_1Y_2$	Spencer, 1940*a*; Hughes, 1938, 1939; Patterson, Stone and Griffen, 1940
Drosophila prosaltans	$X_1X_2Y_1Y_2$	Dobzhansky and Pavan, 1943
COLEOPTERA		
Cicindela spp.*	X_1X_2O	Stevens, 1906, 1909; Goldsmith, 1919
*Blaps lusitanica**	$X_1X_2X_3X_4Y$	Nonidez, 1920 (see also Wilson, 1925)

* In these cases the interpretation is uncertain. Lindner probably misinterpreted the chromosomes of *Schistosomum* (see Ikeda and Makino, 1936 and Niiyamasena, 1940).

premature at the present time. In a great many groups the sex mechanism seems to be extremely stable, the only differences between the X's and Y's of different species and genera being quantitative (variation in the length of the differential region). It is of course quite uncertain to what extent the intergeneric differences in length of the X in a group such as the Empusinae are adaptive. Theoretically one might suppose that since the rest of the genetic system is continually evolving the apparatus which produces an $X : A$ balance must evolve *pari passu*. Thus if we regard the complex of autosomal genes as a 'lock' and the sex-determining differential regions of the chromosome set as a 'key' which switches the mechanism from one state to another, then the evolution of the 'lock' must be accompanied by an evolution of the 'key', even though the essential nature of the mechanism remains the same. No species is known in which the length of the X varies in wild individuals in the way that the Y of *Drosophila pseudoobscura* does—although the variation in number of X's observed in the bed bug is a phenomenon of a similar nature.

That the $X : A$ balance can be upset, even in a group like the Orthoptera, with a 'highly evolved' sex-chromosome mechanism, is suggested by the work of Ohmachi (1935*b*, 1940) on intersexes in a species of *Homoeogryllus*. These crickets normally show a very pronounced sexual dimorphism, but in certain strains male intersexes (i.e. males with some of the external characters such as the tegmina 'feminized') are produced. These intersexes are probably analogous to those known in several species of *Drosophila* where single mutations can upset a system of balanced sex genes.

The evolutionary significance of multiple sex-chromosome systems is not clear, since most of them must have been mechanically inefficient when they first arose, giving rise to a certain percentage of non-disjunctional gametes. Many multiple mechanisms are probably short-lived 'failures' in an evolutionary sense. It is possibly significant that, of the species which are known to have become X_1X_2Y or $X\ Y_1Y_2$ through the inclusion of a pair of autosomes in the sex-chromosome mechanism, no less than three (*Drosophila miranda*, *D. americana* and *Paratylotropidia brunneri*) are extremely rare and localized forms with very small natural populations. In some cases multiple mechanisms have probably been an intermediate stage in the evolution of one type of 'simple' mechanism from another. Although we do not yet know of any actual instance in which a complex mechanism has given rise to a simple one by reversion it is probable that such an event has occurred in the past history of the *obscura* group of *Drosophila*, and it is not difficult to imagine how fusion of the two X's in an X_1X_2 or X_1X_2Y species would produce a new kind of XO or XY mechanism.

CHAPTER XII

SEX DETERMINATION BY MALE HAPLOIDY

In certain groups of animals a method of sex determination exists which does not seem to depend on special sex chromosomes and which consequently bears no resemblance to the mechanisms discussed in the last chapter. The method in question may be described as *haplodiploidy*, since the males develop from unfertilized, haploid eggs, the females from fertilized, diploid ones.

Haplodiploidy may be referred to as *arrhenotoky*, in contrast to *thelytoky* (the production of females by diploid parthenogenesis).* The two phenomena are in reality very different, although they often coexist in the same group (or even, sometimes, in the same species). Thus thelytoky is purely a reproductive device, which does not involve the development of any new sex-determining mechanism, whereas arrhenotoky is a special method of ensuring the production of two sexes. One important difference between haplodiploidy and the sex-chromosome mechanism is that whereas the latter automatically ensures a 1 : 1 sex ratio (apart from minor variations due to differential viability of gametes or zygotes), the former may give any sex ratio from 0 : 100 to 100 : 0 according to environmental or genetic circumstances. Thus from the point of view of reproductive economy haplodiploidy is an infinitely plastic system in which (given sufficient time) selection can bring about any sex ratio which is in the interest of the species.

Thelytoky has undoubtedly arisen repeatedly in most phyla except the Vertebrata, and can be induced experimentally in a variety of ways: arrhenotoky, on the other hand, is only known to have arisen about seven times in the whole history of the Metazoa (five times in insects, once in arachnids and once in rotifers). This is hardly surprising, since the origin of arrhenotoky—although the details are unknown and mysterious—clearly involves the replacement of the old sex-determining mechanism by an entirely new one, an event which can only have taken place under very special circumstances.

The four insect orders which show haplodiploidy (in some or all of their species) are the Hymenoptera, Homoptera, Thysanoptera and Coleoptera. In the Hymenoptera the whole group seems to have adopted male haploidy, the sex of the individual being determined by whether the egg is fertilized or not, so that here the mechanism is probably of great antiquity, and any attempt to speculate as to its origin would be fruitless. In the Homoptera the vast majority

* Some authors have used the terms *arrhenotoky* and *thelytoky* where no parthenogenesis is involved (e.g. in the case of 'monogenic' females in *Sciara*). While such a usage may be etymologically correct it is more convenient to restrict the use of these terms to parthenogenetic forms, employing the words *androgeny* and *gynogeny* in other cases.

of the species (including all the Auchenorrhyncha and the Aphididae) have a sex-chromosome mechanism (usually of the *XO* : *XX* type), but a few aberrant coccids and aleurodids have adopted male haploidy. In the Thysanoptera a haplodiploid mechanism certainly occurs in some forms, but whether all males are haploid in this group is still uncertain. Among the Coleoptera a single species (*Micromalthus debilis*, the only known member of the family Micromalthidae) has male haploidy combined with a very complex life history (see p. 278). Lastly, in the mites the families Gamasidae and Argantidae seem to have diploid males (Sokolow, 1934; Opperman, 1935), while the Tetranychidae and Tarsonedidae have a haplodiploid system (Schrader, 1923*a*; Pätau, 1934, 1936; Cooper, 1937, 1939). The situation in the other families of mites is not known, although some species such as *Cheyletus eruditus* are certainly thelytokous.

When we say that the male of a given species is haploid we usually mean that the germ-line nuclei contain half the number of chromosomes seen in the germ-line of the female. Accurate comparisons between the somatic nuclei have in most cases not been made: in view of the widespread occurrence of endopolyploidy in insects it seems quite probable that most of the somatic tissues in haplodiploid forms are, in actual fact, highly polyploid in both sexes. They have been derived, however, from haploid and diploid cells in the male and female embryos. It is unfortunately not known whether the somatic nuclei of male and female haplodiploids reach the same degree of polyploidy in the course of development, or whether tissues which are octoploid in females are tetraploid in males, and so on. Oehninger (1913) claimed that she could find no differences between the nuclear sizes of male and female Bees, but her work was carried out before the existence of endopolyploidy was known.

In the Hymenoptera the cytology of the sawflies has been studied by many authors, particularly Peacock and Gresson (1931), Sanderson (1933) and Smith (1941). These are the most primitive members of this phylogenetically isolated order, yet all species in which males occur show haplodiploidy and no sex chromosomes have ever been detected (in some sawflies, such as the European species *Pontania proxima*, *Pteronidea hortensis*, *Cimbex connata* and *Croesus brischkei*, males are absent altogether, thelytoky being complete). In a few species of Hymenoptera arrhenotoky and thelytoky coexist (Peacock, 1928), but such a situation seems to be far from common, although a single genus frequently contains both thelytokous and bisexual species. In the bee and in a number of other species it has been shown that virgin females or senile ones which have exhausted the supply of sperm in the seminal receptacle will produce only sons, as was discovered long ago by Dzierzon. In females which still possess a quantity of sperm the sex of the individual offspring probably depends on whether the muscular apparatus of the seminal receptacle contracts or not at the time when the egg is laid, a mechanism which probably operates throughout the order, in spite of considerable variation in the muscular anatomy of the female genital

system (in some species it is possible that fertilized females produce nothing but female offspring).

Since male Hymenoptera are haploid it is clear that they must possess an 'anomalous' meiotic mechanism. The cytological details have been worked out in the sawflies *Pteronidea* (Sanderson, 1933), *Diprion* (Smith, 1941) and *Sirex* (Peacock and Gresson, 1931), the chalcid *Paracopidosomopsis* (Patterson and Porter, 1917), the cynipid *Neuroterus* (Doncaster, 1910, 1911, 1916), the braconid *Habrobracon* (Whiting, 1918; Torvik-Greb, 1935), the ant *Camponotus* (Lams, 1908), the wasp *Vespa* (Meves and Duesberg, 1908) and in several genera of bees such as *Osmia* (Armbruster, 1913), *Xylocopa* (Granata, 1909) and *Apis* (Meves, 1907; Mark and Copeland, 1906; Doncaster, 1906*a*, 1907*a*; Nachtsheim, 1913). In none of these forms does any pairing take place during the prophase of meiosis. A first meiotic spindle is formed, but there is no proper anaphase. In most of the Aculeata the first 'division' merely results in the extrusion from the spermatocyte of a small non-nucleated 'bud' of cytoplasm which undergoes degeneration. In the sawflies even this remnant of a first meiotic division seems to have been lost, since no bud is pinched off from the main cell in *Diprion*, *Pteronidea* and other genera (Sanderson, 1933; Smith, 1941).

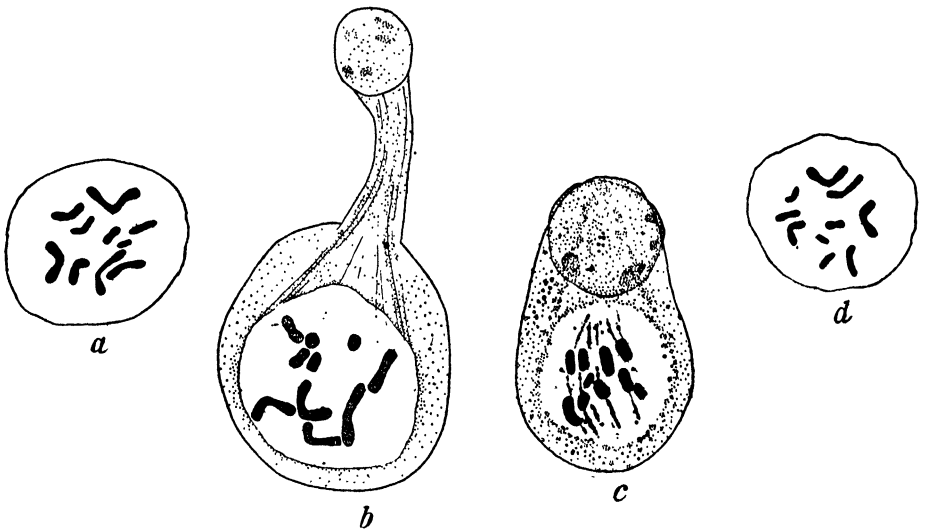
The second meiotic division is a normal mitosis in all the Hymenoptera; it gives rise to two equal spermatids in all families except the true bees (Apidae). In the latter the second division involves an extremely unequal partition of the cytoplasm, so that another small bud (but this time a nucleated one) is cut off from the single functional spermatid. Thus in sawflies, braconids, ants and wasps two sperms are formed from each spermatocyte, while in bees only one is produced.

The functional significance of these cytoplasmic phenomena is far from clear. The bees are morphologically the most 'highly evolved' group of the Hymenoptera, but they have preserved a remnant of the first meiotic division that has been lost in the far more primitive sawflies. Yet when we come to the second meiotic division the bees seem to have acquired a specialized mechanism whereby the cytoplasm is unequally distributed to the two spermatids, one of which is functionless.

A considerable divergence of opinion has existed as to the exact chromosome number of the honey bee, but this controversy does not affect the interpretation of the general course of meiosis, although it had an unfortunate effect in causing doubts as to the interpretation of haplodiploidy in the early part of the century.

In the oogenesis of the Hymenoptera pairing and chiasma formation take place in the usual manner, except in the thelytokous species (Doncaster, 1906*b*; Speicher, 1936*a*; Smith, 1941; Hogben, 1920). Thus in all normally bisexual Hymenoptera crossing-over takes place on the female side, although not on the male.

From a genetical standpoint, male haploidy presents a number of unsolved problems. It will be recalled that in *Drosophila* sex appears to depend upon a balance between male-determining and female-determining genes. At first sight it seems impossible that such a mechanism should be operative in the haplo-diploid scheme, since any genic equilibrium will be exactly the same in both sexes. Moreover, although haploid individuals of *Drosophila* have never been obtained, haploid patches of tissue in a mosaic fly are female in character (Bridges, 1925*a*, *b*, 1930). Thus it appeared for a time as if sex in organisms like the Hymenoptera must depend on a ratio between the chromosomes and the



Text-fig. 113. Meiosis of a haploid male *Habrobracon*. *a*=a spermatogonial metaphase (10 chromosomes); *b*, *c*=first meiotic divisions (pinching off of a cytoplasmic bud); *d*=second metaphase. From Torvik-Greb (1935).

cytoplasm. The whole question was in a very uncertain state (see Schrader and Sturtevant, 1923) when the Whitings (1925, 1927) discovered that in the braconid wasp *Habrobracon juglandis* diploid males could be obtained in certain laboratory crosses. These diploid males were clearly derived from fertilized eggs (and not by diploid parthenogenesis, as might otherwise have been supposed), since they showed genetical characters inherited from both parents. Several beekeepers (e.g. Cuénot, 1909) had previously claimed to have obtained drones showing a mixture of paternal and maternal characters (or paternal characters alone) in interacial bee crosses. It is possible, however, that the queen bees they used in their experiments were themselves of hybrid origin (or were, at any rate, not homozygous) so that segregation could take place in their offspring. This explanation cannot apply in the case of the diploid males in *Habrobracon*, where

the genetic purity of the breeding stocks has been carefully established. Nor can there be any doubt about the diploidy of the 'biparental' males, which has been confirmed cytologically.

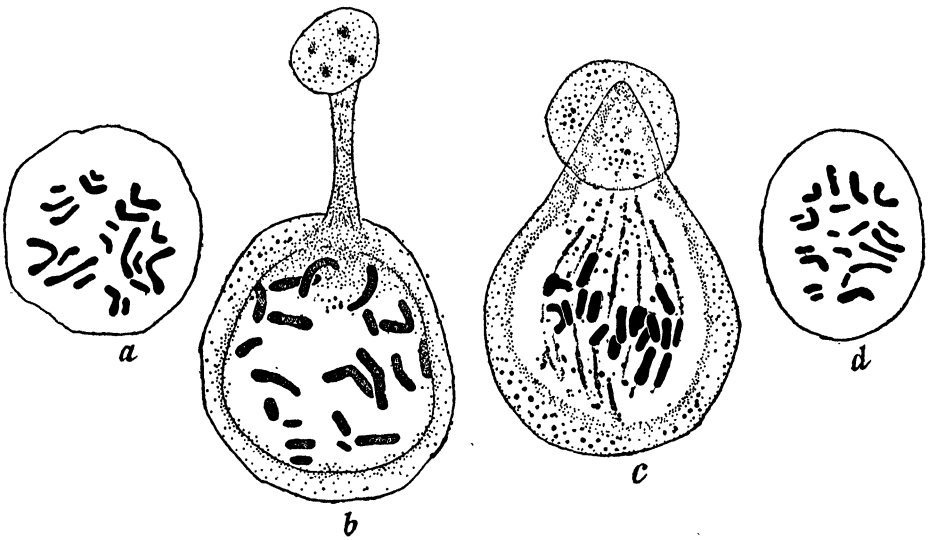
The discovery of diploid males, even though only in a single genus, naturally tended to discredit the idea that maleness in Hymenoptera was a direct consequence of haploidy. As a result of genetical experiments with *Habrobracon* stocks carrying the gene *fused* it was found that the female wasp is heterozygous for a sex factor which is closely linked with *fused*. Thus the females are heterogametic and may be designated x_1x_2, x_2x_3, ..., etc. The normal haploid males are of several phenotypically indistinguishable kinds x_1, x_2, x_3, ..., etc., while the diploid males, which are only obtained by close inbreeding, are x_1x_1, x_2x_2, ..., etc.

On this theory femaleness would depend on some sort of interaction between the different x factors, while all haploid or homozygous individuals would automatically be male. It can be stated quite definitely that no visible cytological difference exists between the chromosomes carrying the different kinds of x factors, but it is by no means certain that the latter are really single genes—they may be very short differential regions, deficiencies or duplications. In the chalcid *Pteromalus puparum* Guhl and Dozorcheva (1934) and Dozorcheva (1936) claimed to have observed visibly distinguishable X and Y chromosomes, but their findings have not been confirmed by any other workers, and it must now be regarded as probable that cytologically distinguishable sex chromosomes do not exist in any of the Hymenoptera. On the other hand, Dozorcheva's genetical evidence strongly suggests that the mechanism of sex determination in *Pteromalus* is of the same general type as in *Habrobracon* (Whiting, 1940).

The special genetic mechanism of sex determination in *Habrobracon* has thus proved to be fairly complex. It is known that crosses between unrelated individuals give a high percentage of viable eggs and no diploid males, whereas crosses between near relatives give many inviable eggs that fail to hatch and a certain number of diploid males. Originally Whiting assumed the existence of a process of 'differential maturation', whereby eggs that had been penetrated by an x_1-bearing sperm eliminated the maternal x_1-bearing chromosome in the polar body and, conversely, that eggs penetrated by an x_2-bearing sperm cast out the x_2-bearing chromosome at meiosis (Whiting, 1935). This hypothesis has now been discarded by its author (Bostian, 1939; Whiting, 1939) on account of further genetical evidence. Whiting's later theory assumed that sex in *Habrobracon* is determined by a series of multiple allelomorphs of different 'potencies'. Heterozygosis for any two of these (or at any rate for most pairs of non-identical allelomorphs) produces a female zygote with a high viability, while homozygosis for any member of the series leads to maleness, but at the same time lowers the viability, so that most of the potential diploid males never hatch from the egg. If this theory is correct it would seem that close inbreeding must be highly

detrimental to a *Habrobracon* population, and that in nature a certain amount of heterozygosity is essential for the maintenance of the species. An extremely neat proof of the theory that femaleness in *Habrobracon* depends on heterozygosis is provided by mosaic males (derived from binucleate eggs) in which there is a certain amount of 'feminization' on either side of the frontier between tissues of different genetical constitution.

In a further paper (1943*a*) Whiting has demonstrated the existence of at least nine different *x* factors which behave as multiple alleles (they may be either single genes or short differential regions in which crossing-over does not take place). These *x* factors have been shown to occupy an interstitial position in a



Text-fig. 114. Meiosis of a biparental diploid male *Habrobracon*. *a*=a spermatogonial metaphase (20 chromosomes); *b*, *c*=first meiotic division (pinching off of a cytoplasmic bud); *d*=second metaphase. From Torvik-Greb (1935).

chromosome which seems to have a genetic length of at least 350 units (Whiting, 1943*a*), and which must, accordingly, have a very high chiasma frequency (this point has not been checked cytologically, since Speicher (1936*a*) only studied the later stages of oogenesis).

One of the most remarkable things about the *Habrobracon* sex-determining mechanism is that none of the various combinations of the $x_1 \ldots x_9$ regions seems to lead to intersexuality; the diploid males, although sterile, are entirely male in appearance. Two types of genetically determined intersexuality are known in *Habrobracon*, but they seem to have nothing to do with the normal mechanism of sex determination; one of them 'feminizes' haploid wasps, the other 'masculinizes' females (Whiting, 1943*b*).

The diploid males are almost completely sterile; their meiosis has been studied by A. R. Whiting (1927) and by Torvik-Greb (1935). Except for the number of chromosomes it follows exactly the same course as in the haploids. No pairing takes place between the homologous chromosomes, and the first meiotic 'division' is of the usual hymenopteran type, resulting in the casting out of a small non-nucleated bud of cytoplasm. It is therefore clear that the peculiar type of meiosis found in the male Hymenoptera is genetically determined, and is not merely an automatic consequence of haploidy (cf. the Iceryine coccids (p. 276), where the reverse is the case). According to Bostian (1936) it is occasionally possible to obtain triploid females by mating diploid males with normal diploid females, so that the sterility of the diploid males is incomplete. In a Japanese species, *Habrobracon pectinophorae*, diploid males were obtained by inbreeding and found to be relatively fertile (Inaba, 1939). They gave rise to triploid female offspring when crossed with normal diploid females.

Although the special genetic mechanism which controls the determination of sex in *Habrobracon* is of considerable interest, there is no evidence that it exists throughout the Hymenoptera. No diploid males are known for certain in other members of the order, nor in the various other groups where haplodiploidy exists. For the time being, therefore, it would seem best to regard haploidy as being male-determining *per se* in these other forms, while admitting that in *Habrobracon* a special genetical mechanism seems to have supplanted the original scheme. Nevertheless, similar genetical mechanisms may be quite common in the Hymenoptera and in other haplodiploid groups. The simplest way to determine whether this is so or not would seem to be to carry out extensive inbreeding in these forms and find out whether diploid males were produced or not. It must be remembered, however, that diploid males seem to have a low viability in *Habrobracon*, and they may be absolutely inviable in some other forms.*

Smith (1941) has argued against the view that the *Habrobracon* mechanism exists throughout the Hymenoptera, on the ground that many thelytokous species are known in which meiosis occurs, the chromosome number being subsequently restored by a fusion of the second polar body nucleus with the egg nucleus. Heterozygosity for an *x*-factor would only be maintained in such

* The work of D: eyfus and Breuer (1944) on the chromosome cycle of the Scelionid Hymenopteran *Telenomus fa, iai* appeared after the above was written. *Telenomus* seems to differ from the other Hymenoptera studied up till now in that it is the second meiotic division in the male which results in the casting out of a nucleated bud destined to degenerate, the first division being an ordinary mitosis. The authors claim to have observed a cytologically distinguishable pair of *X* and *Y* chromosomes in the female, but the evidence is far from convincing, and their account of an unequal division in the spermatogonia even less so. One point of interest is that brother-sister mating seems to be the rule in *Telenomus fariai*, copulation taking place within the egg-shells of the host, *Triatoma* (the Scelionids are egg-parasites). Yet in spite of this obligatory inbreeding no diploid males were observed, thus suggesting that the genetical mechanism of sex determination is not the same as in *Habrobracon*.

forms if a single chiasma were regularly formed between the centromere and the *x*-regions. But it is quite possible that this is just what does happen.

TABLE 14. *Chromosome numbers in* Diprion *sawflies (from Smith,* 1941, 1942)

Species	Type of parthenogenesis	Chromosome no.* ♂	♀
D. polytomum (race A)	Facultative thelytoky	6	12
D. polytomum (race B)	Obligatory thelytoky	7	14
D. abieticolor	Facultative thelytoky	7	14
D. pallidum	,, ,,	7	14
D. nemorum	,, ,,	7	14
D. simile	,, ,,	14	28
Neodiprion sertifer	,, ,,	7	14
N. dubiosus	?	—	14
N. lecontei	?	7	14
N. swainei	?	—	14

* The chromosomes of all these species are metacentric.

It has been suggested by Greenshields (1936) that when the hymenopteran mechanism of haplodiploidy originated the males may have been diploid, the females tetraploid. This, of course, is pure speculation, since the evolutionary origin of the order goes back at least as far as the Trias. The genetical data on *Habrobracon* and the chromosome numbers of present-day Hymenoptera do not provide any support for Greenshields' theory (Speicher, 1936*b*). But in one species of Hymenoptera (out of several dozen that have been studied cytologically from one point of view or another) there is good reason to believe that a diplo-tetraploid state of affairs does exist. The species in question, *Diprion simile*, is one of the sawflies. Whereas most of the species of the two genera *Diprion* and *Neodiprion* have 14 chromosomes in the female and 7 in the male (see Table 14), *Diprion simile* has 28 in the female and 14 in the male (Smith, 1941). The meiosis of the male is of the usual hymenopteran type and bivalents (not quadrivalents) are formed in the eggs. If this species really is a polyploid it is rather difficult to see how it could have arisen from a form in which diploid individuals were female unless some kind of *Habrobracon* mechanism were present (if the diploid males of *Habrobracon* were fertile one could imagine them becoming the foundation of a diplotetraploid race analogous to *Diprion simile*). Smith has suggested that *simile* may have arisen as an allotetraploid, but there is no definite evidence for this. The fact that no quadrivalents are formed in the egg is not an argument against the existence of polyploidy in *D. simile*, since the bivalents are small and the chiasma frequency low. If heterozygosity for an *x* factor determines femaleness in *D. simile* it would be interesting to know how the males are kept homozygous.

We have already described the chromosome cycle in various genera of coccids

in Chapter IX; it will be remembered that in the tribe Llaveini there is an *XO* : *XX* sex-chromosome mechanism, while in the specialized Eriococcidae and Lecaniidae sex chromosomes are apparently absent, although both sexes are diploid. In the tribe Iceryini (which is rather closely allied to the Llaveini) the males are, as far as is known, always haploid (Hughes-Schrader, 1925*b*, 1926, 1927, 1930*a*, *b*; Hughes-Schrader and Ris, 1941; Schrader and Hughes-Schrader, 1926). The chromosome cycle has been worked out in *Icerya littoralis*, *I. montserratensis*, *Echinicerya anomala*, *Crypticerya rosae* and *Steatococcus tuberculatus*; the details appear to be almost identical in all five species. The males have only two chromosomes in their cells, the females four. During oogenesis two bivalents are formed, so that the mature eggs are haploid; if fertilized they develop into females, if unfertilized into males. The meiosis of the male involves a single 'equational' division, so that only two sperms are formed from each spermatocyte.

Icerya purchasi, which is well known as a pest of citrus trees in all warm countries, differs from the other five species so far studied in that the 'females' have become transformed into functional hermaphrodites which produce sperms as well as eggs. The basic facts were discovered by Pierantoni (1913), who unfortunately made a number of errors such as believing that true females as well as hermaphrodites existed; it was left to Hughes-Schrader to clear up the confusion and complete the cytological analysis.

Externally, the hermaphrodites of *I. purchasi* do not differ in general appearance from the females of the other Iceryini, but they possess an ovotestis in which the central part is testicular, the cortex being ovarian. The insects are protandric, since the sperms mature in the nymphs long before the eggs are fully formed.

True males also occur in *I. purchasi*, but are usually very rare, although they may be much commoner in certain localities (Menozzi, 1926; Costantino, 1938*a*, *b*); they are haploid, having only two chromosomes like those of the related species.

The cytology of the hermaphrodite individuals is quite unique in character. They are, in fact, mosaics, the testicular part of the gonad being haploid, the ovarian part and the somatic tissues diploid. The germ cells of the future hermaphrodite are all clearly diploid up to the time of hatching from the egg, but shortly afterwards (i.e. at the beginning of the first nymphal instar) haploid nuclei make their appearance in the gonad. They have presumably arisen by some sort of 'reductional' process, but this has not been actually observed. The haploid cells form the core of the gonad, from which the testis later develops. The spermatogenesis of these cells follows exactly the same course as in the true males, i.e. there is only one meiotic division, which is 'equational'. In two instances, however, Hughes-Schrader observed a few diploid nuclei undergoing spermatogenesis in the gonad of a hermaphrodite; they went through two meiotic divisions instead of one, and, although no bivalents were formed, the chromosome number was halved, and the sperms produced were haploid.

The hermaphrodites of *I. purchasi* seem to be normally self-fertilizing, but they are also capable of copulating with the occasional males which arise from eggs that have escaped fertilization. Since they resemble true females in all external respects their true nature was not suspected until they were studied cytologically. The hermaphrodites are incapable of fertilizing one another, since they have no external male genitalia, and their pattern of behaviour is entirely female.

In seeking to understand the origin of male haploidy in the Iceryini it is clear that we should disregard the hermaphroditism of *I. purchasi*. It is a secondary specialization, superimposed at a later date on the straightforward haplodiploidy of the other Iceryini, which was presumably derived from a chromosome cycle somewhat like that of the Llaveini. Since the latter are *XO* in the males it is probable that the ancestors of the Iceryini also had an *XO* : *XX* sex-determining mechanism. At some stage in the history of the group one set of autosomes was lost in the males, thus leading to the establishment of haploidy. If the diploid number was already four in the females and three in the males, then the 'set' of autosomes which was lost was, in fact, a single chromosome. Thus in the evolution of the chromosome cycle of the Iceryini there were three main steps: (1) the partial disappearance of bivalent formation in the males (which has already happened in the Llaveini), (2) the establishment of male haploidy, (3) the transformation of the female into a hermaphrodite mosaic (a step which, as far as we know, has only taken place in *I. purchasi*). The fact that diploid spermatocytes of *I. purchasi* go through two meiotic divisions suggests that the single equational division of the male Iceryini is not a genotypically determined character, but is merely a mechanical consequence of haploidy (cf. Torvik-Greb's observations on the meiosis of diploid males in *Habrobracon*, see p. 273). *Icerya purchasi* is the only species of animal in which a normal and regular hermaphroditism is known to depend on mosaicism. Whereas other hermaphrodites (e.g. flatworms, pulmonate molluscs, etc.) are 'intersexual' in character (to use Goldschmidt's terminology), it is 'gynandromorphic'. One might expect that a newly arisen haplodiploid system might possibly prove unstable in evolution. If one or other sex were to become an intersexual hermaphrodite it would not be really surprising. But it is clear that the evolutionary origin of hermaphroditism in *I. purchasi* has nothing to do with any imperfection of the haplodiploid system; it was presumably due to a mutation or mutations which produced the special type of reduction division that occurs in the germ-line. The males of this group are very fragile and short-lived, so that any reproductive device which rendered them unnecessary would probably possess a considerable selectional advantage. In the genus *Gueriniella*, which also belongs to the tribe Iceryini, no males are known to exist (Vayssière, 1926), so that diploid parthenogenesis (thelytoky) also exists in this group of coccids.

Only two other instances of normal hermaphroditism are known in insects.

In the stone-fly *Perla marginata* (Schoenemund, 1912; Junker, 1923), the males regularly have a non-functional ovary at the anterior end of the testis, but the chromosomal constitution of this organ is the same as that of the rest of the body. Other species of the genus do not seem to possess this apparently useless gonad.

We have already mentioned the hermaphroditism of the Termitoxeniidae (see p. 246), which has not yet been studied cytologically, but which is presumably functional.

In the white flies (Aleurodidae, order Homoptera) some species have haploid males, but whether all males are haploid in this group is unknown (Schrader, 1920; Thomsen, 1927). In *Trialeurodes vaporarium* there is one race which is arrhenotokous, while a second race consists exclusively of thelytokous females, a state of affairs similar to that found in some sawflies and other Hymenoptera (see p. 268). There is only one 'equational' meiotic division in the haploid males of aleurodids.

The exact status of male haploidy in the Thysanoptera is still rather doubtful. Shull (1917) showed that in *Anthothrips* (=*Neoheegeria*) *verbasci* unfertilized females produced sons but no daughters, thus strongly suggesting that this species is haplodiploid. Unfortunately, he did not work on the cytology of the males and the situation in other species of this order is not known, although a large number of species are certainly thelytokous (Pomeyrol, 1928).

In the mites it has been shown by Schrader (1923*a*), Pätau (1934, 1936) and Cooper (1939) that the species *Tetranychus bimaculatus*, *Pediculoides ventricosus* and *Pediculopsis graminum* have male haploidy. As in the iceryine coccids the chromosome number of these species is very low (haploid number = 3 in the species so far studied). Sokolow (1934) and Opperman (1935) have shown that the Parasitidae (Gamasidae) and Argantidae have diploid males, so that it seems possible to subdivide the Acarina into two great subdivisions according to their method of sex determination. In the spermatogenesis of *Tetranychus*, *Pediculoides* and *Pediculopsis* there is only a single 'equational' meiotic division.

In the rotifers, although it is generally accepted that males develop from unfertilized eggs which have undergone two meiotic divisions, the existence of male haploidy cannot be regarded as finally proven. The literature on the cytology of the Rotifera is in a very chaotic state, and the various papers are in disagreement on many important points, so that it is difficult to arrive at any firm conclusions. Thus in *Asplanchna intermedia*, Whitney (1924) claimed that the somatic (diploid) number in the female was 52, and that the eggs destined to develop parthenogenetically into males contained 26 chromosomes. Tauson (1924, 1927), on the other hand, stated that the somatic number in this species is 24, and that both sexes are diploid. She has described a 'reduction division' occurring in the four primordial spermatogonia (a state of affairs which, if true, would be comparable with the reduction division of the louse). According to

Tauson there is only one meiotic division in the male *Asplanchna*, which is equational in type. Some of the discrepancies between the two accounts may be due to differences in the material—perhaps the American and Russian forms of *Asplanchna intermedia* differ in chromosome number—but it is impossible to reconcile all the disagreements on this assumption. Whitney's later (1929) account of spermatogenesis in *Asplanchna amphora* is completely at variance with Tauson's description of the process in *A. intermedia*. He regards the males as haploid from the beginning, and consequently does not confirm Tauson's account of a reduction division in the primordial spermatogonia. He further reports the presence of two kinds of sperms, large motile ones and small functionless ones. Although his account is more credible than that of Tauson, it is obvious that the whole of this work will have to be repeated before any definite statements can be made about the chromosome cycle in the Rotifera. The work of Shull (1921) and Storch (1924), although interesting, does not help very much to clear up the cytological problem.

A single species of beetle is now known, thanks to the work of Scott (1936, 1938), to possess haploid males. It had earlier been shown by Barber (1913*a*, *b*) that this species (*Micromalthus debilis*), which bores in rotten wood, has a very complicated life cycle, similar in many respects to that of the cecidomyids *Oligarces* and *Miastor*. Some of the larvae are paedogenetic, while others give rise to the sexual males and females. There are two main types of paedogenetic larvae. The first are viviparous and produce only female offspring, the second are oviparous and give rise to males. The adult females were shown by Scott to be diploid, while the males are haploid. It is not known whether the males actually fertilize the females, but they certainly produce sperm. It is thus still an open question whether sexual reproduction takes place in *Micromalthus*—the males may be entirely functionless.

The meiosis of the males is, like that of all haploids, anomalous. At the first meiotic division a unipolar spindle is formed, to the 'base' of which all the chromosomes are attached. This 'division' is entirely abortive, since neither chromosomes nor cytoplasm divide. The second division is a normal mitosis, so that two sperms are formed from each spermatocyte.

Since *Micromalthus debilis* is the only member of its genus and family it would clearly be useless to speculate as to the origin of its peculiar reproductive and chromosomal cycle. One would like to know what has happened to the sex chromosomes, but Scott's account does not contain any information bearing upon this point, although the haploid number is 10 and the parthenogenetic eggs which will develop into females contain 20 chromosomes.

In theory, at any rate, the evolutionary genetics of organisms with male haploidy should be very different from that of groups in which both sexes are diploid. In the latter recessive mutated genes can and do exist in wild populations in the heterozygous state. Thus most wild populations of *Drosophila* species

contain numerous recessive genes, most of which would be deleterious or lethal if present in the homozygous condition. There is thus a reservoir of 'hidden variation' in wild populations of diploid species, and it is probable that a certain number of these deleterious recessives eventually become 'neutral' or even 'beneficial', either as a result of changes in the genetic constitution of the species or as a result of changes in the environment.

In a species with haploid males there can be no 'reservoir of hidden variability', since all recessives will be subject to the full effects of selection in the males. In this respect they will resemble the sex-linked genes of *Drosophila*. It is now known that sex-linked mutants are only very rarely found in wild populations of *Drosophila*, and it seems likely that the females of haplodiploid organisms must be far more homozygous in nature than those of animals with diploid males. On the other hand, a 'beneficial' mutation will, other things being equal, have a better chance of spreading through a population and establishing itself in a species with haplodiploidy than in one with diploid males. It is, of course, possible that the chromosome sets of the Hymenoptera contain numerous and extensive 'repeats', in which case a reservoir of hidden variability could exist in respect of all those loci situated in repeated regions (which would be present twice in males and four times in females).

Recessive mutants that are sex limited in their expression, so that they produce no effect in the male, will be in a special position in organisms with male haploidy. Such mutations may exist in wild populations for a long while, even though deleterious, since in the males they will not affect the phenotype. This fact may possibly explain why in the social Hymenoptera the males are all of one type while the females are differentiated into several castes. We are not suggesting here that the various female castes are genotypically different—merely that a large number of mutants whose effects are limited to the female sex may have accumulated in the species, gradually building up a genotype that is very plastic in the female sex (producing several entirely different phenotypes according to the environment and nutrition of the larvae). In termites, where both sexes are probably diploid (although their cytology has never been fully worked out), the males as well as the females are differentiated into several castes (Light, 1942).

To what extent structural rearrangements are able to establish themselves in organisms with male haploidy is still unknown. Most of the groups in which haplodiploidy occurs are not particularly suitable for detailed work on chromosome structure, and the chromosome sets of the Hymenoptera, iceryine coccids and mites, at any rate, seem to be rather uniform, with few obvious differences between closely related species.

CHAPTER XIII

THE EVOLUTION OF PARTHENOGENESIS*

In the previous chapter we have described one type of parthenogenesis, that which is associated with male haploidy. We have now to consider thelytoky, of which two main types exist, *complete parthenogenesis* (where only females exist and every individual arises from an unfertilized egg) and *cyclical parthenogenesis* (where one or more parthenogenetic generations alternate with a bisexual one throughout the seasons).

Complete parthenogenesis constitutes a highly distinct genetic system in which sexuality has been entirely abolished, and recombination of genes is no longer possible. It occurs sporadically in a large number of groups, but never seems to have become widely established in any of the major groups of the animal kingdom. Since it has clearly arisen on many different occasions in the course of evolution it is natural that the cytological details should show considerable variation. Parthenogenetic forms seem to be frequently successful in the struggle for existence, but sooner or later the inherent disadvantages of this type of genetic system must be expected to lead to a lack of adaptability, followed by extinction, or perhaps sometimes by a return to sexuality. Nevertheless, there are a great number of forms, apparently highly successful at the present time, in which males are completely unknown. Thus we often see two 'races' of the same species, one bisexual and the other parthenogenetic, and in other cases we have genera containing both bisexual and parthenogenetic forms. On the other hand, there are very few instances of large groups all the members of which show complete parthenogenesis (the rotifers of the group Bdelloidea (see Winkler, 1920) are almost the only example of such a state of affairs, as far as the Metazoa are concerned).

Some of the immediate advantages of parthenogenesis are fairly obvious: by dispensing with the need for mating it allows the whole of the adult life to be devoted to feeding and reproduction. The prolificity of parthenogenetic organisms is thus nearly always higher than that of related sexual forms: even if the average number of offspring per female is the same the potential increase in numbers per generation is double that of a bisexual species, since there are no males. A number of other possible advantages which a parthenogenetic system may possess have been discussed by Dobzhansky (1937*d*, 1941*a*), who points out that in a thelytokous form advantageous combinations of genes which may arise

* No general review of the cytology of natural parthenogenesis has been published since those of Vandel (1931) and Ankel (1927, 1929), to which the reader is referred for much detailed information not included in this chapter.

by mutation are not liable to be broken up by crossing-over before they have had a chance to spread through the population (although advantageous combinations of genes are much less likely to arise in a parthenogenetic form). In some cases parthenogenesis permits the establishment of triploid or aneuploid chromosome sets which would be incompatible with a functioning meiotic mechanism. This may or may not be an advantage, according to whether the particular triploid or aneuploid condition increases or diminishes viability.

The great disadvantage that parthenogenetic species suffer from is, however, the fact that new combinations of genes cannot be built up by selection within the population, so that selection in thelytokous organisms lacks the constructive character which it possesses in species with cross-fertilization.

Animals with cyclical parthenogenesis seem to have established a compromise which reaps the advantages of both methods of reproduction. They are enabled to increase very rapidly in numbers during the thelytokous part of the life cycle (which usually corresponds to the warm summer months)—while during the sexual generation recombination of genes can take place. We thus find that cyclical parthenogenesis, where it occurs, is generally characteristic of whole groups, such as the aphids, gall wasps (Cynipidae) and certain rotifers. Even in these groups, however, there are some species which seem to have secondarily lost the sexual part of the cycle, becoming permanently thelytokous.

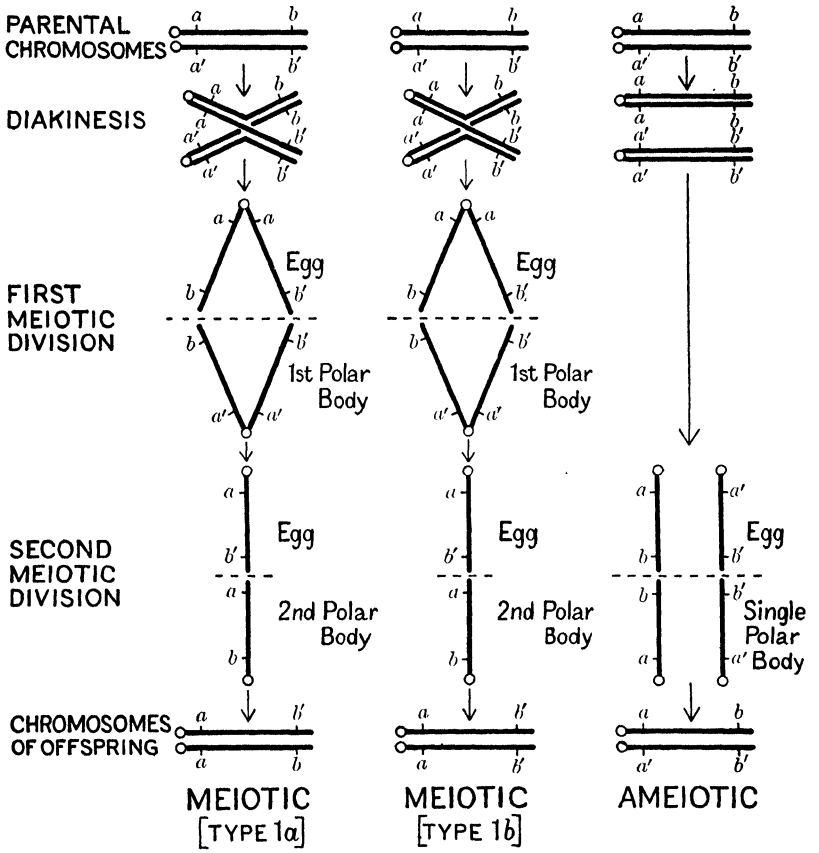
Darlington (1939*b*), writing primarily from a botanical standpoint, has treated the evolutionary significance of parthenogenesis in a somewhat different way. He regards it as an 'escape from sterility'—a sterility which may be due to 'anisopolyploidy' or to incompatibility of gametes arising from genetic or other causes. While this may be the main reason for the prevalence of asexual methods of reproduction in certain groups of plants, there is little reason to suppose that it has played any part in the evolution of parthenogenesis in arthropods, nematodes and rotifers.

Before considering the theoretical implications of parthenogenesis any further, it is desirable to describe the cytological details. Weismann (1886, 1887) claimed that the essential difference between the maturation of parthenogenetic eggs and those requiring fertilization was that the former only gave off a single polar body. This is undoubtedly true for most types of parthenogenesis; no reduction in chromosome number occurs during maturation, and the egg nucleus contains a diploid set of chromosomes identical with the set possessed by its mother. On the other hand, there are a number of instances in which eggs that are destined to develop parthenogenetically do undergo a true meiosis, giving off two polar bodies. In these cases the somatic chromosome number is restored, either by a fusion of one polar body with the egg or by a fusion of the early cleavage nuclei in pairs.

We may thus draw a distinction between two main types of parthenogenesis: (1) the *meiotic* type (in which meiosis occurs, the chromosome number being

somehow doubled at a later stage), and (2) the *ameiotic* type (in which meiosis has been entirely suppressed).

It is interesting to consider the theoretical genetics of parthenogenetic organisms. In ameiotic parthenogenesis genetic segregation will not occur. Recessive mutations and structural rearrangements will tend to accumulate indefinitely in such organisms, there being no mechanism for their elimination



Text-fig. 115. Diagram showing the genetical consequences of the three main types of parthenogenesis. In each case the parental pair of chromosomes is supposed to be heterozygous for two pairs of genes *a a'* and *b b'*. Further explanation in text.

by natural selection (unless the rearrangements produce a position effect in the heterozygous condition). As a result these forms must be expected to become gradually more and more heterozygous, but all the offspring of a single female will resemble their mother exactly except for newly arisen dominant mutations and differences due to the action of the environment. If we suppose an ameiotic

form evolving for a very long period of time we might imagine its two chromosome sets becoming completely unlike, so that it could no longer be considered as a diploid either in a genetical or cytological sense. Ameiotic parthenogenesis is genetically equivalent to clonal or vegetative reproduction. Since no pairing of chromosomes takes place it is not necessary that such forms should be diploid—they may be triploid or aneuploid.

Meiotic parthenogenesis may be divided into two subtypes. In the first of these (1 *a*) the doubling of the chromosome number results from an ineffective second division (i.e. re-fusion of the second polar nucleus with the egg nucleus). In the second subtype (1 *b*) the doubling of the chromosome number is accomplished by an ineffective cleavage division.

Types 1 *a* and 1 *b* must be expected to behave differently from a genetical standpoint. In both of them segregation may occur in the offspring of a single female if she is heterozygous. But in type 1 *b* all individuals must be completely homozygous, except for mutations that have arisen in them during their own lifetime. In type 1 *a*, on the other hand, it is possible for an individual to inherit heterozygosity from its parent. Nevertheless, all organisms with meiotic parthenogenesis will tend to remain extremely homozygous, whatever the method of post-meiotic doubling: in this respect they possess a genetic system which is the antithesis of that found in species with ameiotic parthenogenesis.*

In Chapter 1, when defining the species-concept, we said that species were breeding units. If that is so one might expect that the concept would break down in groups where cross-fertilization does not take place. This is exactly what we do find in those plant genera, such as *Hieracium*, where asexual methods of reproduction are of general or universal occurrence; a great number of closely similar forms are found, but they cannot be grouped into definite systematic entities, and it is purely a matter of individual taste whether we designate them as varieties, subspecies or species, since no definitions are possible, and all degrees of divergence exist.

In animals 'complete' parthenogenesis does not seem to have established itself in any group for long enough to have permitted the *Hieracium* condition to develop. Thus in most parthenogenetic coccids, weevils, sawflies and stick insects we can speak of 'species' without impropriety, since many of the specific characters are probably older than the asexual method of reproduction, and have been handed down from the time when these forms were bisexual.

Having considered some of the theoretical consequences of parthenogenesis,

* Prof. J. B. S. Haldane points out to me that in meiotic parthenogenesis of type 1 *a*: 'the progeny of a heterozygote is heterozygous if, and only if, there is post-reduction at the locus concerned. The frequency of this event, say p, varies from 0 near the centromere to $\frac{2}{3}$ at some distance from it. It is doubtful whether it ever exceeds $\frac{2}{3}$. Thus the frequency of heterozygosis falls off in a geometrical series whose common ratio is $\frac{2}{3}$ or less. For genes where $p < \frac{1}{2}$, i.e. fairly near the centromere, the process is quicker than self-fertilization. It is *always* quicker than brother-sister mating.'

we may proceed to describe the cytological details in the main types that have been studied. It is useful for this purpose to draw a distinction between *facultative* and *obligatory* parthenogenesis. In the facultative type the eggs are still capable of being fertilized, but if not penetrated by a sperm will develop parthenogenetically. In the obligatory type the eggs are incapable of being fertilized. Thus the mature egg is usually haploid in facultative parthenogenesis, but undergoes a secondary doubling of the chromosome number if no sperm enters it within a certain length of time. On the other hand, in obligatory parthenogenesis the mature egg usually shows the somatic chromosome number. The two types correspond in general to the meiotic and ameiotic categories, but there are some exceptions. We shall describe the chromosome cycle in cases of facultative parthenogenesis first, since it deviates less from the usual sexual cycle.

In the facultatively parthenogenetic race of the coccid *Lecanium hesperidum* (Thomsen, 1927, 1929), the meiosis of the egg is of the usual type and two polar bodies are formed; but if the egg is not penetrated by a sperm the second polar body re-fuses with the egg and a pseudo-fertilization takes place which restores the somatic number. A similar mechanism probably exists in those sawflies (Hymenoptera) which show facultative parthenogenesis (Peacock, 1928; S. G. Smith, 1938*a*, *b*).

As we pass from facultative to obligatory parthenogenesis we should expect to find that the useless second division would tend to disappear. Thus in the moth *Solenobia pineti* (Seiler, 1923), in the race of *Artemia salina* from Cette (Artom, 1931), and in two species of nematodes of the genus *Rhabditis* (Bělař, 1923, 1924), we find that the early stages of meiosis in the parthenogenetic egg are quite normal. The chromosomes pair and bivalents are present in diakinesis. At first metaphase segregation occurs, i.e. the whole and undivided centromeres pass to opposite poles. Following on the formation of the first polar body a second metaphase occurs, but this second division is entirely abortive: the centromeres divide and the half-chromosomes fall apart, but there is no anaphase and no second polar body is given off. Genetically, of course, this type of meiotic parthenogenesis is exactly similar to the last.

In obligatory parthenogenesis the chromosomes usually do not pair to form bivalents. There has thus been a genetically determined suppression of all that distinguishes meiosis from mitosis. At the stage corresponding to diakinesis all the chromosomes are univalent, and the single division which occurs when the polar body is extruded is an ordinary mitosis. Since the centromeres divide this division seems to represent the second meiotic division, the first one having disappeared.

In *Aphis palmae* (de Baehr, 1920) and *A. rosae* (Paspaleff, 1929) it has been stated that the chromosomes pair at zygotene to form bivalents, but that they fall apart again before diakinesis. If true this probably indicates that pairing has

survived, while crossing-over has been suppressed. In other aphids, such as *Pemphigus* (de Baehr, 1920) and *Phylloxera* (Morgan, 1906, 1908, 1909*a*, *b*), no pairing takes place in the parthenogenetic egg.

In the stick insects (Phasmoidea) many species are obligatorily parthenogenetic. Nevertheless, it is generally accepted that two polar bodies are given off (de Baehr, 1907; Nachtsheim, 1925; Pehani, 1925). It has been stated that both 'meiotic' divisions take place with the somatic number of chromosomes, and are hence mitotic in character. This is unlikely on *a priori* grounds, and Pehani's figures suggest that true bivalents are present at the first division in *Carausius morosus*. It is thus probable that a restoration of the somatic chromosome number takes place by a fusion of the cleavage nuclei in pairs.

Since obligatory parthenogenesis involves the disappearance of both meiosis and the sex-determining mechanism, it removes two of the main barriers that prevent the establishment of polyploidy in bisexual organisms. We consequently find that a number of parthenogenetic species or races are triploid or tetraploid, as can be seen very clearly by a comparison of their chromosome numbers with those of related bisexual forms.

One of the best-known examples of parthenogenesis combined with polyploidy is the small branchiopod crustacean *Artemia salina*. Owing to the fact that it is restricted to waters of very high salinity, such as occur in some lakes and 'salt pans', *Artemia* has a very discontinuous distribution. In the Old World it occurs in the south of France, Italy (several different localities), Cadiz, Balearic Islands, North Africa, Syria and South Russia (Odessa), while in America it is found in Great Salt Lake, Utah and in the Gulf of California. The various forms from these different localities are usually regarded as forming a single complex species, although some of them are bisexual, while others are parthenogenetic. The cytological details have been worked out by Brauer (1894), Artom (1908, 1928, 1931), Gross (1932) and Barigozzi (1934, 1935).

The bisexual race (which occurs in many localities) consists of males and females with a somatic number of 42. It has been stated that a tetraploid bisexual race occurs at Odessa, but very little is known of this form, and it may really be diploid. Meiosis in the ordinary bisexual form is normal in both sexes, and the egg will not develop without fertilization.

The parthenogenetic races fall into three groups, according to whether they are diploid, tetraploid or octoploid. At Margherita di Savoia (Italy) all three exist together (Barigozzi, 1935). These races consist almost entirely of females, males being encountered only as very rare anomalies.

In the oogenesis of the parthenogenetic races the chromosomes pair so as to form bivalents: thus in the oocytes of diploids there are 21 bivalents, in those of tetraploids 42 and in those of octoploids 84 (Barigozzi, 1934). Each bivalent is a small quadripartite body in which the chromosomes are apparently held together by a single chiasma. Multivalents are not formed, presumably for one

of the reasons discussed on pp. 87–88. At the first meiotic division a polar body is given off which takes no further part in the development of the egg.

Behaviour at the second meiotic division is highly variable. The latter is always abortive, however. An anaphase may occur, but a second polar body is never extruded. Thus the somatic number is restored by a fusion of the two products of the second division.

Artemia is a classical example of meiotic parthenogenesis (Type 1 *a*). It may be regarded as a polytypic species which, no doubt partly as a result of its discontinuous distribution, has broken up into a number of races. Apparently there are slight morphological differences between these forms, although the degree of salinity of the water and other environmental factors may also affect the appearance of the animals. No doubt the bisexual race represents the original condition; unfortunately, nothing is known about its method of sex determination, so that it is scarcely worth while speculating as to the way in which occasional males are produced in the parthenogenetic races.

It is interesting to compare with the case of *Artemia* that of the isopods of the genus *Trichoniscus* (= *Spiloniscus*) studied by Vandel (1928, 1934, 1940). In this genus there are a number of bisexual species (*elizabethae*, *provisorius*, *biformatus*, *darwini*) with a diploid number of 16 and a triploid parthenogenetic form (*coelebs*) with 24 chromosomes, which is regarded by Vandel as a 'race' of *elizabethae*. In central and southern France the bisexual and parthenogenetic forms overlap in distribution, but probably do not interbreed. In the south of France the bisexual species occur only in damp mountainous localities, while *coelebs* is found in isolated colonies in the arid 'garrigues' of the Mediterranean region, which are very unsuitable for a crustacean whose life depends on the presence of water. Thus the parthenogenetic form seems able to maintain a precarious existence in regions where the bisexual species would not be able to live. Parthenogenetic strains of *Trichoniscus* are also found much farther north than the bisexual forms, and even reach the Baltic countries, Scandinavia and Iceland, so that they are probably more resistant to cold as well as to drought; whether this resistance depends on triploidy or on the parthenogenetic mode of reproduction is, of course, unknown.

Whereas the diploid race of *elizabethae* has a sex ratio of about 1 : 1, *coelebs* consists almost exclusively of females, but there are a few males (1–2% of the population), which are also triploid. The triploid females are ameiotic: their chromosomes do not pair during oogenesis and only one polar body is formed as a result of an equational division. Thus the eggs which develop without fertilization possess the somatic number of 24 from the beginning. The establishment of ameiosis must almost certainly have preceded the development of triploidy; it is hardly likely to have been an automatic consequence of the latter, so we must assume that a bisexual parthenogenetic race became ameiotic, and that it was then replaced by a triploid form. Perhaps this hypothetical diploid

but parthenogenetic form is extinct—on the other hand, it may yet be found elsewhere in Europe, just as the diploid parthenogenetic form of *Solenobia triquetrella* (see p. 290) was found by Seiler and Schaeffer many years after its existence had been predicted on theoretical grounds.

The triploid males which are occasionally met with constitute an interesting problem. It is not known whether their chromosomal constitution is exactly the same as that of the triploid females. In any case the mechanism of sex determination in isopods is quite obscure, since no sex chromosomes can be detected in the species that have been studied (Radu, 1930; Mir, 1937; Callan, 1940; Imai and Makino, 1940). The meiosis of the triploid males is naturally anomalous: there is no chromosome pairing, but two meiotic divisions occur, both of which are said to be equational (i.e. mitotic in character). Thus the sperm of such males contains the somatic number of chromosomes (24). Triploid males can be induced to cross with triploid females, but their sperm is not functional; they will not usually copulate with females of the diploid race.

Artemia and *Trichoniscus* are not the only Crustacea in which polyploidy is associated with parthenogenesis. It was shown by Schliep (1909) that the parthenogenetic ostracod *Cypris fuscata* has 24 chromosomes, while related bisexual forms have 16. Although there is no proof here it seems likely that *C. fuscata* is triploid. Lastly, in *Daphnia pulex*, Schrader (1925) studied a parthenogenetic race with a somatic number of 24. The diploid number of the bisexual form of this species is probably 8, so that the parthenogenetic form may be hexaploid. Mortimer (1935) has, however, questioned the reliability of the work on the bisexual form, so that this case requires further investigation. A number of species of *Apus* (= *Lepidurus*) are known to be parthenogenetic, but no cytological investigation has been carried out as yet.

In the Mollusca a single instance is known where polyploidy is probably combined with parthenogenesis. The British form of *Potamopyrgus jenkinsi* has a somatic number of approximately 36–44 (Sanderson, 1940; Peacock, 1940), while the continental form is stated by Rhein (1935) to have 20–22 chromosomes. The material obviously presents great technical difficulties, and it is possible that mistakes may have been made in counting the chromosomes, but if the facts are as stated it would appear that the British form is a tetraploid. The only other case of parthenogenesis in the Mollusca that has been investigated cytologically is that of the American species *Campeloma rufum* (Mattox, 1937), which has a somatic number of 12; there is no suggestion that this species is a polyploid.

In insects polyploidy is associated with parthenogenesis in some Coleoptera, Lepidoptera, and possibly in other orders. Suomalainen (1940*a*, *b*) studied the cytology of a number of species of weevils (Curculionidae). Whereas all the bisexual species had a somatic number of 22, the parthenogenetic ones showed 22 (one species), 33 (five species) and 44 (three species). The oogenesis of the

parthenogenetic forms was always ameiotic, only one polar body being extruded. There are a few other parthenogenetic Coleoptera such as the chrysomelid *Adoxus vitis* (Jolicœur and Topsent, 1892), but parthenogenesis is undoubtedly very rare in this order.

In the Odonata and Heteroptera parthenogenesis seems to be entirely unknown. A few isolated instances in other insect orders have been listed in Table 15 (in

TABLE 15. *Miscellaneous cases of thelytoky in insects (no cytological data as yet)*

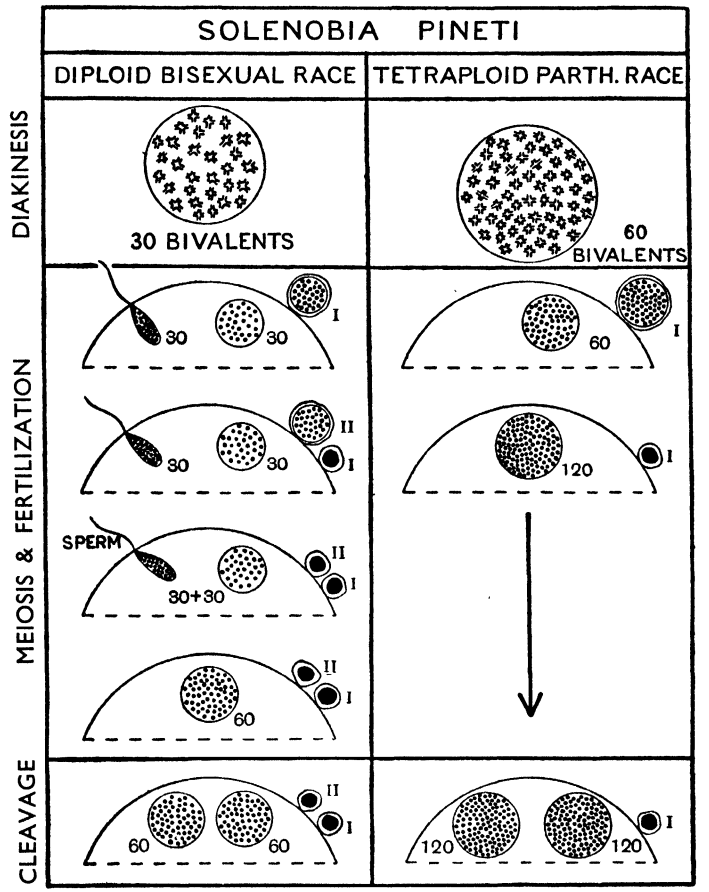
EPHEMEROPTERA	
Ameletus ludens	Needham, 1924
Ephemerella feminina	,, ,,
SALTATORIA	
Myrmecophila acervorum	Schimmer, 1909
PSOCOPTERA	
Ectopsocus briggsi var. *meridionalis*	Ribaga, 1904
THYSANOPTERA	
Heliothrips haemarrhoidalis (and many other species)	Pomeyrol, 1928; Eddy and Clarke, 1930
HOMOPTERA (Coccoidea)	
*Orthezia insignis**	James, 1939
Saissetia nigra	,, ,,
TRICHOPTERA	
Apatania muliebris and *A. arctica*	McLachlan, 1880
DIPTERA	
Chironomus clavaticus	Edwards, 1919
Ochthiphila polystigma	Sturtevant, 1923
Lonchoptera furcata	,, ,,

* Probably bisexual in some countries.

TABLE 16. *Polyploidy in weevils (data of Suomalainen, 1940a, b)*

	Oogonial chromosome number (observed or calculated)	Sex chromosomes in male
BISEXUAL SPECIES		
Strophosomus capitatus	22	*XO*
Otiorrhynchus arcticus	22	*XY*
Polydrosus pilosus	22	*XY*
Hylobius abietis	22	*XO*
PARTHENOGENETIC SPECIES		
Polydrosus mollis	22	
Otiorrhynchus ovatus	33	
O. ligustici	33	
Strophosomus melogrammus	33	
Trachyphloeus bifoveolatus	33	
Sciaphilus asperatus	33	
Otiorrhynchus dubius	44	
O. scaber	44	
Barynotus obscurus	44	

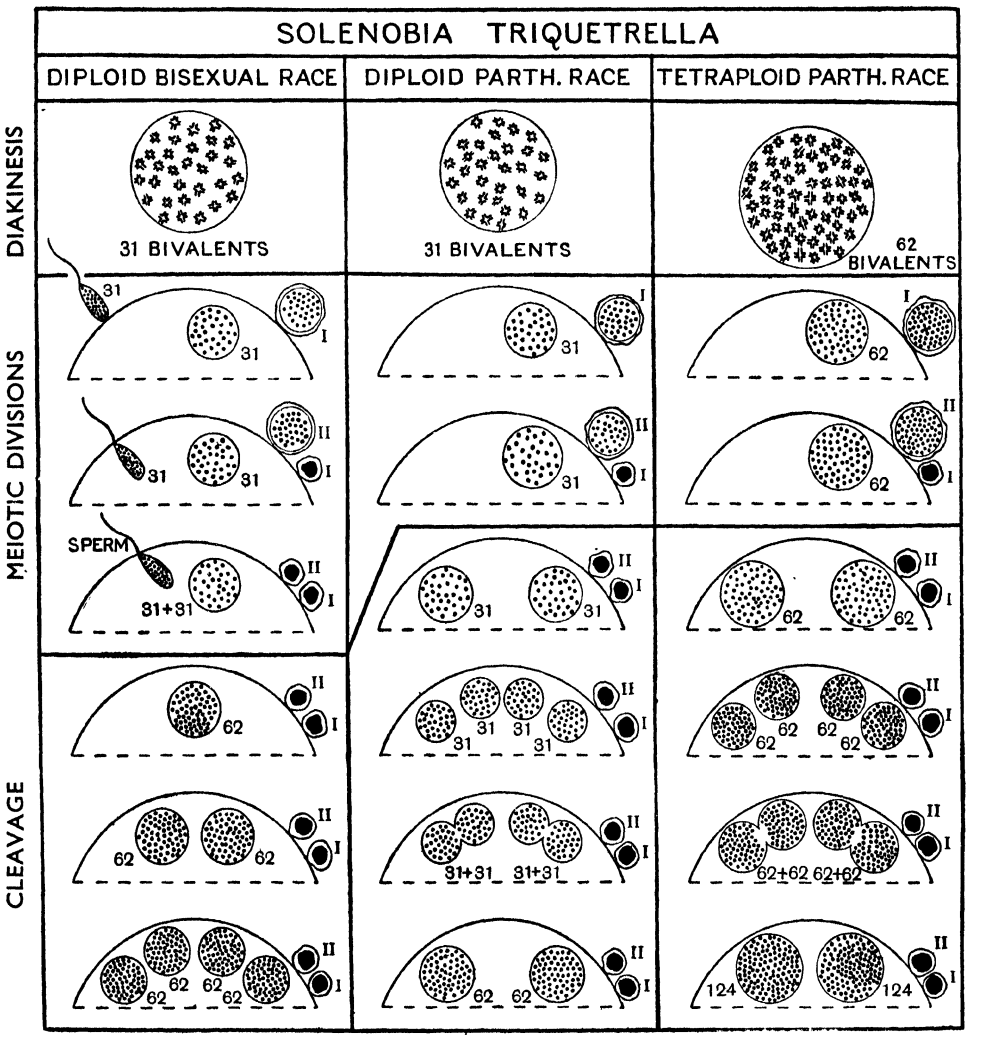
all these cases thelytoky seems to be the normal method of reproduction and males are either unknown or very rare). By far the greater number of cases of thelytoky in insects occur in the Lepidoptera and Hymenoptera, where the number of species showing this method of reproduction is too great to be tabulated conveniently.



Text-fig. 116. Diagram of oogenesis and cleavage in the bisexual and the parthenogenetic race of *Solenobia pineti* (based on the work of Seiler (1923)). The chromosome number is not known with complete certainty, but is probably 30 or 31 in the bisexual race. In the tetraploid, parthenogenetic race there is only one cleavage division. I, II = first and second polar bodies, respectively. For the sake of simplicity no division of the first polar body is shown.

Among the Lepidoptera the cytology of parthenogenesis in the small psychid moths of the genus *Solenobia* has been studied very thoroughly by Seiler (1923, 1927*a*) and Seiler and Schaeffer (1938, 1941). In *S. triquetrella* three races are

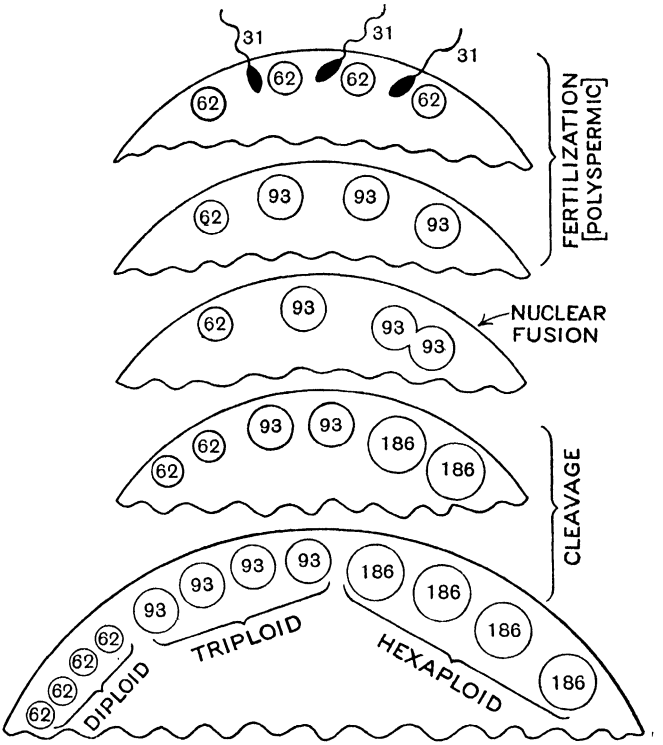
known, a bisexual one with a haploid number of 31, a diploid parthenogenetic strain and a tetraploid parthenogenetic race with a somatic number of 124.



Text-fig. 117. Diagram of oogenesis and cleavage in the bisexual and the two parthenogenetic races of *Solenobia triquetrella* (based on the work of Seiler and Schaeffer (1938, 1941)). In all three races two polar bodies are given off (I and II). In the parthenogenetic races the somatic number is restored by fusion of the cleavage nuclei in pairs.

The first, which we must regard as the ancestral form, is confined to a small area in the south of Germany. The second has only been found in one locality near Zürich, while the third (which consists exclusively of females) has a wide

area of distribution throughout northern Europe. The distribution of the three forms suggests that the tetraploid parthenogenetic form has largely replaced the more primitive races which only linger in a few localities.



Text-fig. 118. Diagram showing how fertilization of an egg of the tetraploid parthenogenetic race of *Solenobia triquetrella* by several sperms of the diploid bisexual race gives rise to a mosaic hybrid. Based on the work of Seiler (1927*a*).

The eggs of the parthenogenetic females (whether of the diploid or the tetraploid race) undergo a true meiosis in which two polar bodies are cast out. The chromosomes pair to form either 31 or 62 bivalents, as the case may be, and after reduction the egg contains half the somatic number of chromosomes. The first few cleavage divisions take place with this number, but the nuclei then fuse in pairs so as to restore the original somatic number.

The parallel between this case and that of *Artemia* is obvious, although the method of restoration of the chromosome number is not the same. One interesting point to which no answer can be given is the following: since in Lepidoptera the females are normally *XO* or *XY*, how is it that in the diploid parthenogenetic race individuals which must be completely homozygous are nevertheless female?

In moths which only show parthenogenesis occasionally, such as *Porthesia similis* (Garbowski, 1904), *Lymantria dispar* (Goldschmidt, 1917) and *Bombyx mori* (Conte, 1911; Lecaillon, 1918), unmated females produce both sons and daughters. Presumably in these cases *XX*, *XY* and *YY* offspring are produced, according to the method of restoration of the chromosome number. It is possible that in some instances tetraploidy may have been advantageous to a parthenogenetic lepidopteran, since by abolishing heterogamety it would ensure that all the offspring were *XXYY* (i.e. genetically female). The work of Astaurov (1940) and Frolova (1940) on artificial parthenogenesis in the silkworm, *Bombyx mori*, is of some interest in this connection. These authors found that they could induce parthenogenesis in this species by heat-treatment. The unfertilized eggs only underwent a single meiotic division and almost all (37,139 out of 37,152) developed into females, 27·5% of which were apparently tetraploid, possibly as a result of fusion between cleavage nuclei.

In *Solenobia triquetrella* Seiler (1927*a*) was able to perform the interesting experiment of crossing the bisexual race with the tetraploid parthenogenetic one. Since polyspermy is normal in *Solenobia* several sperms penetrated each of the parthenogenetic eggs. Their nuclei fused with the four 62-chromosome female nuclei to give triploid nuclei with 93 chromosomes. The subsequent development was rather chaotic, since in some instances these triploid nuclei fused in pairs, so as to give rise to hexaploid tissue. The hybrids were thus queer, malformed insects, basically triploid, but in actual fact mosaics of triploid, tetraploid, hexaploid and octoploid regions. They were intersexual and often asymmetrical.

In a related species, *Solenobia pineti*, there is also a diploid bisexual race and a tetraploid parthenogenetic one, but the latter has a much more restricted distribution area than is the case in *S. triquetrella*. We have already described (p. 284) the meiosis of the thelytokous form of *pineti*, which is of a somewhat different type to that of *S. triquetrella*, suggesting that parthenogenesis has arisen quite independently in the two species. Parthenogenesis also occurs in a number of other psychids (Trautmann, 1909), but it is not known whether it is generally associated with polyploidy in this group.

In the orthopteroid groups of insects there are a number of instances in which polyploidy may be combined with parthenogenesis, but none of them has been conclusively proven.

In the large wingless tettigoniid, *Saga serrata* (= *S. pedo*), which inhabits the Mediterranean region, only two or three males have been reported. The species is thus normally parthenogenetic. Matthey (1939*a*, 1941) has studied the details of oogenesis. There is no pairing of the chromosomes and only one polar body is extruded, the parthenogenesis being clearly of the ameiotic type. The somatic number is 68 (12 chromosomes metacentric), which is far higher than that of any other tettigoniid previously studied (Text-fig. 68). Matthey thus makes the plausible suggestion that *S. serrata* is tetraploid (34 would be a 'normal'

somatic number for the group and 20 chromosome limbs in the haploid set would compare with 16 in most Decticinae and 18 in some Pseudophyllinae). If this suggestion be true, it raises the interesting question: what was the chromosomal constitution of the males which have occasionally been captured? Some other species of *Saga* are bisexual, so that it should eventually be possible to ascertain definitely whether *serrata* is tetraploid by comparison with the chromosome number of a bisexual member of the genus. Most, if not all, of the so-called males which are occasionally found in the parthenogenetic species of stick insects are probably intersexes (Cappe de Baillon and de Vichet, 1935). They may contain testes, but their chromosomal constitution is unknown.* Possibly the males of *S. serrata* are similar in character.

S. serrata is the only species of tettigoniid in which parthenogenesis is known to be firmly established as the normal method of reproduction, but in the absence of a male, females of some other species (e.g. *Leptophyes punctatissima*) will lay eggs that sometimes hatch (Cappe de Baillon, 1939).

Saga serrata is an interesting species, not only on account of its parthenogenetic method of reproduction, but also because of its extreme rarity. The genus to which it belongs contains about 17 species and has its headquarters in Turkey, Syria and Palestine. *S. serrata* seems to have spread over a much wider area, since it occurs from Spain to the Caucasus and the southern Urals. On the other hand it seems to be a 'relict' species, since the localities in which it occurs are very discontinuous and the individual populations of very small size. Thus after a period of successful dispersal it has apparently become extinct over the greater part of its range, surviving only in isolated colonies. It may be worth pointing out that on theoretical grounds a tetraploid species which reproduces by ameiotic thelytoky is in a very peculiar genetical state. In such an organism mutation will have almost ceased to be an effective agent in evolution, since all newly arisen mutations will be almost completely recessive (in the presence of three doses of the original allelomorph), and will stand no chance of becoming homozygous. Thus if *S. serrata* has failed to adapt itself to changing conditions and is now on the verge of extinction, at any rate in the western part of its range, the reason is not (as it probably would be in a diploid sexual species of comparable rarity) that disadvantageous mutations are establishing themselves by 'drift'; rather, the evolution of *S. serrata* seems to have become 'frozen' by its peculiar genetic system. It is significant that, apart from the weevils studied by Suomalainen, the other thelytokous tetraploids which we have considered

* In a later paper on the cytology of stick insects, Cappe de Baillon and de Vichet (1940) have published a comparison between the males of *Leptynia attenuata* (normally bisexual) and a single male of *L. hispanica* which occurred among a very large number of parthenogenetic females. Whereas meiosis in the males of *attenuata* was entirely normal, the spermatogenesis of the male *hispanica* was highly irregular and abnormal, no functional sperms being formed. It is thus probable that this individual was an intersex whose genic balance was upset (rather than a true male).

(*Artemia*, *Solenobia*) all have meiotic mechanisms, so that the mutations which arise in them are bound to become homozygous. It is interesting to compare the geographical distributions of the parthenogenetic forms in the genera *Saga*, *Trichoniscus* and *Solenobia* with those of their diploid, bisexual relatives. In every case the parthenogenetic forms exist over a much wider area. Vandel has assumed in the case of *Trichoniscus* that the triploid, parthenogenetic form has a wider distribution because it is more hardy. But a more likely explanation in all these genera is that the parthenogenetic forms have found it easier to expand their range just because they were parthenogenetic, so that every individual accidentally transported to a new locality was able to breed and there was no 'reproductive wastage' however sparse the population.

It is still uncertain whether any of the parthenogenetic Phasmoidea show polyploidy. In this group, although many or perhaps all species are capable of occasional parthenogenesis in the absence of a male, it is only in a few genera such as *Eurycnema*, *Clonopsis*, *Bacillus* and *Carausius* that parthenogenesis has become the regular method of reproduction in some species. In a general way it does seem that the parthenogenetic forms have higher chromosome numbers than the bisexual members of the group (see Table 17), but in most instances they are not an exact multiple of a lower chromosome number. In the family Bacillidae, *Bacillus rossii* (parthenogenetic) has the same chromosome number as *Phalces longiscaphus* (bisexual), while in the genus *Carausius* the form known as *theiseni* (parthenogenetic) probably has the same number as *juvenilis* (bisexual). Of course the forms of *Carausius* with very high chromosome numbers (64–100) may be triploids, pentaploids or even irregular polyploids in which some chromosomes are represented three or four times, others only twice, but there is no certain evidence of this. *Phobaeticus sinetyi*, however, does really look like a tetraploid, since its chromosome number is exactly twice that of the related species *Dubreulia lineata*. *Leptynia attenuata* and *L. hispanica* are an interesting pair of species; it certainly looks as if the second is an 'irregular polyploid' (see Table 17). It is thus possible that some species of parthenogenetic phasmids are diploids while others are tetraploids or irregular polyploids with inconstant chromosome numbers. Cappe de Baillon, Favrelle and de Vichet (1934*b*) found a number of instances of apparent genetical segregation in several of the parthenogenetic species; perhaps these were due to variation in chromosome number.

From the cytogenetical standpoint one of the most thoroughly studied cases of facultative parthenogenesis is that of the grouse locusts (Tettigidae) investigated by Nabours (1919, 1925, 1929, 1930) and Robertson (1925, 1930, 1931). The situation in various species of *Apotettix* and *Paratettix* seems to be exactly the same, so that the observations made on different species may be combined to give a composite account of the phenomena.

Normally, the tettigids are not parthenogenetic, but unfertilized females lay

eggs which frequently hatch. To what extent this occurs in nature is not known. The fatherless offspring are nearly always female, but once in several hundred individuals a male is produced (in *A. eurycephalus* Nabours obtained 13 males in about 5,000 partheno-produced offspring). Robertson found that these males have 13 chromosomes instead of 14, as in the females—that is to say they are true *XO* males and not intersexes or sex-reversed females.

TABLE 17. *Examples of chromosome numbers in bisexual (B) and parthenogenetic (P) phasmids*

(Data from de Sinéty (1901); Cappe de Baillon, Favrelle and de Vichet (1934*a*, *b*, 1935, 1937, 1938); and Cappe de Baillon and de Vichet (1940))

Family	Somatic number in female (observed or calculated from male number)
BACILLIDAE	
Phalces longiscaphus B.	36
Bacillus rossii P.	36
Leptynia attenuata B.	36
L. hispanica P.	52–56*
PHYLLIIDAE	
Phyllium bioculatum B.	34
BACUNCULIDAE	
(1) Clitumninae	
Dubreulia lineata B.	26
Phobaeticus sinetyi P.	52
Baculum artemis P.	68–76*
(2) Lonchodinae	
Carausius theiseni P.	40–42*
C. juvenilis B.	42
C. furcillatus (race I) P.	64–73*
C. furcillatus (race II) P.	85–100*
C. (Greenia) rotundato-lobatus B.	22
BACTERIIDAE	
Sipyloidea panaeticus B.	22
Parasosibia parva B.	54

* Exact number not determined—perhaps not constant?

The fatherless offspring, whether male or female, seem to develop from eggs in which only one meiotic division has taken place. Presumably the division which fails is the second one, which is normally stimulated to occur by the entrance of the sperm. Genetical analysis shows that the progeny are homozygous; this presumably implies that the loci of all the genes so far analysed are close to a centromere.

Individuals that have arisen parthenogenetically show 14 chromosomes (or 13 if they are males) when in the later instars or fully adult. The homologous chromosomes usually have a tendency to lie side by side, as in the Diptera—

a tendency which is not seen in biparentally produced individuals. The younger nymphs which have arisen from unfertilized eggs show varying numbers of chromosomes (from 7 to 14) in their nuclei, but where 13 are present one is double the width of a normal chromosome, where there are 12 two are broader than usual, and so on—if there are only 7 chromosomes they are all double the usual width.

It thus appears that although the second division may be ineffective, the chromosome split is not inhibited in the parthenogenetic eggs, so that the 'broad' chromosomes consist of four, instead of two, chromatids, lying alongside one another, and probably only held together by an undivided centromere. They have the same structure as the 'diplochromosomes' produced by irradiation, abnormal temperatures or other environmental agencies (White, 1935*a*, *b*; Barber, 1940). Sooner or later the four chromatids fall apart so as to give two normal chromosomes which still, however, show a tendency to lie side by side in subsequent divisions. Thus the diploid number of bodies is gradually restored.

The mode of origin of the occasional males in parthenogenetic families is not properly understood, but it seems probable that they are produced by some type of non-disjunction.

There are certain peculiarities about the parthenogenesis of the nematoda which place it in a special category, rather different from the various types that we have so far considered. In many species of this group the egg has to be stimulated to develop by the penetration of a sperm, but the latter then degenerates, so that it plays no further part in development, and no true fertilization can be said to have occurred. The phenomenon is known as *pseudogamy* or *pseudo-fertilization* and is not known elsewhere in animals,* although an analogous phenomenon occurs in some plants (Darlington, 1939*b*).

The majority of the nematoda are bisexual, the males being heterogametic. There is usually a well-developed sex-chromosome mechanism (see Chapter XI for details). In three families, however (Anguillulidae, Rhabdonemidae and Mermithidae), hermaphroditism or parthenogenesis occurs in some species.

The Anguillulidae are free-living worms most of which inhabit the soil. In the genus *Rhabditis* there are some bisexual forms, while other species consist of

* The problematical case of the cyprinodont *Mollienisia formosa* (Hubbs and Hubbs, 1932; Meyer, 1938) should perhaps be mentioned here. This small fish from the Gulf coast of Mexico is morphologically intermediate between *M. sphenops* and *M. latipinna*, and it has been suggested that it arose as a natural hybrid between them. *M. formosa* consists entirely of females—no male has ever appeared, either in collections made in the wild or in controlled breeding experiments. Nevertheless, the females *M. of formosa* will not breed until they have been fertilized by the male of one of the other two species. It is not known whether this 'fertilization' involves the penetration of the egg by the foreign sperm, but it is unlikely that the latter plays any part in development, since the offspring are always female and show no resemblance to the male 'parent', even after several generations of 'backcrossing'. Whether this is a true case of pseudogamy cannot be decided until a thorough cytological investigation has been made: Hubbs and Hubbs interpreted it in this sense, while Meyer has put forward a more complex interpretation which seems on *a priori* grounds less probable.

hermaphrodites with a few rare males (recalling the situation in *Icerya purchasi*, although the cytological basis of hermaphroditism is quite different). There are also many species of Anguillulidae which consist only of females, no males having ever been found (Maupas, 1900): it must be presumed that these are thelytokous forms. A very unequal sex ratio does not necessarily imply parthenogenesis, however. Thus it has been shown by Bělař (1923, 1924) that in *Rhabditis monohystera*, where the males only form about 6–7% of the population, unmated females do not produce offspring. The eggs usually undergo a single meiotic division and are then stimulated to further development into females by the penetration of a sperm which degenerates. If an egg undergoes two meiotic divisions it becomes capable of being fertilized, and after fusion of the two pronuclei a male worm is produced. In some other species of the genus, such as *Rh. gurneyi* and an unnamed species referred to by Bělař as '*Rhabditis XX*', there are no males at all, but the females form a certain quantity of sperm in their ovaries, i.e. they have become partially converted into hermaphrodites. The sperms which arise in this way stimulate the eggs to begin development, but the sperm nuclei degenerate without contributing to the germ-plasm of the embryo.

In *Rhabditis* '*XX*' the eggs only undergo a single meiotic division. The chromosomes do not pair during the growth phase, and at the metaphase of meiosis each univalent splits as in an ordinary mitosis. The meiosis of the spermatocytes in the ovotestis follows a somewhat different course: two meiotic divisions occur, but since pairing seems to be highly irregular and incomplete the number of chromosomes passing into the sperms is variable. Since these sperms only function for a short while as stimulating agents and play no further part in heredity this is probably not important. In an evolutionary sense the degeneration of the functions of the sperm has rendered possible a degeneration of meiosis, the regularity of pairing and segregation having disappeared.

Another interesting species is *Rh. pellio*. Here no parthenogenesis normally occurs, but in a laboratory stock cultured by Hertwig (1920) a strain of parthenogenetic females suddenly arose by mutation or segregation. These female worms were entirely sterile in the absence of males, since their eggs were unable to develop unless penetrated by a sperm. Clearly such a strain could only perpetuate itself in nature if the ovaries developed the power to produce sperms that could activate the eggs. This is apparently what has happened in those species of *Rhabditis* in which the females have become hermaphroditic.

In *Rh. monohystera* which, as we have already seen, is bisexual (although the males are in a minority), there is only one meiotic division in the egg, but pairing is normal and the 20 chromosomes form 10 bivalents. The somatic chromosome number is restored by a splitting of the chromosomes which takes place during the telophase of the single meiotic division. The degeneration of meiosis has not gone so far in this species as in '*XX*', where no pairing occurs during oogenesis. The oogenesis of a form called '*XIX*' by Bělař follows the same

course as in *monohystera*, but in '*XIX*' there are no males and the eggs are capable of developing spontaneously, without pseudo-fertilization.

In some species of nematodes there is an alternation between a bisexual and a hermaphrodite generation, although no parthenogenesis occurs; this type of life cycle is characteristic of many of the Rhabdonemidae. These cases may be considered here for the sake of convenience. Thus in *Angiostomum* (*Rhabdonema*) *nigrovenosum* (Boveri, 1911; Schliep, 1911), the male and female individuals are free-living, while the hermaphrodites are parasitic in the lung of the frog. Anatomically, these hermaphrodites are obviously modified females, their general structure being quite different to that of the males, although they produce sperms in an ovotestis.

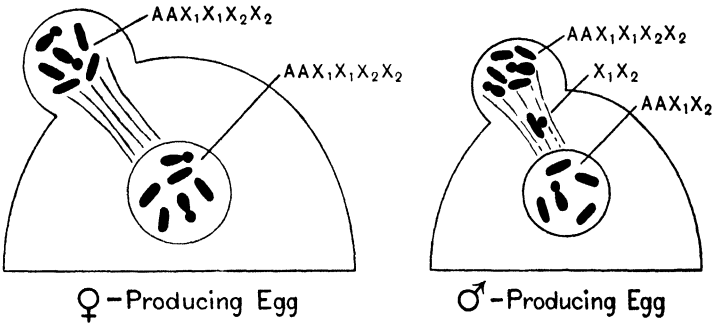
The females and hermaphrodites have a diploid set of 12 chromosomes. During oogenesis two meiotic divisions occur, so that the eggs are haploid and contain six chromosomes. The males have 11 chromosomes of which one is an *X*. *Angiostomum* thus clearly possesses an *XO* : *XX* sex-determining mechanism. In the spermatogenesis of the free-living males two kinds of sperms are formed, with and without an *X*-chromosome. The latter seem, however, to be incapable of fertilizing the eggs, so that all eggs are fertilized by *X*-bearing sperms, and the hermaphrodites arising from these eggs are all *XX* like the females. The spermatogenesis which goes on in the ovotestis follows a different course to that which occurs in the males. One *X*-chromosome becomes nucleinated faster than the other (it is not clear whether this is the maternal or the paternal *X*). No sex bivalent is formed during this meiosis, and the two *X*'s pass to opposite poles at the first anaphase. All the sperms come to contain an *X*, but in half of them the *X* is extruded and lost at the time when the sperm separates from its residual cytoplasm. Thus the *XX* hermaphrodites produce one kind of egg, but two kinds of sperm, and by fertilization of these eggs the *XX* and *XO* individuals of the sexual generation are produced once again.

The chromosome cycle of *Rhabdias fülleborni*, described by Dreyfus (1937), is very similar to that of *Angiostomum*. The parasitic hermaphrodites which live in the lungs of toads have 12 chromosomes: these form 6 bivalents in oogenesis, but in spermatogenesis the two *X*'s do not pair and both *X*'s divide in the first meiotic division. Thus all second metaphases contain a haploid set of autosomes and two *X*'s. At the second division one or both *X*'s are lost from some cells, so that sperms with 5 and 6 chromosomes are formed. Thus the fertilized eggs that will develop into the males and females of the sexual generation have 11 and 12 chromosomes respectively.

In the human parasite *Strongyloides stercoralis* and in *S. papillosus* from the sheep, which also belong to the family Rhabdonemidae, the parasitic generation consists not of hermaphrodites but of parthenogenetic females. These lay eggs which pass out with the faeces and develop into the males and females of the bisexual, free-living generation. In *S. stercoralis* males are frequent, but in

S. papillosus they form only about 0·05% of the population (Brumpt, 1921). Unfortunately, the chromosome cycle has not been studied in *Strongyloides*, so that the method of sex determination is not known.

The most typical examples of cyclical parthenogenesis occur in the aphids and cynipids. The life cycle of the aphids usually consists of a series of parthenogenetic summer generations, alternating with a single sexual generation which occurs during the colder part of the year. We may take *Tetraneura ulmi* (Schwartz, 1932) as a typical representative of the group. At the beginning of May the small black nymphs of this species form galls on the leaves of the elm, inside



Text-fig. 119. Diagram of the first meiotic division in male- and female-producing eggs of the aphid *Phylloxera caryaecaulis*. Based on the work of Morgan (1912).

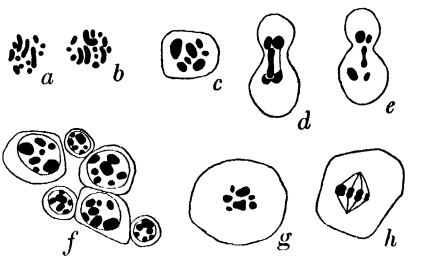
which they become adult and produce by parthenogenesis about forty female offspring. These wingless, gall-making individuals are known as *Fundatrices*: their offspring develop wings and make their way out of the galls. They then migrate to the roots of various species of grasses—whence their name of *Emigrantes*. On this second host plant they give rise parthenogenetically to several generations of *Exules*. These latter finally give rise to *Sexuparae*, winged forms that fly back to the elm, where they produce male and female individuals (again by parthenogenesis). All the fundatrices, emigrantes, exules and sexuparae are females—the mechanism of thelytoky never seems to break down and produce a male by accident.

The males and females of the winter generation (*Sexuales*) pair and from the fertilized eggs arise the gall-making fundatrices of the next year.

The cytology of *Tetraneura* has been studied in considerable detail by Schwartz. All the different types of thelytokous females have a diploid number of 14, consisting of three large and four small chromosome pairs. The sexual females have the same number of chromosomes as the parthenogenetic ones, but the males have one chromosome less, so that there is an $XO : XX$ sex-determining mechanism, all the different types of females being XX. The eggs of the fundatrices, emigrantes and exules only undergo one meiotic division,

which is non-reductional. The sexuparae differ from the other types of parthenogenetic females in that they produce two different kinds of eggs which will develop into males and females respectively. In *Tetraneura* a single sexupara produces eggs of both kinds, but in some other aphids there are two kinds of sexuparae, male-producing and female-producing. The two kinds of eggs both undergo a single meiotic division, but whereas in the female-producing eggs all the chromosomes split as in an ordinary mitosis, in the male-producing eggs the two X chromosomes pair to form a bivalent which remains in the middle of the anaphase spindle after the other chromosomes have passed to the poles. One half of this XX bivalent then passes into the polar body, the other half remaining in the egg. Thus the XO condition in the male arises through the X chromosome alone undergoing reduction at the single meiotic division.

The meiosis of the males is of a highly characteristic and anomalous type. All the autosomes pair to form bivalents, so that at the metaphase of the first meiotic division there are six autosomal bivalents and the X univalent. The latter becomes stretched between the two cells at anaphase, appearing as a bipartite body lying in the long axis of the spindle. Although it has the appearance of a body under considerable tension it eventually passes into one of the daughter nuclei without dividing. Thus two kinds of secondary spermatocytes are formed, one possessing an X chromosome, the other lacking one. The former receive far more cytoplasm than the latter, so that the no-X spermatocytes are very much smaller. Only the larger cells undergo a second meiotic division, the smaller ones simply degenerating without forming sperms. Thus, although the males are XO, they are actually homogametic, producing only one kind of sperm. This explains why all aphids arising from fertilized eggs are female. According to Ris (1942) the unequal division of the cytoplasm is caused by the X chromosome, which is stretched in the axis of the spindle and prevents the cleavage-furrow from cutting through the middle of the cell.



Text-fig. 120. *Tetraneura ulmi*. a = somatic metaphase in male embryo (13 chromosomes); b = somatic metaphase in female embryo (14 chromosomes); c = first metaphase in the male; d = first anaphase with the X chromosome stretched on the spindle; f = a group of three large and three small cells between the first and the second divisions (the latter lack an X chromosome and will undergo degeneration without undergoing a second division); g, h = second meiotic division. From Schwarz (1932), redrawn.

The above account may be regarded as valid in all essentials for any species of aphid except those that have lost the sexual part of the cycle (see p. 301). The meiosis of the males, in particular, always seems to be of the same type (Tannreuther, 1907; Stevens, 1905*b*, 1906*b*; Frolova, 1924; Lawson, 1936; Honda, 1921; de Baehr, 1908, 1909; Shinji, 1931; Morgan, 1906, 1908, 1909*a*, *b*,

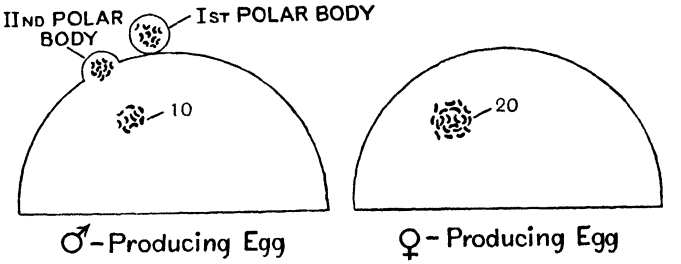
1912, 1915; Suomalainen, 1933). In some species such as *Phylloxera caryaecaulis* there is an $X_1X_2O : X_1X_1X_2X_2$ system, and in *Euceraphis betulae* there is an $X_1X_2X_3X_4O$ mechanism, but all the different X's behave in exactly the same way as the single one in other species.

Certain questions remain, however, completely mysterious. Thus in *Tetraneura ulmi* it is not known why some eggs of a particular sexupara get rid of one X chromosome at meiosis (and therefore produce males), while other eggs of the same individual retain both X's and give rise to females. In some other aphids, such as the species of *Phylloxera*, there are two kinds of sexuparae, each kind producing only male or only female eggs (Morgan). It is not known whether a cytological or genetical difference exists between the two kinds of sexuparae in these cases; Morgan (1912) thought that a portion of one of the X's was eliminated during the meiosis of eggs destined to give rise to male producers, but his observations have never been confirmed, and Ris (1942) thinks that any elimination which takes place is merely a casting out of surplus nucleic acid (as in *Pediculopsis*) and not the loss of a part of the protein framework of the chromosome.

Although most aphids have an alternation of generations, in some species the sexual part of the cycle has been lost. Thus in the subfamily Pemphiginae most species have a sexual generation which forms galls on the Mediterranean shrubs of the genus *Pistachia*, the parthenogenetic part of the cycle taking place on the roots of certain grasses, but in northern Europe (where *Pistachia* does not occur) species of permanently parthenogenetic Pemphiginae exist which are entirely confined to grass roots. According to the theory of Mordwilko (1935) these forms originally had an alternation of generations like the Mediterranean species, but when the Ice Ages drove the vegetation of the warm pre-glacial period out of northern Europe the sexual part of the cycle was abolished in one part of the range of the species, the permanently parthenogenetic ('anholocyclic') forms being restricted to a single host plant.

The cyclical parthenogenesis of the gall wasps (Cynipidae) differs from that of the aphids in several respects. Thus in *Neuroterus lenticularis* (Doncaster, 1910, 1911, 1916) there are two generations a year. The fertilized eggs give rise in the spring to parthenogenetic females which, although they all look alike, are in reality of two different types, male producers and female producers. In both cases the chromosomes pair during oogenesis and form ten bivalents. In the eggs of male producers (which are destined to give rise to haploid embryos), at least one and possibly two meiotic divisions occur (Doncaster thought two, but Dodds (1939), who has reinvestigated the matter, thinks only one division takes place). The eggs of the female producers seem to be entirely unique in not giving off a polar body at all (Doncaster and Dodds are in agreement on this). Thus if femaleness in *Neuroterus* depends on heterozygosity as in *Habrobracon* this heterozygosity could be transmitted by female producers to their daughters.

The sexual generation of *Neuroterus* pair and produce diploid larvae which develop into male and female producers once more in the following spring. Doncaster showed that each sexual female always gives rise to either male producers or female producers, but not both, so there are presumably two



Text-fig. 121. Diagram showing meiosis in the male- and female-producing eggs of the gall wasp *Neuroterus lenticularis*. In the first, two polar bodies are given off, in the second none. Based on the work of Doncaster (1910, 1911).

genetically different types of sexual female, outwardly similar. No cytologically distinct sex chromosomes have been demonstrated in *Neuroterus*, and in view of what we have said in Chapter XII it is unlikely that any exist.

In *N. lenticularis* the eggs of the sexual females must be fertilized if they are to undergo further development, and all the eggs laid by sexual females give rise to parthenogenetic females. In *N. contortus*, however, Patterson (1928) bred 10 males and 231 females from eggs laid by sexual females; no pairing took place between these males and the females of the parthenogenetic generation, so that the sexual instincts of the latter had apparently been lost. The distinction between male-producing and female-producing parthenogenetic females which is rigid in *N. lenticularis* and *N. irregularis* breaks down in *Andricus operator*, where the same parthenogenetic female produces both sons and daughters. In other species an intermediate condition exists, each female producing offspring which are mainly of one sex, with a few exceptions. The whole system of unisexual progenies seems to depend on a genetical mechanism which has developed within the Cynipidae, and reaches its final state in species like *Neuroterus lenticularis* and *irregularis* where no 'exceptional' offspring are produced and each parthenogenetic female is exclusively of one type or the other.

It is not known whether the cytological details are the same in all species of *Neuroterus*. In another cynipid, *Dryophanta erinacei*, the work of Wieman (1915) suggests that the chromosome cycle is of the same fundamental type.

A number of Cynipidae, belonging to several genera (*Cynips*, *Andricus*, *Rhodites*, *Phanacis*, etc.), have become anholocyclic, males being unknown or very rare and probably functionless. The cytology of *Rhodites rosae*, one of these anholocyclic species, has been studied by Henking (1892), Schliep (1909) and Hogben (1920), all of whose results are incomplete and somewhat contradictory.

CHAPTER XIV

CONCLUSIONS—CYTOLOGY AND EVOLUTIONARY PATTERNS

We have now completed our survey of existing knowledge about the changes which the chromosomes have undergone in the evolution of the Metazoa. This knowledge is fragmentary and incomplete in almost every respect, but it at least shows that the physical basis of evolution has itself undergone an evolution of its own, and is, in fact, still evolving. In the past it has been customary to explain the 'patterns' of evolution as largely or entirely determined by environmental factors. The theory of 'adaptive radiation', together with the various hypotheses that have been put forward to account for the extinction of once dominant groups like the Dinosaurs and the Ammonites, are examples of this tendency. Much less attention has been paid to the inherent properties and potentialities of particular genetic systems considered as limiting factors in evolution. No doubt all evolutionary 'patterns' are the result of interaction between environmental factors and genetic systems (rather than between the environment and *single* genes); we really know very little about this kind of interaction, although it is the very kernel of the whole evolutionary problem. Some of the phenomena formerly grouped under the term *orthogenesis* may possibly be eventually interpreted in terms of the intrinsic properties of cytogenetical systems. As Huxley (1942) has put it: 'Comparative evolution is destined to become as important a part of biology as comparative anatomy.' At present we can only dimly apprehend the scope of this new field, but there is every reason to be hopeful as to its future development.

Each set or complement of chromosomes, characteristic of a particular species, may be regarded as a genetical system which, like a chemical compound, has certain fixed characteristics (mutation rates, recombination index, liability to spontaneous breakage and so on). These properties, which depend on its molecular composition and organization, must collectively determine the capacity of the whole system to undergo evolutionary change. To some extent, also, they may determine the direction of change. In general the genetic systems of closely related species will be very similar, in spite of many single-gene differences, although special exceptions no doubt occur (e.g. where one species is bisexual and the other parthenogenetic, or where chromosomes which are autosomal in one species form part of the sex-chromosome mechanism in the other).

It is to be hoped that the time is not far distant when all the main types of genetic systems (including the bizarre chromosome cycles of the coccids and cecidomyids, the complex sex-chromosome mechanisms of many groups and the special types of structural heterozygosity met with in the evening primroses

and the grasshoppers of the genus *Trimerotropis*) will be seen as parts of a complete system of evolutionary theory. At present two tendencies exist which must be regarded as unfortunate. On the one hand there are those who altogether ignore or neglect the view that different types of genetic systems have different evolutionary potentialities and limitations, and tend to regard the patterns of evolution as determined solely by the extrinsic factors such as population size, selection pressure, geographical isolation and so on. This tendency is to a certain extent shown in the writings of some biologists who have made noteworthy contributions to the mathematical theory of natural selection. We cannot yet say with certainty how the mechanisms of speciation in the groups with haploid males differ from the corresponding mechanisms in groups where both sexes are diploid; but we can say with a fair degree of certainty that some general differences of this sort must exist, although they are not necessarily obvious to taxonomists engaged in studying the end-products of speciation rather than the process itself.

On the other hand, there are those who, while recognizing that 'evolution has had an evolution', fail to appreciate the complexity of the processes involved, and are satisfied with rather simple *a priori* explanations for the existence of different types of genetic systems. As illustrations of this kind of tendency we may take the view that parthenogenesis is an 'escape from sterility' (Darlington, 1939*b*) and the theory that chiasma frequencies are mainly determined by direct natural selection (see p. 84). Where a particular process or phenomenon is not immediately susceptible of experimental investigation it is always tempting to invent *a priori* interpretations. This kind of thinking does no harm, and may actually be useful in suggesting new lines of investigation so long as we are clearly aware of its limitations and do not mistake hypotheses for facts. In particular, we must bear in mind the probability that the same type of genetic system may have arisen under quite different circumstances in different groups. Thus parthenogenesis has arisen again and again in many different phyla, and it is at least highly unlikely that the causative factors have been the same in all cases. It has not arisen in the Vertebrata, except perhaps in the very special case of *Mollienisia formosa* (see p. 296)—a fact which merely emphasizes our ignorance of evolutionary pattern-making, since most vertebrate eggs can be artificially stimulated to develop without fertilization.

It is thus clear that the process of evolution is vastly more complex than the early geneticists imagined. In particular it is far more variable from group to group, and this variability probably exists at all levels in the systematic hierarchy. A given species may be evolving more rapidly in one part of its range than in another, one subsection of a genus may be splitting up into a great many species, while in another speciation is going on much more slowly, and so on. To a considerable extent, of course, these differences will depend on the extrinsic factors. Speciation is almost certain to occur far more rapidly in an archipelago or in a complex system of mountain ranges than in a uniform 'continental' area,

and if a species has a wide range its evolutionary history in different parts of that range may depend on climatic or geographical factors, presence or absence of predators and parasites and so on. Nevertheless, closely allied forms sometimes possess very different genetic systems which cannot obviously be correlated with the environments they occupy (although a hidden connection may nevertheless exist). Thus the llaveine and iceryine coccids are externally very similar, and have the same kind of life history, yet the males are diploid in the former and haploid in the latter. Even in the genus *Icerya* itself, males are necessary in most species but superfluous in *I. purchasi*, where the female has become converted into a hermaphrodite. The diploid males of *Habrobracon*, the occasional males in various species of parthenogenetic phasmids, and perhaps the sexual adults of *Micromalthus* are further examples of individuals which are strictly unnecessary but nevertheless persist as 'imperfections' of the genetic system in which they occur. But until a complete investigation has been made in each case we should be unwise to assume that they are completely functionless.

In a few instances, perhaps, we can establish a connection between geographical distribution and the type of genetic system present in a particular group of organisms. Thus in the *Trimerotropis* grasshoppers, it seems that the species of the Atlantic coast of the U.S.A., the Mississippi Valley and the Great Plains are cytologically homozygous, while those of the Sonoran and Rocky Mountain region, with its complex system of mountains, valleys and deserts, are structurally heterozygous. But this correlation may be purely accidental, and in any case much more work on the population-dynamics of these forms is needed before their speciation can be interpreted. It would certainly be interesting to know why large inversions are common in natural populations of *Sciara impatiens* but unknown in other species of the genus such as *ocellaris* and *coprophila*.

It may be worth while at this point to call attention to the fact that there are certain types of genetic systems that are well known in the higher plants but which have never been shown to exist in animals. Thus no well-authenticated case of natural allopolyploidy is known in the Metazoa, all the animal polyploids (*Artemia*, *Solenobia*, *Trichoniscus*) being apparently autopolyploids. The distinction between auto- and allopolyploidy is not, of course, an absolute one, and if a doubling of the chromosome number followed on crossing between two subspecies or strains of the same species it would be difficult to decide whether the resulting form should be called an auto- or an allopolyploid. If any allopolyploids exist in animals they are probably border-line cases of this kind.

One type of genetic system which has arisen independently in several orders of higher plants is *complex heterozygosity*. In complex heterozygotes such as many species of *Oenothera*, *Rhoeo discolor* (Commelinaceae) and *Hypericum punctatum* each chromosome of the diploid set is homologous to parts of two others, so that a single continuous ring of chromosomes (instead of a number of

separate bivalents) is formed at meiosis (see Darlington (1937*b*) or White (1937*a*, 1942*b*) for details). The whole system has clearly arisen as a result of a number of translocations. There seems to be no theoretical reason why complex heterozygosity should not also arise in animals, although the absence of self-fertilization may constitute an impassable barrier to the establishment of such a mechanism. If one day a ring-forming species of animal is discovered it will probably be in a group with the following characteristics: (*a*) low chromosome number, (*b*) all chromosomes metacentric, each arm having a chiasma frequency of 1·0, (*c*) no morphologically distinct sex chromosomes.

In very general terms the modern view as to the genetical mechanisms of species formation in animals may perhaps be formulated as follows:

(1) Speciation is not a sudden process but represents a rather definite stage or discontinuity in evolutionary divergence.

(2) The essential feature of speciation is the origin of a new isolating mechanism which partly or completely cuts off one group of individuals from another with which it would previously interbreed.

(3) Isolating mechanisms may depend on structural rearrangements of the chromosomes, but most of them are probably polygenic, arising in several stages.

(4) Geographical isolation between populations is the most important precondition for the establishment of biological isolating mechanisms such as those depending on intersterility, etc. Ecological isolation is also important, in some groups at any rate.

These four propositions may be regarded as common to most schools of evolutionary thought, and would probably be acceptable to nearly all modern geneticists. It is unfortunate that a proper classification of the different types of isolating mechanisms is still lacking, although a preliminary classification has been drawn up by Muller (1942) who uses the term 'hybrid incapacitation' to include both hybrid sterility and hybrid inviability. Various authors (e.g. Hogben, 1940) have suggested that mutations changing the time of the breeding season may initiate a state of biological isolation between the old and the new forms. It is possible that the importance of this type of isolating mechanism has been rather exaggerated, owing to the fact that it can easily be studied by field naturalists without the necessity of performing special experiments.

There can be very little doubt that the three main types of biological isolating mechanism in animals are: (1) a lack of sexual attraction between the males of one form and the females of another, i.e. a 'mating barrier'; (2) inviability of hybrids; and (3) hybrid sterility. In practice two or more types of isolating mechanism often exist together, mutually 'reinforcing' one another. Thus form *A* may show an 'aversion' to mating with form *B*, but if it should occasionally do so the cross may be infertile or the hybrids may be sterile, so that the two forms are kept distinct in spite of a certain amount of interbreeding.

Very little is known of the physical basis of sexual attraction in most groups

of the animal kingdom. In some (birds, spiders) complicated patterns of behaviour seem to play a major role, while in other groups chemical stimuli (odours) seem to be mainly responsible. In the genus *Drosophila* it is known that some species will mate readily in the dark while others will not do so, thus proving that visual stimuli may be essential for reproduction in one section of a genus and unimportant in another section. It is possible that mutations affecting the mechanism of sexual attraction may constitute one of the most important methods whereby incipient species come into existence, but there is very little concrete evidence on this subject.

Sturtevant (1938), in a stimulating essay, has raised the question: Which comes first in the speciation process—physiological isolation of the two forms or sterility of the hybrid between them? If, as there is now some reason to believe, both sexual isolation and hybrid sterility usually have a polygenic basis, then the antithesis may have little meaning. If both types of isolating mechanism arise by a fairly large number of separate steps, then they can evolve *pari passu*, and it becomes less important whether the first step was one affecting the mating habits of the parents or the fertility of the offspring. In some groups, however, it appears that interspecific hybrids and *a fortiori* those between races and subspecies of the same species are partially or fully fertile (see Chapter x). Unfortunately, we have no information as to whether the 'mating barrier' is unusually strong in these groups under natural conditions (it must be possible to cross the two forms in the laboratory, otherwise we should not know that the hybrids were fertile). It is conceivable that in some groups speciation involves nothing more than the building up of 'mating barriers', while in others intersterility or hybrid-sterility mechanisms are built up at the same time.* In that case the genus *Drosophila* would be an example of a group in which mating barriers, intersterility and hybrid sterility all participate in speciation, while those groups in which interspecific crosses give fertile hybrids would represent a different type of evolution in which nearly allied species are kept apart solely by mating barriers or other habit differences.

The nature of the 'raw materials' of evolution (i.e. gene-mutations and structural rearrangements) is no longer in doubt; but it is still far from clear just what role the latter have played in speciation. Some authors seem to have assumed rather lightly that structural rearrangements were one of the main agents of species formation. The opposite view (that they are mere epiphenomena of the evolutionary process, without any great significance in speciation) seems to be even more widely held at the present time. As far as *Drosophila* is concerned the truth probably lies somewhere between these extremes. The fact that even the most closely allied species always seem to differ in gene-sequence suggests

* It is probable that intersterility and hybrid sterility always develop *eventually*: it is merely a question of whether they grow up during that stage of evolutionary divergence which we call speciation.

that structural rearrangements do occur during the speciation period. But there is no evidence that the essential 'first steps' in speciation are always, or even usually, structural rearrangements. What does seem certain is that during the initial stages of speciation the number of individuals included in the new potential species will usually be small. Under such circumstances there will be a good opportunity for structural rearrangements to establish themselves as a result of 'drift'. When the number of individuals belonging to a species has become very large the chance of an inversion spreading through its whole range will be extremely small: on the other hand, inversions may establish themselves in local populations at any time during the history of the species. We cannot, of course, measure the antiquity of structural rearrangements by their frequency in species at the present day; but rearrangements which are present in all the individuals of a species and which distinguish that species from its nearest relatives (such as the large inversion in chromosome III which distinguishes *D. simulans* from *D. melanogaster*) must usually be of great antiquity and probably arose during the speciation period, when the number of individuals was still small.

It is still very uncertain how we should regard 'minute' rearrangements. Are they the outward and visible sign of certain types of gene-mutation, or are they to be looked upon as similar to the larger rearrangements but on a much smaller scale? And in any case what is their role in evolution?

None of the ordinary mutations known in *Drosophila* seem to alter in any way the appearance of the bands with which they are associated—that is to say, homozygotes and heterozygotes for ordinary gene-mutations cannot be distinguished in salivary preparations. This does not necessarily mean, however, that some true mutations may not induce visible changes in the appearance of the bands.

The wild populations of most species of animals are probably more heterogeneous genetically than cytologically; that is to say the number of different gene-sequences existing in the population at any one time will be smaller than the number of single gene differences. The condition met with in *Drosophila pseudoobscura* (where as many as 21 different sequences exist for a single chromosome) is probably rather exceptional, but may be expected to occur in other species that exist in nature as small colonies which are normally isolated from one another by geographical barriers.

We have as yet no real knowledge as to how far structural rearrangements determine evolutionary pattern-making. We may draw a distinction between groups in which the chromosome morphology varies very greatly from species to species and others in which it is much more constant, but this distinction does not seem to be obviously correlated with different types of evolutionary pattern. In the insects the archaic orders such as the Odonata, Plecoptera and the orthopteroid groups seem to have relatively few species and rather constant chromosome numbers, while in some of the 'modern' orders (Trichoptera,

Lepidoptera) there are more species and the chromosome numbers are less constant. But there seem to be far too many exceptions to this correlation for it to have any general validity or significance. Thus the Diptera (a 'modern' order including a very large number of species) seem to have rather constant chromosome numbers, and among the arachnids the scorpions (a very archaic group) show great variations in chromosome number. The only conclusion which can justifiably be drawn is that in some groups the gross morphology of the chromosomes seems to be extremely stable, while in others it is much less so; it may eventually be possible to establish general correlations with the speciation patterns of the various groups, but it would certainly be premature to do so at present.

The significance of 'repeats' in determining the long-range patterns of evolution may be considerable. The immediate effects of a duplication in the chromosome set will be to upset the genic balance of the organism. If this unbalance is serious the duplication will hardly stand a chance of establishing itself. But if a duplication does manage to undergo fixation it may be regarded as a source of new genetic potentialities not present in the original chromosome set. To what extent repeats have actually governed the patterns of speciation in particular groups can, of course, only be guessed at.

Another type of structural change which, although very rare, should on theoretical grounds have far-reaching genetical and evolutionary effects is the transference of regions from autosomes to sex chromosomes and vice versa.

Muller (1943) has recently suggested that the general mutation rate of the organism should depend in part on the length of the *X* chromosome (or, strictly speaking, on the number of active genes in the *X*). The argument is, briefly, as follows: mutations increasing the general mutation rate will tend to be eliminated because they lead to the production of too many 'freaks' of low viability. But they will only be eliminated when they occur in individuals which are phenotypically abnormal, i.e. in (*a*) individuals homozygous for an autosomal recessive, (*b*) those heterozygous for an autosomal dominant, (*c*) *XO* or *XY* individuals carrying a sex-linked mutation. Since the last category will be much more numerous where the *X* contains many genes Muller concludes that in a species like *Drosophila pseudoobscura*, where an originally autosomal chromosome arm has been included in the *X*, the general mutation rate will be forced to a lower level. The same will, of course, occur where a group adopts haplodiploidy, a mechanism which renders all the genes 'sex-linked'.

Goldschmidt (1940) has recently put forward an entirely new theory of the mechanism of evolution, to which we have referred several times. He regards the differences between species as entirely different in kind from those between subspecies and races and believes that true species arise by sudden 'systemic mutations'. The exact nature of the latter is left somewhat vague, but apparently they are supposed to involve a 'repatterning' of the chromosomes.

Now this repatterning really does occur (by multiple rearrangements), but in *Drosophila*, *Sciara*, and *Chironomus* it seems to occur within species as well as between them. Moreover, to anyone who has carefully studied the modern literature on speciation in *Drosophila* (which represents by far the most complete body of evidence on the 'species problem', since it includes cytological, genetical, ecological and biometrical data as well as detailed knowledge about hybridization and other types of information not usually taken into account by systematists), it must surely be clear that no hard and fast line can be drawn between species and lower categories such as subspecies. All degrees of isolation and morphological divergence exist, and the amount of 'repatterning' which the chromosome set has undergone depends, in general, on the degree of evolutionary divergence. In all this work there is nothing to suggest that species are fundamentally different in kind from subspecies, or that they arise by some special kind of intrachromosomal cataclysm. It is true that the gene-sequences of *pseudoobscura* and *miranda* are very different (a point stressed by Goldschmidt), but differences of exactly the same kind (although not so numerous) exist between subspecies, local races or strains of the same species. The only respect in which species do really seem to differ from the lower categories is in being true breeding units. In some instances a sudden cytological change such as a translocation may have ushered a new species into the world, but there is no reason to suppose that most species have arisen in this kind of way, or that a sudden change of this sort would usually create a new isolation mechanism. Most structural rearrangements probably have to exist for many generations in the heterozygous state before undergoing fixation in a local population, and the very fact that they are able to do so implies that they do not give rise to a new 'breeding unit'. On the other hand, if a particular rearrangement causes a lowered fertility or viability when heterozygous but has a satisfactory viability and fertility in the homozygous state (a condition which occurs in many translocations), we have a situation in which any mutation leading to an isolation between the old type of chromosome and the new will have a particularly good chance of undergoing fixation and thus giving rise to a new 'incipient species'.

Although, in the present state of our knowledge, it is difficult to make general statements about the rather diverse phenomena included in the term position effects, it is clear that they are all expressions of the *continuity* of the chromosome. In the early days of *Drosophila* genetics the emphasis was entirely on discontinuity (effects of single genes conceived of as discrete units). More recently certain writers such as Goldschmidt have swung to the opposite extreme, thinking that all genetical phenomena should be regarded as expressions of a continuous molecular pattern in the chromosomes and that all mutations are nothing but position effects resulting from minute structural rearrangements. The truth, for *Drosophila* at any rate, would appear to lie somewhere between these extreme viewpoints. For maize, on the other hand, the older viewpoint

seems to be almost completely true, since no undoubted position effects are known, in spite of the fact that a number of structural rearrangements have been studied. Perhaps the 'internodes' between the genes are longer or at any rate more completely devoid of genetic properties than they are in *Drosophila*.

It is unfortunate that we have no information about position effects in animals other than *Drosophila*. Even the fact that no position effects are known in grouse locusts, birds or rodents is hardly significant, since so few structural rearrangements have been studied. The extent to which changes of gene-sequence are able to establish themselves in evolution must depend largely on whether or not they lead to position effects, and if so on whether those effects are superficial or profound, advantageous or disadvantageous. In *Drosophila* perhaps 90% of all structural rearrangements have a detrimental effect on viability or fertility, so that they do not stand a reasonable chance of establishment, even in a small population. It would be unwise, however, to assume that this situation necessarily exists in other groups. It is unlikely on *a priori* grounds that position effects are confined to one genus of insects, but until we have far more exact knowledge as to their prevalence and intensity in other groups it is difficult to form any opinion as to their significance in evolution.

Although it seems undesirable to follow Goldschmidt in his complete rejection of the gene-concept, it is becoming increasingly clear that some regions of the chromosome possess general properties which it is difficult to interpret except in terms of a general molecular pattern which is superimposed on the genes. Thus all the loci of the *white-notch* region of the *X* in *melanogaster* exhibit mottling when brought into proximity with a heterochromatic region. These genes do not seem to show any other characteristic in common; some of them affect the colour of the eyes, others the development of the wings, and so on.

From time to time the hope has been expressed that chromosome cytology may become an important aid in taxonomic work. As far as plants are concerned, this situation already exists: chromosome studies are frequently employed in the discrimination of species and particularly in establishing their relationships to one another. Breeding work on wheat, cotton, rice, bananas and other economically important plants is now largely based on chromosome counts, which are essential to the understanding of phylogeny in a group where hybridization and polyploidy have occurred in the course of evolution.

In animals cytology has not been employed by taxonomists to anything like the same extent. In order to see the problem in its proper perspective it is necessary to understand the objectives of the taxonomist. In the first place he wishes to establish criteria for the identification of species and subspecies, in the second place he aims at determining the relationships of the species to one another, and in the third place he usually wants to have some idea of the relationships between the higher categories (genera, families, etc.).

For the first purpose polytene 'salivary-gland' chromosomes provide the ideal

technique of investigation, but since these only exist in the Diptera, the method is very restricted in application. Nevertheless, in this one group (or at least in those dipterous families where 'workable' salivaries exist) it is to be hoped that the discrimination of species and subspecies will come to be based more and more on accurate descriptions of salivary chromosomes.

Outside the Diptera the application of cytological methods to taxonomic practice depends on studies of the 'gross' morphology of the chromosomes—their number, shape, position of centromere, extent of heterochromatic segments and so on. In groups where the chromosome set varies very greatly from species to species it is probable that cytological methods will often be useful in taxonomic work. Thus in genera such as *Gammarus*, *Erebia*, *Limnophilus* and *Lethocerus* (see Table 8) it is quite possible that counts of chromosome numbers might be one of the best ways of distinguishing some 'difficult' species. They might also enable subgenera to be created where this has not previously been possible. On the other hand, in many large genera this method would be quite useless, since all the species have the same chromosome number. Conversely, in some genera like *Drosophila*, where the chromosome sets vary very greatly from species to species, it is not always safe to base one's ideas on the affinity of species on cytological data alone (see Text-figs. 54 and 55 for several instances of closely related *Drosophila* species with very different chromosome sets).

In a few complex or polytypic species such as *Gryllotalpa gryllotalpa* and *Sciurus carolinensis* cytological work may enable us to distinguish 'cryptic' forms or to establish the phylogenetic relationships of the various races. Thus in all difficult taxonomic problems it is worth considering whether a cytological investigation is worth undertaking. In many instances the answer will be in the negative, but in some cases cytological work may throw an entirely new light on the problem, since chromosomal characters are not necessarily correlated with ordinary morphological ones. Where a particular structural rearrangement can be shown to exist in a number of species we can safely assume that it arose on a single occasion and is hence monophyletic; but a mere chromosome number may easily be polyphyletic in a particular group. Thus the *a* and *b* inversions which exist in all the native American species of the *Drosophila virilis* group did not arise on several different occasions, and the *X*-autosome translocation occurred once only in the phylogeny of the Mantinae; but the chromosome number 3 has arisen on quite a number of occasions in different sections of the genus *Drosophila*.

Where an author attempts to produce a complete taxonomic monograph (e.g. Warren's (1936) *Monograph of the genus Erebia*), an effort should always be made to include some account of the chromosomes in the various species. If a preliminary investigation suggests that all the species have very similar chromosome sets the matter may be left at that: but if considerable differences are discovered a more extensive survey is warranted. Cytology is a tool that deserves more attention by taxonomists than it has received in the past, but as

far as animals are concerned it is certainly not a magic key that will unlock all taxonomic problems (except in those Diptera which possess workable salivaries, where cytology can probably answer all problems of discrimination of 'difficult' species).

For obtaining an understanding of the phylogenetic relationships of genera, families and so on, chromosome morphology *by itself* is usually an unreliable guide. But if we take into account not merely the shapes and sizes of the chromosomes, but the details of their mitosis and meiosis, a great deal more can be learned. Some examples have already been given in Chapters VIII, IX and XII—the subdivision of the Nematocera into those with normal and those with abnormal meiosis and of the Acarina into those with sex chromosomes and those with haplodiploidy represents instances where cytology has thrown new light on the phylogeny of the groups in question. In the coccids the work of the Schraders suggests that the group should be divided into three main sections: (1) those genera which retain an $XO : XX$ sex-chromosome mechanism, (2) those with male haploidy, and (3) those which have lost their X chromosomes, one haploid set being heteropycnotic in the males. It can hardly be doubted that such a classification is more 'fundamental' and represents phylogenetic relationships better than one based on rather trivial external characters such as the number of facets in the compound eye (i.e. characters which, by analogy with *Drosophila*, may well be due to single gene mutations, and which, in any case, are far more likely to be polyphyletic than a fundamental alteration in the whole genetic mechanism of the organism).

The nature, origin and functions of heterochromatin constitute one of the major unsolved problems of cytogenetics at the present time. We say unsolved, because in spite of the fact that we already know a great deal about the general behaviour of heterochromatin we are quite ignorant of its precise significance in the metabolism of the cell and in the evolution of genetic systems.

It is probable that rather too much stress has been laid on the antithesis between eu- and heterochromatin. It is at any rate certain that in most organisms there are several different kinds of heterochromatin, and it is possible that what we ordinarily call eu- and heterochromatin are merely the end terms of a series that includes a number of intermediate types of protein framework (as suggested by Poulson and Metz, 1938 and by Pontecorvo, 1943).

It can hardly be doubted that the heterochromatin plays a part in the general protein and nucleic acid metabolism of the cell. It is, indeed, probable that all chromosomal regions do this, but the heterochromatic segments seem to be particularly active in this respect. Neither can it be doubted that the alternation of different types of protein framework in the chromosome is in some way bound up with the occurrence of crossing-over (although here the connection is still imperfectly understood). But these by no means exhaust the possible functions of heterochromatin. We have seen that in many instances heterochromatic

regions or chromosomes possess 'vestigial' genetic functions, and it is possible that these properties are closely connected with the heterochromatin itself, i.e. that they could not be shown by euchromatic parts of the chromosome.

For a long time the *Y* was the only known example of genetically inert chromosomal material. When inert regions began to be discovered in other chromosomes (Muller and Painter, 1932) it was natural that these should have been regarded at first as having been derived (by translocation) from the *Y*. This was the view held by Muller (1932), who had previously pointed out that a chromosome like the *Y*, which does not undergo crossing-over and is always heterozygous, might be expected to undergo degenerative changes owing to the fact that it is 'shielded' from the effects of natural selection.

It is now clear that this conception of the origin of the heterochromatic regions was far too simple. In many organisms there exist heterochromatic segments in the other chromosomes which must surely have developed *in situ*. Thus in the case of the Acrididae, not only is a *Y* totally absent, but the autosomal heterochromatin is of a different type to that in the *X*, and must hence be presumed to have had an autosomal origin.

In some insects there is an obvious difference between *X* heterochromatin and *Y* heterochromatin. Thus in many Heteroptera such as *Picromerus bidens* the *X* and the *Y* are very much the same size and are both heteropycnotic at meiosis (Geitler, 1939*a*, *b*). But in the somatic resting nuclei only the *Y*'s are heteropycnotic, there being no heteropycnotic bodies in the female somatic nuclei. Even in *Drosophila melanogaster*, where all the heteropycnotic regions are sufficiently alike to form a chromocentre, there are certain differences between the heterochromatin of the autosomes and that of the *X* and *Y*. Thus translocations between the IVth chromosome and the heterochromatin of the sex chromosomes give rise to a *cubitus interruptus* position effect, while those between the IVth and the heterochromatin of the other autosomes do not (Khvostova, 1936). Moreover, Kaufmann (1942) has shown that the variegation of the eye facets known as *roughest*[3] depends on a rearrangement by which a particular locus is brought next to that part of the inert region of the *X* which contains the nucleolar organizer and the centromere. The remaining part of the inert region does not give rise to this position effect.

The ultimate origin of the inert regions is still wrapped in mystery. The earlier view (due mainly to Muller) was that a heterochromatic chromosome such as the *Y* had become inert through each of its genes mutating to an inactive (and stable) allelomorph. 'Becoming inert' was thus held to be a progressive change, each step of which was a gene-mutation.

Since no gene has ever 'become inert' in this sense in the laboratory the theory now looks rather doubtful. It now appears as if the essential difference between inert and active chromosomal regions is that the latter contain far fewer genes per unit of mitotic length. These genes are hence far 'longer' and,

correlated with this, they produce more nucleic acid at certain stages of mitosis.

When once they have arisen, heterochromatic regions can increase or decrease in the course of evolution, by duplication or deletion. They will be more likely to undergo changes of this kind than the active regions, since 'plus or minus changes' will have comparatively slight phenotypic effects. Within each group it is usually possible to distinguish species with much heterochromatin from those with relatively little. The former may be called megaheterochromatic species, the latter microheterochromatic ones (White, 1943). *Drosophila virilis*, *D. melanopalpa*, *Edessa irrorata* (Pentatomidae) and *Corixa punctata* seem to be all megaheterochromatic, while some other species of all these genera are relatively microheterochromatic. No suggestion can be put forward at present to explain why these species have acquired extensive heterochromatic regions while in others the amount of heterochromatin has been reduced in the course of evolution.

In some groups the amount of heterochromatin varies considerably from one individual to another owing to the prevalence of duplications or deletions of inert regions, supernumerary chromosomes and so on. In grasshoppers, especially, 'unequal bivalents' are very common in many species, the 'unequal' region being usually, or perhaps always, heterochromatic. The genetic systems of grasshoppers seem to be extremely tolerant of plus and minus changes of the total amount of heterochromatin. In *Drosophila* species, on the other hand, this type of variation does not seem to occur in natural populations (although in some species several types of *Y*, of different lengths, occur). It is thus probable that in *Drosophila* the amount of heterochromatin is fixed within much narrower limits, the degree of tolerance to deletions and duplications being much lower. Thus in the genus *Drosophila* we find interspecific variation in the amount of heterochromatin, while in some grasshoppers and in the bed-bug this variation is intraspecific.

It has been pointed out by Dobzhansky that if the mutation rate in man were the same per unit of time as in *Drosophila* a disastrous accumulation of lethal mutations would take place. It is thus probable that there is some kind of adaptation of the total mutation rate of an organism to the length of its life cycle. Nevertheless, we have very few data on the relative mutation rates of different species, and still fewer on the frequency of 'spontaneous' chromosome fragmentation. It is, however, probable that these rates play some part in determining evolutionary patterns. We now know that certain genes may affect the mutability of all the others, and it is probable that there are also genes which affect the frequency of chromosome fragmentation (*sticky* in maize is an example, but it also has other effects). Genes which greatly increase the mutation rate or the frequency of structural rearrangements will probably be too deleterious to survive in wild populations for more than a few generations, but even if they

only last a short while mutations of this kind may give rise to a sudden outburst of genetical or cytological variation, not all of which is eliminated by selection. Whether species that have remained constant over long periods of geological time have unusually low rates of mutation and chromosome breakage cannot, of course, be decided from any evidence available at the present time, although it seems most unlikely that the explanation will prove to be as simple as this.

It is known that extreme temperatures and temperature-shocks may increase mutation rates, but the evidence for an effect of temperature on the rate of production of structural rearrangements is mostly negative.

In the evolution of the sex-determining mechanism we may, perhaps, draw a primary distinction between *monogenic* and *chromosomal* (i.e. polygenic) mechanisms. A monogenic mechanism depends solely on a difference at a single locus, such as seems to exist in *Habrobracon*. Chromosomal mechanisms, on the other hand, involve the acquisition of differential regions which may render the X and Y visibly distinct under the microscope. Obviously, where the differential region is very short it may be extremely difficult to be certain that one is not dealing with a monogenic mechanism. In *Habrobracon* it is still uncertain which type of mechanism exists, although the balance of opinion seems to be in favour of the view that the x-factors are short differential segments rather than single genes. Monogenic mechanisms probably exist in teleosts, Amphibia and the lower Diptera (Chironomidae, Culicidae, Cecidomyidae and Sciaridae, where the distinction between the X and X' chromosomes appears to constitute a monogenic mechanism).* Many monogenic mechanisms seem to depend, not on a single allelomorph, but on a series of alleles of different strength. Thus such mechanisms frequently involve unisexual broods or at least broods showing sex ratios that vary according to the genetical constitution of one or both parents. In fact wherever we find fluctuating sex ratios or unisexual broods (as in *Pediculus* (Hindle, 1919; Buxton, 1940), *Chrysomyia* (Roy and Siddons, 1939) and the terrestrial Isopoda (Vandel, 1941; Howard, 1942)) there is reason to suspect the existence of a monogenic mechanism.†

Chromosomal mechanisms of sex determination may be looked upon as more 'advanced' than genic ones, the differential segments having been gradually built up by accumulation of genic differences, duplications and losses of heterochromatin and so on. Nevertheless, the monogenic mechanisms which we observe

* In the Chironomidae there is good evidence from salivary gland studies that no differential segments exist: in the other groups cited there is no really critical evidence that would enable a distinction to be drawn between short differential segments and single sex-determining genes.

† Howard has suggested that the various types of females in the Isopod *Armadillidium* ('androgenic', 'gynogenic' and 'amphogenic' according to whether they produce males only, females only or mixed broods) may differ in respect of a cytoplasmic factor, but it seems more in line with what we know of the inheritance of sex in other forms such as *Habrobracon* and *Sciara* to suppose that a single gene or short differential region determines femaleness, different allelomorphs of it (or different modifiers) regulating the sex of the offspring through some mechanism of 'differential maturation'.

at the present day were almost certainly evolved (as 'reversions') in groups with well-developed sex chromosomes, the monogenic mechanism overriding the chromosomal one which, being rendered superfluous, was subsequently lost. Thus the lower Diptera are not to be looked upon as remnants of a primitive state in which morphologically distinct sex chromosomes were absent: they are almost certainly descended from a group of 'panorpoid' or neuropteroid insects with a chromosomal method of sex determination. In all probability the change-over from male to female heterogamety (in the ancestors of the Trichoptera and Lepidoptera) also involved the replacement of a chromosomal by a monogenic mechanism, the latter subsequently evolving into a new chromosomal system, in which the female is the heterogametic sex. An analogous substitution seems to have occurred in the 'higher' scale insects (see p. 198), although it has not yet led to a 'chromosomal' heterogamety in the females.

Looking at the matter in a quantitative way, we may classify the various types of sex-determining mechanisms according to the number of sex-linked genes relative to the total number of genes (Table 18). This fraction seems to range from under one-hundredth to about one-third (not counting haplodiploid groups in which all the genes are 'sex-linked').

TABLE 18. *Percentage of the total number of genes which are sex-linked in various animals*

(Rough calculations based on various types of evidence)

Phigalia pedaria (Lepidoptera), some decapod Crustacea	Less than 1 %*
Man	Less than 4 %†
Drosophila melanogaster	18·4 %‡
D. pseudoobscura	36·5 %‡

* Estimated from the fact that all the chromosomes are about the same size and the haploid number is 100 or over.

† Estimated from the length of the *X* and the combined length of the 23 pairs of autosomes. There is a complication, due to the fact that some of the genes in the *X* are only partially sex-linked (see p. 238).

‡ Calculated from the number of bands in the salivary chromosomes (see Table 1). In *pseudoobscura* it is assumed that the *X* is equivalent to the *A* and *D* elements of *melanogaster* and that the total number of bands is the same in the two species.

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