Ph.D. Entomology

Cytogenetics in relation to taxonomy within the family Gryllidae (Orthoptera), with observations on some artifically induced changes

By

Hai-Choo Lim

Abstract

Testes from nymphs of the last three instars of twenty species belonging to two subfamilies of Gryllidae were studied to determine the number, morphology and behaviour of their chromosomes. Karyotypes of different species are described in detail with illustrations and idiograms. The male diploid numbers ranged from seven to thirty-one.

Gryllus campestris and a population of "G. bimaculatus" from Singapore showed anomalies in chromosome number and structure. Chromosomal polymorphism was quite common. Polyploid cells, and chromosome gaps and bridges occurred occasionally in some species. One or two supernumerary chromosomes occurred in some individuals of Gryllus veletis, the chromosome number of this species thus varying from 2n♂=29 to 31. Chromosome evolution within the family Gryllidae is discussed.

Various chemical and radiation treatments were applied in order to induce chromosomal abnormalities in some species. Chromosome breakage, stickiness, bridges and lagging, and multipolar spindles, polyploidy, unequal segregation etc. were the main abnormalities produced by these treatments. The sensitivity to chemicals and radiation varied between different species.

The need for further study to evaluate the cytogenetic effects of environmental contamination is stressed.

Ph.D. Entomology

Études Cytogénétiques en relation de taxonomie chez les Gryllides (Orthoptères), avec des observations sur des changements induits artificiellement

par

Hai-Choo Lim

Résumé

La morphologie du nombre, et du comportement des chromosomes de vingt espèces appartenant à deux sous-familles des Gryllides a été étudiée à l'aide des testicules prélevés sur des larves parvenues aux trois dernières stades larvaires. La description détaillée des caryotypes des diverses espèces s'snompagne d'illustrations et d'idiogrammes. Le nombre diploïde de chromosomes chez les mâles varie de sept à trente-et-un.

Des anomalies dans le nombre et la structure des chromosomes furent observées chez Gryllus campestris ainsi que dans une population de G. bimaculatus en provenance de Singapour. Le polymorphisme chromosomique s'avéra répandu. Des cellules polyploïdes et des cassures chromosomiques ont été rencontrées occasionnellement chez quelques espèces. Un ou deux chromosomes surnuméraires fusent trouvés dans quelques spécimens de Gryllus veletis; fasisant ainsi varier de nombre chromosomique de vingt-neuf a trente et un. Une discussion sur l'évolution des chromosomes chez les Gryllides est présentée.

Divers traitements chimiques et d'irradiation furent appliqués afin de produire des anomalies chromosomiques chez quelques spécimens. Les principaux effets observés sont: cassures de chromosomes; adhésivité; ponts; ralentissment; faisceaux multipolaires; polyploïdee; répartition inégale; etc. La sensitivité à ces traitements varie d'une espece à

l'autre.

La nécessité d'investigations plus approfondies de l'évaluation des effets cytogénétiques de la contamination biotopique est fortement soulignée.

CYTOGENETICS IN RELATION TO TAXONOMY WITHIN THE FAMILY GRYLLIDAE (ORTHOPTERA), WITH OBSERVATIONS ON SOME ARTIFICALLY INDUCED CHANGES

By

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I. INTRODUCTION

Since the beginning of twentieth century, the application of cytological data to different fields of biological science, especially to taxonomy, has become more and more important and useful. In many well-known groups of animals and plants, a study of the chromosomes has served as a valuable adjunct to taxonomic research.

A critical re-examination of the taxonomy of many insect groups has been carried out during recent years. This has long been necessary, because much of the classification in use at the present time is, of necessity, still based largely or wholly upon preserved specimens, i.e., for the greater part, on external morphological characters. This limited approach has frequently resulted in more than one biological species being included under a single name, or in a single polymorphic species having more than one name. Great difficulty and confusion for subsequent workers has often resulted. Therefore, a combination of morphology, cytology, ecology, biogeography and other factors now form, wherever possible, the foundation of modern taxonomy. The present study is part of such an integrated approach to cricket taxonomy (Kevan *et al.*, 1964).

Chromosome number is usually considered to be the most important cytological character of interest to taxonomists, but size, shape and behaviour of the chromosomes may throw more light on a taxonomic problem than the number alone, particularly in groups, such as the Acrididae (*s.str.*), in which the chromosome number is virtually constant. The most favourable situation is that in which the structure

of the individual chromosome can be studied in detail, so that a great number of characters can be taken into account.

Stebbins (1950) stated: " The chromosomes, because they are bearers of hereditary factors, should be considered as somewhat more fundamental than other structures on which relationship is based. " It is unnecessary, and indeed incorrect, however to assume that complex chromosomal systems are correlated with a complexity of macroscopic structure, or that species very similar in their general morphology must have very similar chromosomes. Nevertheless, in many cases, chromosomes do show co-variation with other characters exhibited by organisms, especially those associated with the accumulation of morphological changes which culminate in speciation.

Cytology has provided valuable data concerning the origin and nature of the chromosomal differences that exist at various taxonomic levels, and it has proved extremely useful in the study of closely related species groups, sibling-species complexes and polymorphic species. On the other hand, the effects of certain external environmental factors — such as various chemicals, including pesticides and other polluting agents, and radiation — can also be detected cytologically. Recently there has been a great increase in interest in this field, which has resulted in the publication during the last three decades of a number of papers dealing with the results of research into the cytological effects of environmental factors.

Investigations into radiation-induced chromosomal aberrations are of great fundamental importance. Not only do they assist in a

proper understanding of the possible mechanisms involved in the production of structural changes in chromosomes, such as occur, usually less frequently, in untreated populations, and which are inevitably involved in evolutionary processes, but they also allow one to assume the genetic effects of different qualities and dosages of radiation. Further, they enable one to determine the approporiate dosages to use in experiments intimately connected with physiology, therapy and protection against radiation harzards.

Study of the effects of chemicals on chromosomes have a similar value to studies on radiation, and, in addition, enable one to estimate genetically tolerable limits for the accumulation of pollutants such as pesticides. Further, such studies provide a better understanding of DNA, RNA and protein synthesis and the nature of gene mutation.

It is obvious, from almost any survey of biological literature, that an extensive study of cytology with modern techniques is extremely desirable in order to promote an understanding of both taxonomic and ecological problems. The present work attempts to relate these two aspects. The main purpose of the study was to increase our knowledge of cytogenetic and chromosomal aberrations induced by powerful ecological factors, namely toxic chemicals and radiation, with particular reference to Gryllidae, a group which has recently received much attention in the field of experimental taxonomy, both at McGill University (Macdonald Campus) and elsewhere. As a necessary major preliminary part of the work, an attempt was made to elucidate certain taxonomic questions, and, on the basis of cytological

differences between them, to confirm some previous findings regarding certain members of the family. This included an investigation of chromosomal variation occurring ' naturally ' within populations.

Thirteen species of Gryllinae were investigated, of which four are native to North America and two to the West Indies; the remainder are Old World species, of which three are established in the Americas. Six native North American species and one New Zealand species of Nemobiinae were also studied.

II. CYTOGENETIC STUDIES IN RELATION TO TAXONOMY

A. Literature Review

1. Cytological Review:

Since the beginning of the present century, and especially over the last twenty years, cytological studies of crickets (Grylloidea, mostly Gryllidae) have been carried out by a number of investigators. Earlier studies (i.e., those published 25 or more years ago) included a number on various species of Gryllinae (belonging, for the most part, to the genera now recognized as Gryllus, Acheta, Gryllodes, Loxoblemmus, Brachytrupes, Teleogryllus and Melanogryllus) by Baumgartner (1904), Gutherz(1907,1909), Brunelli (1909), Meeks (1913), Honda (1926), Ohmachi (1927,1929,1932a,b,1935), Tateishi (1932), Honda and Iriki (1932), Suzuki (1933), Momma in 1942 (as cited by Makino, 1951,1956) and Toledo Piza (1945); one on a species of Nemobiinae ("Nemobius" (=Allonemobius)) by Baumgartner (1929); two on Eneopterinae, viz. one species of "Apithes" (=Hapithus) by Baumgartner (1917) and one of Eneoptera, by Toledo Piza (1946); three, involving two species of Oecanthus, Oecanthidae, by Johnson (1922,1931) and Makino (1932); and three in respect of two species of Mogoplistinae (Ohmachi, 1927,1935; Tateishi,1932). Several species of "Pteronemobius", Nemobiinae, are also referred to by Honda (1926), Ohmachi (1927,1929,1932b, 1935) and Tateishi (1932); Ohmachi (1935) surveyed the chromosomes of 28 or more species of Grylloidea, including those of some genera, such as Cyrtoxiphus, Trigonidiinae, not referred to above.

More recently, for Gryllinae, Ohmachi (1950) and co-workers (1953) have studied three Japanese Teleogryllus species; Ohmachi and Ueshima (1955) examined a species of Loxoblemmus; Randell and Kevan (1962) added further species of Gryllus and one of Scapsipedus to the list of species investigated; Sharma (1963) referred, under the name Gryllus, to one species each of Modicogryllus and Plebeiogryllus; and Leroy (1967) also studied several species of Gryllinae, including the genera Gryllus, Teleogryllus, Modicogryllus, Platygryllus, Scapsipedus, Tartarogryllus and Loxoblemmus. Sotelo and Wettstein (1964) studied the fine structure of the chromosomes of a species of Gryllus. For other subfamilies, Ray-Chaudhuri and Manna (1950) refer to Euscyrtus spp. and to Seychellesia, Phalangopsinae, and Claus (1956) to Eneoptera, Eneopterinae. Davenport (unpublished,1960) investigated several North American species of Nemobiinae. Also, in the last decade, various grylloid insects of several genera, belonging to different families and subfamilies have received considerable attention in India from Manna and his collaborators (1964,1965,1966,1968,1969) and by Bhattacharjee and Manna (1967,1969). The genera studied included Gryllus, Gryllodes and Brachytrupes (Gryllinae), "Pteronemobius" (Nemobiinae), Anaxipha and Trigonidium (Trigonidiinae), Oecanthus (Oecanthidae) and Ornebius and Ectatoderus (Mogoplistinae).

Lim et al. (1969), followed almost simultaneously by Fontana and Hogan (1969), have published more comprehensive accounts of two Australasian species of Teleogryllus, which have been very recently augmented by Lim (1970). The last author has also provided further information on several genera of Nemobiinae (Lim,1971).

Ohmachi (1935) was the first worker to make a comparative study of the relationship between chromosomes and taxonomy in Gryllidae, nearly thirty species being considered. Makino (1951,1956), in his "atlases" of the chromosome numbers in animals, included a review of more than fifty grylloid species. More recent, similar reviews, restricted to the Grylloidea, have been published by Ohmachi (1958) and by Bhattacharjee and Manna (1967).

The male diploid chromosome number so far recorded for crickets ranges from 29 to 7. At the upper end of the scale are included Gryllus veletis (Alexander and Bigelow) and G. pennsylvanicus Burmeister, both of which have the same male diploid chromosome number, 29 (Randell and Kevan,1962). This chromosome number is also reported for G. pennsylvanicus (as G. assimilis) by Baumgartner (1904) and Ohmachi (1935), and for other Gryllus species: G. assimilis (Fabricius) (presumably) (Toledo Piza,1945); G. assimilis, sensu stricto (Randell and Kevan,1962; Leroy,1967); G. campestris Linnaeus (Ohmachi,1929,1935); G. bimaculatus De Geer (Tateishi,1932; Ohmachi,1935; Leroy,1967); G. rubens Scudder (Randell and Kevan,1962); G. fultoni (Alexander) (Randell and Kevan,1962); G. bermudensis Caudell (Leroy,1967); G. capitatus Saussure (Leroy,1967); G. insularis Scudder (Leroy,1967); G. peruviensis Saussure (Leroy,1967). Randell and Kevan (1962) pointed out that all the Gryllus species examined by them had the same chromosome number (i.e. $2n\delta=29$), but that they found it possible only to identify the X chromosome and the largest pair of autosomes, the remaining autosomes being too small to associate in pairs.

In species currently referred to the genus Teleogryllus, the spermatogonial chromosome number of T. mitratus (Burmeister), T. commodus (Walker), T. emma (Ohmachi & Matsumura), T. oceanicus (Le Guillou) and T. taiwanemma (Ohmachi & Matsumura) has been reported to be 27 by Honda (1926), Ohmachi (1927,1950), Tateishi (1932), Ohmachi et al. (1953), Lim et al. (1969), Fontana and Hogan (1969) and Lim (1970). However, that of T. oceanicus was recorded to be $2n♂=29$ by Leroy (1967), and another (Japanese) species of Teleogryllus, T. yezo-emma (Ohmachi & Matsumura), was observed by Ohmachi et al. (1953) to have $2n♂=25$. T. mitratus was, however, found by Honda and Iriki (1932) to vary: the chromosome number was $2n♂=25$ in a population from Manchuria and $2n♂=27$ in specimens from Kyoto, Japan. One grylline species, purportedly the type species of Teleogryllus from central Africa, T. posticus (Walker), was reported by Leroy (1967) to have $2n♂=19$. (If this is true, our present concept of Teleogryllus will have to be changed - see p. 48,53). My own analysis of the chromosome complements in Teleogryllus showed that acrocentric chromosomes and achromatic gaps were very common in T. oceanicus but rather rare in T. commodus, except in a population from Victoria, Australia; polyploid cells and lampbrush chromosomes also occurred in the intra- and interspecific hybrids of T. commodus and T. oceanicus (Lim et al.,1969; Lim,1970).

Twenty-one chromosomes occur in spermatogonial metaphase in the following species (names corrected where appropriate): Acheta domesticus (Linnaeus) (Baumgartner,1904; Gutherz,1907,1909; Meeks,1913; Randell and Kevan,1962); Gryllodes sigillatus (Walker) (Ohmachi,1927, 1935; Tateishi,1932); Scapsipedus marginatus (Afzelius et Brannius) (Randell and Kevan,1962; Leroy,1967); Melanogryllus desertus (Pallas)

(Brunelli,1909); Modicogryllus confirmatus (Walker) (Sharma,1963); M. uncinatus (Chopard) (Leroy,1967); Plebeiogryllus guttiventris (as Gryllus configuratus Walker) (Sharma,1963); Platygryllus lineaticepes (Walker) (Leroy,1967); Tartarogryllus burdigalensis (Latreille) (Leroy,1967).

A male diploid chromosome number of 19 is found in some Nemobiinae. Davenport (unpublished,1960) indicated that ten species of "Nemobius" occurring in the eastern United States of America should be separated on cytological grounds into three subgenera, as proposed earlier on the basis of external morphology by Hebard (1913): namely, Neonemobius, Allonemobius and Eunemobius, with male diploid chromosome numbers of 19, 15 and 7 respectively. Neonemobius was considered by Davenport (unpublished,1960) to be the most primitive member of the group and Eunemobius to be the most advanced. Allonemobius lay between them, and its karyotype was presumably derived from one similar to that of Neonemobius, in which a process of centric fusion might have occurred. Further centric fusion was postulated by Davenport as having occurred during the evolution of the karyotype of Eunemobius from an Allonemobius-like ancestor. His conclusion regarding the above relationships were supported by stridulation and specialization of habitat. Davenport's findings have recently been largely confirmed and the subgenera elevated to genera (Vickery and Johnstone, 1970; Lim,1971). Much earlier, Baumgartner (1929) had studied Allonemobius fasciatus (De Geer) in detail and had found that all of the autosomes were rod-shaped. They could grouped into two classes

according to the tetrad formation: three pairs formed rod tetrads and the other four equatorial rings or double crosses. The X chromosome was large and U-shaped.

Ohmachi's (1935) review of the chromosome complements of eight Old World species of Nemobiinae indicated 17 to be the most common male diploid chromosome number in this subfamily, and 15 the next. Only one species had 19 and one had 11 chromosomes. More recently, Bhattacharjee and Manna (1967) made a further brief review of the chromosome complements of eleven Old World species of Nemobiinae. The most common male diploid number reported by them was 15, only one species had 19, two had 17 and three had 11. Their paper is referred to and updated by Lim (1971).

Variable chromosome numbers are reported in the nemobiine genus Pteronemobius. Manna (1969) stated that this genus was the most heterogeneous amongst the Gryllidae. This was also stated by Vickery and Johnstone (1970) and Vickery (1971, in preparation) and was clearly indicated by Lim (1971). P. furumagiensis (Ohmachi and Furukawa) was recorded by Ohmachi (1927,1935) having a 2n♂ complement of 19, the autosomes consisting of two pairs of V's and seven pairs of rods and a slender U-shaped sex chromosome. Sixteen autosomes (two pairs of V's and six pairs of rods) and a V-shaped X chromosome were observed in P. flavoantennalis (Shiraki) (Ohmachi,1929,1935). A further three species of Pteronemobius having the same chromosome number are: P. nitidus (Shiraki) (Ohmachi,1927,1935), P.csikii (Bolívar) (Honda,1926), and P. fascipes (Walker) (Ohmachi,1927,1935;

Tateishi,1932). Two other species, P. taprobanesis (Walker) (Manna and Bhattacharjee,1964) and P. mikado (Shiraki) (Ohmachi,1927,1935) have $2n\delta$=15. P. ohmachii(Shiraki) possesses the lowest chromosome number, $2n\delta$=11, among so-called Pteronemobius species; all the chromosomes were V-shaped in this species (Ohmachi,1927,1935). Pteronemobius clearly includes species of more than one genus (Lim,1971) but only partial revisions have yet been attempted (Vickery and Johnstone,1970; Vickery, in preparation). It may be noted that P. fascipes will become the type species of a new genus. P. hargreavesi Chopard, P. occidentalis Chopard, P. nitidus and P. csikii should probably also be placed in the new genus (Vickery, in preparation).

Variability within "species" had also been recorded. The chromosome number of the grylline Loxoblemmus arietulus Saussure has been variably reported by different workers. It was given as $2n\delta$=13-15 by Honda (1926), 11-13 by Ohmachi (1927,1932b), 14 and 15 by Suzuki (1933) and 13-17 by Ohmachi and Ueshima (1955). All agreed that the variation of the chromosome number was due to the occurrence of multiple chromosomes. "L.arietulus", however, probably comprises more than one species, and, indeed, Ohmachi and Ueshima (1955) (without giving them formal names) distinguished three sibling species — "Tanbookame", "Moriokame" and "Haraokame" — in Japan. The chromosome number ranged from $2n\delta$=13 (consisting of X plus four pairs of metacentrics and two pairs of acrocentrics) to 17 (X plus one pair of metacentric and seven pairs of acrocentrics). The extra three pairs of metacentrics in the individuals with $2n\delta$=13 were multiple

chromosomes which were formed by the linkage of two non-homologous euchromosomes. Multiple chromosomes have also been observed in Brachytrupes portentosus (Lichtenstein). The male diploid number is reported to be either 15 or 17 by Momma in 1942 (as cited by Makino, 1951,1956); 14,15 or 20 by Ohmachi (1932a,1935); and 13,14 or 15 by Tateishi (1932).

Cytological studies of the hybrids between certain American field crickets were undertaken by Randell and Kevan (1962). The hybrid crosses between G. assimilis and G. pennsylvanicus, and between G. assimilis and "Texas half-triller" (a species not yet formally named) showed great variation in the chromosome number in metaphase II. A double bridge was found in anaphase I of the hybrids obtained by crossing G. fultoni and G. veletis. These chromosomal aberrations, it was presumed, might be caused by the failure of synapsis and incomplete pairing in the hybrids.

The sex-determining mechanism appears to be XX♀-XO♂ in most Grylloid species. Multiple sex chromosomes ($X_1X_1X_2X_2$♀-X_1X_2Y♂) have, however, been reported in Euscyrtus sp., E. concinnus (Haan) and Seychellesia sp., Phalangopsinae (Ray-Chaudhuri and Manna,1950; Manna and Ray-Chaudhuri,1965). During meiotic division in the male, one of the small univalents (supposed to be the Y chromosome) goes to one pole and the other two (one large and one small acrocentric, supposedly the X-complex, X_1X_2) move near to the opposite pole. Multiple sex chromosomes also occurred in Encoptera surinamensis (De Geer), Encopterinae (Toledo Piza,1946; Claus,1956). According to Claus (1956)

the multiple sex chromosome was $X_1X_1X_2X_2♀-X_1X_2Y♂$, rather than $XX♀-X_1X_2Y♂$ as reported by Toledo Piza (1946). X_1 was a small metacentric, X_2 an acrocentric and Y was a large metacentric; both X chromosomes went to the same pole, opposite to the Y chromosome, and no pairing was observed between them. A pseudo-multiple sex chromosome was studied by Smith (1953) in an Indian phalangopsine gryllid Euscyrtus sp.

Natural heterozygotes have been recorded in the Gryllinae, Plebeiogryllus guttiventris, P. sp. near guttiventris, Modicogryllus confirmatus, Teleogryllus commodus and T. oceanicus and in the Nemobiinae, Paranemobius sp., Pteronemobius bicolor (Saussure), P. taprobanesis, Neonemobius palustris (Blatchley) and Eunemobius carolinus (Scudder) (Manna and Bhattacharjee,1964,1966; Bhattacharjee and Manna, 1969; Lim et al.,1969; Fontana and Hogan,1969; Lim,1970,1971). The heteromorphic bivalents can be identified by their hook-shaped appearance in metaphase I.

The fine structure of meiotic chromosomes was studied, for Gryllus argentinus Saussure, by Sotelo and Wettstein (1964). Electron-microscope investigation demonstrated that the medial component was integrated by three longitudinal planes of filaments and each plane was integrated by two units: longitudinal in the frontal view and transversal in the lateral view.

In addition to investigations directly involving a study of chromosomes, a few other publications involving the cytology of crickets have appeared. In studies on the spermatogenesis of Acheta domesticus, using phase-contrast microscopy, Nath and Bhimber (1953)

found that the Golgi body was either granular in form or vesicular in appearance. Mitochondria varied in form during the development of the sperm and fused to form a mitochondrial body in the spermatid. The acroblast appeared as a large vesicle and the nucleus of the mature sperm was spiral in structure. Many secondary spermatocytes did not undergo cytokinesis, and spermatids had one, two, or more nuclei. However, Levine (1966) found that cytokinesis does occur in most of the primary spermatocytes and in all spermatogonia.

Under the electron-microscope, the nuclei of the early oogonia of Acheta domesticus have been shown to contain several small DNA bodies, whereas in the later stages (leptotene, zygotene and pachytene), the young oocytes have only one large DNA body; the DNA body exhibits a filmentous shape during metaphase and anaphase (Kunz, 1969). Several workers have analysed the extra DNA in the female germ cells of Acheta domesticus (Nilsson, 1966; Heinonen and Halka, 1967; Bier et al., 1967; Lima-de-Faric et al., 1968; Cave and Allen, 1969). Lima-de-Faric et al. (1968), however, found that every oocyte of Acheta domesticus contained a DNA body, which increased in size during the early meiotic prophase but which began to disintegrate by breaking into several small pieces at the end of the diplotene. By late diplotene, the whole body disappeared and had released DNA, histone and RNA into the nucleus. These authors stated that there was no comparable structure in the male meiotic prophase. Kunz (1969) also pointed out that, although the X chromosome of the male germ cells is very similar to the DNA body of the female, there is no regular

contact between the sex chromosome and the nucleolus. Cave and Allen (1969) found that the DNA body in oocytes of Acheta was intimately associated with one or more chromosome pairs and that at diplotene, large quantities of nucleolar material accumulated at the periphery of the body. Synthesis of this extra DNA continued long after DNA synthesis was completed by the chromosomes during early meiotic prophase. Poletaeva et al. (1970) found that there was no change in the amount of DNA during prophase I in A. domesticus, but the amount of histones increased progressively.

In conclusion, it may be mentioned that Tyrkus (1971) has recently developed a new cytological technique for the study of the morphology of the mitotic chromosomes with particular reference to Acheta domesticus. Insect haematocytes, instead of germ cells, are used for karyotypic analysis.

2. Taxonomic Review (with reference to the genera here studied):

The field and house crickets here studied all belong to the gryllid subfamily Gryllinae, tribe Gryllini, subtribe Gryllina, as defined by Randell (1964), to whom reference for details of classification may be made. Native field crickets occur commonly in relatively open places over much of the world between a little over 50°N. and a little under 45°S., and, in most of North, Central and South America, they can be found almost everywhere within these limits.

The first description of an American field cricket was that of Acheta (now Gryllus) assimilis, from Jamaica, published nearly two

centuries ago by Fabricius (1775). No less than forty-seven species were described from North and South America and the West Indies between 1775 and 1903. In 1903, seventeen names were applied to American field crickets (Rehn and Hebard, 1915). Lutz (1908) and Rehn and Hebard (1915), after studying a great series of specimens, concluded that only one highly variable species was represented and all the American species were reduced to synonymy under the name Gryllus assimilis (Fabricius). For many years all American field crickets were almost universally known by this specific name.

During this time there was also considerable confusion in the generic nomenclature of grylline crickets, the name Acheta Fabricius, 1775, to which genus the house cricket, Gryllus (Acheta) domesticus Linnaeus, 1758, is now referred, being generally regarded as a synonym of Gryllus Linnaeus, 1758; various species now referred to Gryllus, s. str., were referred to Liogryllus Saussure, 1877. Uvarov (1935) clarified the position regarding Gryllus, by implication synonymized Liogryllus with it, and proposed a new generic name, Gryllulus, for domesticus, which he regarded as being generically distinct, and this name had fairly wide acceptance. Roberts (1941), however, pointed out that Acheta Fabricius was available, with domesticus* as its type species, so that Gryllulus fell as its synonym. Gurney (1951) transferred assimilis back to Acheta, and North American workers followed his lead. The criterion defining the limits of Acheta (merely the arrangment

* Originally written domestica, a practice which survived for a long time, but Acheta is masculine, and in concurrence with the International Code of Zoological Nomenclature, the spelling was emended by Kevan (1955).

of the ocelli) was unsatisfactory, however, and, for reasons given in a footnote to their paper, Jobin and Bigelow (1961), at the suggestion of Dr. D.K.McE. Kevan, indicated that North American field crickets should be referred to the genus Gryllus if the classification were to be natural. Randell (1964) tacitly confirmed this. He found that the structures of the male genitalia of the species localized naturally in North America were more similar to G. campestris Linnaeus (the type species of Gryllus) and other Old World species than to Acheta domesticus.

As indicated above, since the work of Rehn and Hebard (1915), the native North American field crickets were, for many years, all lumped together under the name Gryllus (or Acheta) assimilis. Field observations, however, had suggested to some workers that this was not acceptable. Criddle (1925), for example, recognized formally two different 'races' of field crickets in Manitoba; called by him the spring cricket, G. assimilis pennsylvanicus Burmeister, and the fall cricket, G. a. luctuosus Serville. No interbreeding between these two seasonal populations occurred. Fulton (1952) confirmed Criddle's finding and wrote that at least four distinct populations of field crickets were distributed in the State of North Carolina. They were reproductively isolated from each other and differed biologically, physiologically and ecologically. Fifty hybridization experiments were made and all gave negative results. Fulton did not, however, assign formal specific names to his various populations. Behavioural differences between populations were further demonstrated by Alexander

(1957), who revised the taxonomy of field crickets of the eastern United States of America, reinstating several of the specific names that had fallen into synonymy and describing one new species, Acheta (now Gryllus) fultoni, for which no previous name was available. Alexander and Bigelow (1960) believed that the subspecies established by Criddle (1925) had become reproductively isolated through a seasonal separation of adults ("allochronic speciation"), and gave them full specific status as sibling species. The spring cricket they described as Acheta (now Gryllus) veletis (since no existing species name was available). The fall cricket was designated as typical A. pennsylvanicus; luctuosus, the name used by Criddle (1925), being a synonym (Alexander, 1957).

The first biological hybridization for field crickets was reported by Cousin (1933), who crossed Gryllus campestris and G. bimaculatus. A series of hybridizations were later carried out by the same author: G. bermudensis Caudell females crossed with G. campestris males (Cousin, 1946); G. (as Acheta) peruviensis Saussure with G. campestris (Cousin, 1954a); and G. (as Acheta) argentinus with G. campestris (Cousin, 1954b, 1955). The fertility of the hybrid generations was reduced in all of these crosses. Bigelow (1960) studied interspecific crosses among four species of American field crickets and found that hybrids were produced when he crossed G. rubens females with both G. veletis males (in his paper referred to as "WSS") and G. assimilis males; G. assimilis females crossed with both G. rubens males and G. pennsylvanicus males; G. veletis females with G. rubens males; and

G. pennsylvanicus females with G. assimilis males. All other attempts to cross the four species in different combinations (notably G. pennsylvanicus with G. veletis) gave negative results. Eight similar crosses between Gryllus species were also made by Randell and Kevan (1962).

Crossing experiments with house crickets, Acheta, s.str., by Ghouri and McFarlane (1957) showed that a Pakistani and a Canadian population were reproductively isolated. Geographic isolation and behavioural differences (failure of insemination, differences in action during courtship or, may be, in the odor of the male) were considered to be involved. It is now clear that two distinct species were involved, only the Canadian population being referable to the cosmopolitan house cricket species, A. domesticus. The Pakistani 'strain' has now proved to be A. hispanicus (Rambur), a widely distributed but less common Old World species (Dr. A.S.K. Ghouri, personal communication, 1970).

In addition to the field and house crickets of the subtribe Gryllina, one member of the tribe Gryllini belonging to the subtribe Sciobiina, Tartarogryllus burdigalensis (Latreille), was studied in the present work. No special comment on its taxonomy is called for, except to note that Randell (1964) established its systematic position within the Gryllinae.

'Ground crickets' belong to the subfamily Nemobiinae. Several small North American species of these were long confused under a single specific name, Nemobius fasciatus (De Geer). Fulton (1931, 1933, 1937), after a series of studies, pointed out that the 'species'

N. fasciatus was divisible into three physiological or ecological 'races'. The races were isolated from each other by their habitats and they did not interbreed in the areas of overlap. He designated one of these races as typical N. fasciatus and another as N. fasciatus tinnulus (Fulton); the third, N. allardi, was described by Alexander and Thomas (1959), who cleared up certain misunderstandings in the specific nomenclature.

With reference to generic names, all North American species were long regarded as belonging to one genus, Nemobius. However, Hebard (1913) proposed three subgenera, namely Allonemobius, Neonemobius and Eunemobius, for the Nearctic species, all being distinct from typical Old World Nemobius. He also proposed a fourth subgenus, Brachynemobius, to contain some Mexican species. Members of all but this last group have been available for the present study.

Fulton (1931) indicated that genitalic characters supported Hebard's separation, and Davenport (unpublished, 1960) agreed on cytological grounds (see p. 9). Recently, Vickery and Johnstone (1970), on the basis of the stridulation, genitalia and other morphological characters, have shown that the species of Nearctic Nemobiinae, formerly placed in Nemobius, and later transferred to Pteronemobius by Chopard (1967), belong to (at least) four distinct genera (not one genus with three subgenera). These are Hebard's Neonemobius, Allonemobius and Eunemobius together with a new genus, Pictonemobius. None is very closely related either to Nemobius, s.str., or to Pteronemobius, although they have more in common with the latter and belong to the

same tribe (Pteronemobiini). Their generic status is confirmed on cytological grounds by Lim (1971).

Johnstone and Vickery (1970) have also made certain corrections in the specific nomenclature of North American Nemobiinae, particularly in respect of the species name palustris (Blatchley). All of the species in which the males have subdistal tibial glandular spines (including those belonging to the Nearctic genera referred to above) are now included by Vickery (in preparation) in the tribe Pteronemobiini.

With reference to the systematics of the single New Zealand species of Nemobiinae studied, little can be said at present, except that it belongs to the Nemobiini. This tribe is in very serious need of revision. Johns (1970) indicates the present unsatisfactory taxonomic situation regarding the New Zealand species, but his suggestion that the species should be referred to Pteronemobius, rather than to Nemobius as formerly, is (at least partially) incorrect. The species here considered can only be referred tentatively to a systematic position possibly associated with the Australian "Nemobius" bivittatus (Walker) (see Chopard,1951), but apparently not to the genus Nemobius, s. str.

B. Materials and Methods

1. Materials:

The systematic positions, origin and history of the species used in this study are as follows:

Subfamily Gryllinae

Tribe Gryllini

Subtribe Gryllina

Genus	Species	Origin	History
Gryllus	veletis (Alexander & Bigelow, 1960)	S.W. Quebec	reared in the laboratory since 1969
	pennsylvanicus Burmeister, 1838	S.W. Quebec	reared in the laboratory since 1969
	assimilis (Fabricius, 1775)	Antigua Jamaica	both reared in the laboratory since 1959
	bimaculatus De Geer, 1773	Azores (Sta Maria) Singapore	reared in the laboratory since 1965. field collected in 1968 by Dr. T.W. Chen
	bermudensis Caudell, 1903	Bermuda	reared in the laboratory since 1959
	rubens Scudder, 1902	Florida	field collected in 1970 by Dr. T.J. Walker
	campestris Linnaeus, 1758	Hungary	field collected in 1970 (spent a short time in insect house in Budapest Zoo before received from Dr. B. Nagy)
	firmus Scudder, 1902	Florida	reared in the laboratory since 1962
Acheta	domesticus (Linnaeus, 1758)	S.W. Quebec (cosmopolitan, Old World)	reared in the laboratory since 1967
Gryllodes	sigillatus (Walker, 1869)	Pakistan (tropicopolitan, Old World)	reared in the laboratory since 1956
Scapsipedus	marginatus (Afzelius et Brannius, 1804)	Jamaica (Africa, introduction)	reared in the laboratory since 1959

Melanogryllus	desertus (Pallas, 1771)	Hungary	field collected in 1969 by Dr. B. Nagy and subsequently reared in the laboratory in Budapest and, in 1970, Macdonald College
Subtribe Sciobiina			
Tartarogryllus	burdigalensis (Latreille, 1802)	Azores (Sta Maria)	reared in the laboratory since 1965
Subfamily Nemobiinae			
Tribe Pteronemobiini			
Neonemobius	palustris (Blatchley, 1900)	Lac Carré, Quebec	reared in the laboratory since 1968
	sp. near mormonius (Scudder, 1896)	Florida	field collected in 1969 by Dr. T.J. Walker
Allonemobius	fasciatus (De Geer, 1773)	Pincourt, Quebec	field collected in 1969 by Dr. V.R. Vickery
	allardi (Alexander & Thomas, 1959)	Pincourt, Quebec	field collected in 1969 by Dr. V.R. Vickery
	griseus griseus (E.M. Walker, 1904)	N.D. du Laus, Quebec	field collected in 1969 by Lyman Museum Staff
Eunemobius	carolinus carolinus (Scudder, 1877)	Pincourt, Quebec	field collected in 1969 by Dr. V.R. Vickery
Tribe Nemobiini			
'Nemobius'*	sp.? near bivittatus (Walker, 1869)	Kaikoura, New Zealand	field collected in 1970 by Dr. P. Johns

* Pteronemobius of Johns (1970), but not this genus; agrees better with current concept of Nemobius, which is, however, in need of revision (Dr. V.R. Vickery, personal communication, 1971).

Unless otherwise stated, the stocks from which laboratory cultures originated were field collected at different times by various members or former members of the Department of Entomology, McGill University.

Throughout the study, nymphs of the last three pre-adult instars were used to provide both testes and ovaries for cytological examination. All the data recorded, however, were obtained from testicular follicle cells, because, in immature ovaries, mitotic cells are rare and no meiotic division occurs. The oogonial metaphase was used merely to confirm the expected female diploid chromosome number.

2. Methods:

a. Culture and rearing

The culture and rearing methods used through the present study were the standard ones adopted in previous studies on crickets in the Department of Entomology, McGill University (Ghouri and McFarlane, 1957).

b. Cytological studies

After anaesthetizing the crickets with ethyl acetate, the gonads were dissected from living individuals in insect saline (Baker, 1950), fixed in Farmer's fluid or Carnoy's fluid (Smith, 1947) for 24 hours, and then stained according to Snow's method (Snow, 1963). Temporary squashed preparations were made in most cases. The coverslips were ringed with a mixture of paraffin and vaseline, and the slide thus prepared remained in a satisfactory state for four to five weeks.

A permanent dry-ice-freezing method (Darlington and La Cour, 1962) was also used occasionally for special purposes. For further details of the methods used, see Lim (1968).

c. Analysis of data

Drawings of chromosome complements were made with the aid of a camera lucida at a magnification of 1250X. The chromosome number was determined by first counting the number in the spermatogonial metaphase, and then confirmed by determining the haploid number in both the first and the second meiotic divisions. The chromosomes were differentiated into four groups according to the position of the centromere and the arm ratio, as proposed by Levan et al. (1964) and modified by Lim (1968): (1) metacentric (M): arm ratio=1.00-1.30; (2) submetacentric (SM): arm ratio=1.31-1.70; (3) subtelocentric (ST): arm ratio=1.71-7.00; (4) acrocentric (A): arm ratio=7.00-∞. Centromeric index (i) was calculated from the formula $i=100s/c$ where s the length of short arm and c total length of the chromosome (Levan et al., 1964).

A side-screw divider and a triangular boxwood metric scale (both supplied by The Hughes-Owens Co., Montreal) were used as tools to measure the lengths of the chromosomes (mainly from drawings). The total chromosome length (TCL), arm ratio and centromeric index were then calculated. Idiograms of the karyotypes were made according to the data obtained. In the idiograms, the chromosomes were arranged in order of descending length of the short arm. The "fundamental number" is the total number of arms occurring in the autosomes of the

diploid set (Matthey,1951). The ratio of X/LA is the length of the X chromosome divided by that of the largest autosome.

During diakinesis, all the chromosomes become condensed and can be distinguished individually. The shape and structure of the chromosomes are more or less constant at diakinesis, which is the best stage for studying the frequency of ring-formed chromosomes. Thus, all of the analysis of this type of data was carried out on cells of this stage. The frequencies of unequal bivalent, terminal and interstitial chiasmata were measured at metaphase I because these characters could be observed most clearly at this stage. During the diplotene, the chromosomes usually show maximum chiasma frequency and each chromosome can be distinguished; chiasmata were thus most conveniently studied during this phase.

As all the chromosomal characters undergo some change during the different stages of meiosis, the data presented for each character apply only to the particular stages of development indicated above.

C. Results

1. Chromosome Numbers:

The chromosome numbers of the species studied are listed in the following table (mm=mitotic metaphase; MI=meiotic metaphase I; MII=meiotic metaphase II).

Subfamily	Genus	Species	mm♂	mm♀	MI♂	MII♂
Gryllinae	Gryllus	veletis	29,30,31	-	15,16	14,15,16
		pennsylvanicus	29	30	15	14,15

Subfamily	Genus	Species	mm♂	mm♀	III♂	III♂
Gryllinae	Gryllus	assimilis	29	30	15	14,15
		bimaculatus	29	30	15	14,15
			27,29	-	variable	variable
		bermudensis	29	30	15	14,15
		rubens	29	30	15	14,15
		campestris	29	-	15	14,15
		firmus	29	30	15	14,15
	Acheta	domesticus	21	22	11	10,11
	Gryllodes	sigillatus	21	22	11	10,11
	Scapsipedus	marginatus	21	22	11	10,11
	Melanogryllus	desertus	21	-	-	-
	Tartarogryllus	burdigalensis	19	20	10	9,10
Nemobiinae	Neonemobius	palustris	19	20	10	9,10
		sp. near mormonius	19	-	10	9,10
	Allonemobius	fasciatus	15	16	8,9	7,8,9
		allardi	15	16	8	7,8
		griseus griseus	15	16	8	7,8
	Eunemobius	carolinus carolinus	7	8	4	3,4
	'Hemobius'	sp.? near bivittatus	21	-	11	-

chromosomes at the same pole as the X chromosome (Fig. 25); (iv) two supernumerary chromosomes, one at the opposite pole and one at the same pole as the X chromosome (Fig. 26). Only 6 individuals (out of 20 studied) were without a supernumerary chromosome. The male diploid number was 29 ($n\delta$=15) (Figs. 27a,b) in these individuals as previously reported by Randell and Kevan (1962). In some individuals (7 out of 20 studied), one or two supernumerary chromosomes occurred in some cells but not in others, even of the same individual. During anaphase I, the supernumerary chromosomes, in some instances, moved to the same pole as the X chromosome (about 42.9%), while in others, they moved to the opposite pole (about 49.7%) or remained at the equator area (7.4%) (Figs. 28a,b). At telophase I, the supernumerary chromosomes either moved to the end of the poles or remained at the equatorial plate. They formed small vesicles with a structure similar to that of the X chromosome at interkinesis (Fig. 29).

Polyploid cells (Fig. 30) and sticky bridges at anaphase I (Fig. 31) occurred occasionally. All of the chromosomes were homomorphic (Fig. 32), no heteromorphic pair was observed. The frequencies of the chiasmata and ring-formed chromosomes are summarized in Tables XXI, XXII, XXIII, Fig. 194.

(2) G. pennsylvanicus

No supernumerary chromosome was observed in this species. The diploid chromosome number was 29 in the male and 30 in the female. There were only three acrocentric pairs (1,2 and 10); seven subtelocentric pairs (5,6,7,8,9,12 and 13); two submetacentric pairs (4 and

9); and two metacentric pairs (3 and 14). The X chromosome was the largest metacentric. The mean TCL was 147.45μ, ranging from 135.92μ to 158.56μ. The fundamental number was 50. The ratio X/LA was 2.63 and the average length of each chromosome was 5.08μ (see Tables I,III, Figs. 2,19,33).

All of the chromosomes were connected to each other and closely associated with the nucleolus during early meiotic prophase (Fig. 34). At metaphase I, a single unequal bivalent appeared in some cells (about 30%, from 16 individuals) (Fig. 35). A sticky bridge configuration occurred in some of the anaphase I cells (Fig. 36). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(3) G. assimilis

(a) Antigua population:

The spermatogonial complements showed 29 chromosomes. The karyotype consisted of four acrocentric pairs (1,4,5 and 11); seven subtelocentric pairs (2,3,6,7,8,9 and 10); one submetacentric pair (12); and two metacentric pairs (13 and 14). The X chromosome was the largest metacentric with an arm ratio of 1.12. The mean TCL was 156.01μ, ranging from 141.68μ to 178.40μ. The fundamental number was 48. The ratio X/LA was 2.33 and the average length of each chromosome was 5.37μ (see Tables I.IV, Figs. 3,19,37).

The size and the shape of the spermatid (Figs. 38a,b) and of the early sperm (Fig. 39) were quite different from those of other

Gryllus species described previously. The spermatids were almost rectangle-shaped instead of oval- and spindle-shaped, as in other Gryllus species. The X chromosome sometimes was cross-shaped instead of V-shaped at metaphase I (Fig. 40). No heteromorphic chromosome occurred (Fig. 41). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(b) Jamaica population:

The morphology and behaviour of the chromosomes were similar to those of the Antigua population, as expected. All of the chromosomes were homomorphic(Fig. 42). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(4) G. bimaculatus

(a) Azores population:

This species has the smallest-sized chromosomes among the Gryllus species studied, and there was very little difference in length between each chromosome pair. The male diploid chromosome number was 29. The karyotype consisted of nine pairs of acrocentrics (1,2,3,4,6,7,8,10 and 13); five pairs of subtelocentrics (5,9,11,12 and 14); and a metacentric X chromosome. The mean TCL was 104.97μ, ranging from 95.84μ to 114.32μ. The fundamental number was 38. The ratio X/LA was 2.84 and the average length of each chromosome was 3.59μ (see Tables I,V, Figs. 4,19,43).

The nucleolus (1 or 2 in number) was always found to be

associated with the X chromosome during meiotic prophase and they remained in the nucleus until early diakiensis. All of the chromosomes were homomorphic(Fig. 44). The shape of the early spermatid was triangular (Fig. 45) instead of oval -shaped as in most Gryllus species. The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(b) Singapore population:

The population from Singapore survived through one generation only. No egg was produced by any female of the F_1 offspring.

Cytological aberrations were observed in the F_1 generation and the chromosome number varied even within a single individual. The male haploid chromosome numbers scored from 6 F_1 individuals were as follows:

chromosome number (n♂)	13	14	15	16	17	18
no. of cells involved	6	100	110	54	28	2
per cent	2.0	33.3	36.7	18.0	9.3	0.7

The stickiness of the chromosomes in the F_1 (Fig. 46) was much greater than in the Azores population; the chromosomes of most of the cells formed a mass, so that no detail could be observed. Other chromosomal aberrations such as unequal segregation (Fig. 47), asynapsis, fragmentation (Fig. 48), polyploid cells (Fig. 49), chromosomal bridges at anaphase I (Fig. 50) and telophase I (Fig. 51), multinuclei (Fig. 52) and lagging chromosomes at telophase I (Fig. 53) were observed in the F_1 male offspring. The F_1 female offspring showed abnormal oogenesis and had only sterile ovaries.

Two males from the parent generation were also studied. More than half of the cells (about 68.7%) had a diploid chromosome number of 27 ($n\delta$=14) instead of the normal number 29. Achromatic gaps occurred at metaphase I (Fig. 54).

(5) G. bermudensis

Twenty-nine chromosomes were counted in spermatogonial metaphase. The chromosome pairs of 2,12 and 14 were short to long submetacentric; those of pairs 3,5,6,7,8,9 and 11 were subtelocentric; the remaining four pairs (1,4,10 and 13) were acrocentric of varying length. The X chromosome was the only metacentric. The mean TCL was 145.44μ, ranging from 120.72μ to 183.04μ. The fundamental number was 48. The ratio X/LA was 3.10 and the average length of each chromosome was 5.10μ (see Tables I,VI, Figs. 5,19,55).

At anaphase I, the X chromosome had a cross-shaped appearance and it sometimes still remained at the equator area when all of the autosomes had moved to the poles (Fig. 56). No heteromorphic occurred (Fig. 57), but polyploid cells were observed occasionally (Fig. 58). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(6) G. rubens

The male diploid number was 29 in this species. The karyotype consisted of seven acrocentric pairs (1,2,5,6,7,9 and 11); two subtelocentric pairs (8 and 12); four submetacentric pairs (3,4,10 and 13); and one metacentric pair (14). The X chromosome was the

largest metacentric with an arm ratio of 1.19. The mean TCL was 120.17μ, ranging from 110.80μ to 130.72μ. The fundamental number was 42. The ratio X/LA was 2.65 and the average length of each chromosome was 4.14μ (see Tables I,VII, Figs. 6,19,59).

The sticky substance which formed the interbivalent connections was very pronounced in this species. It was found to occur not only at prophase I, but was also observed at metaphase I (Fig. 60). In some cases, a non-homologous association occurred, involving the centric end of one bivalent and the non-centric end of another (Fig. 61). The phenomenon was quite unusual in the 'normal' (laboratory) population, although the interbivalent connection was found to be a chromosomal abnormality frequently produced by chemical or radiation treatments (as described later in Chapters III and IV). Achromatic gaps and, occasionally, chromosome breaks were observed at metaphase I (Fig. 62). Sticky bridges (in about 7.6% of the cells) occurred at anaphase I and telophase I (Fig. 63). One or two heteromorphic bivalents occurred (Fig. 62). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(7) G. campestris

Two specimens collected in the field some 15 km N. E. of Budapest, Hungary (and subsequently transferred to the insect house at the Budapest zoological park before transmittal to Canada) were studied. The male diploid chromosome number was 29, as reported for the species by Ohmachi (1929,1935). There was very little variation in length between different pairs of autosomes, and most of the

chromosomes were rod-shaped. The karyotype consisted of nine acrocentric pairs (1,2,3,4,5,6,7,9 and 12); three subtelocentric pairs (8,10 and 11); one submetacentric pair (13); and one metacentric pair (14). The X chromosome was metacentric with a secondary constriction on the proximal end of the short arm. The mean TCL was 119.33μ, ranging from 96.56μ to 137.36μ. The fundamental number was 38. The ratio X/LA was 2.64 and the average length of each chromosome was 4.11μ (see Tables I,VIII, Figs. 7,19,64).

The chromosome mass of the two individuals studied was extraordinarily abnormal. The chromosomal abnormalities included: breaks (Fig. 65), anaphase bridge (Fig. 66), stickiness (Fig. 67), c-mitosis (Fig. 68), polyploidy (Fig. 69), numerous univalents (Fig. 70), lagging chromosomes (Fig. 71), non-disjunction (Fig. 72) and unequal segregation (Fig. 73). The frequency of the abnormalities is recorded in Table IX. The degree of stickiness varied from a few light staining thread-like connections between bivalents forming a pseudomultivalent (Fig. 74), to a condition in which all the chromosomes were clumped into a large dense mass (Fig. 75) or a few small mass groups (Fig. 76). All cells were polyploid or showed chromosomal abnormality in some testicular follicles (Fig. 77) in one of the individuals. The chromosomal abnormalities in the scanty material studied for this species were similar to those produced by chemical treatment, especially by phenol compounds (see Chapter III).

(8) G. firmus

The male diploid chromosome number was determined as 29, but

no study of the details of the chromosome structures was made.

(9) Gryllus hybrids

Hybrids between several species of Gryllus were studied cytologically by Randell and Kevan (1962) and various abnormalities in the chromosomes were described. No effort was made, therefore, to duplicate the particular crosses already made by these authors, but, since the present work is largely concerned with chromosomal abnormalities, numerous and repeated attempts were made to produce hybrids from other crosses between available species. None of these hybridization experiments was successful and no progeny (and, therefore, no cytolgoical material for the present study) was obtained, although some interspecific pairing occurred in some cases and oviposition of infertile eggs sometimes occurred. Thus, although the production of hybrids from several different crosses between Gryllus species is possible (see pp. 18 and 19), other species seem to be genetically incompatible.

The following were the unsuccessful crosses attempted: G. bimaculatus, female X G. veletis, male; G. veletis, female X G. bimaculatus, male; G. assimilis, female X G. bermudensis, male; G. bimaculatus, female X G. assimilis, male; G. bermudensis, female X G. assimilis, male; G. bermudensis, female X G. bimaculatus, male.

ii. Genus Acheta

A. domesticus

Twenty-one chromosomes were counted in spermatogonial

metaphase. The karyotype consisted of four acrocentric pairs (1,2, 4 and 5); one subtelocentric pair (3); two submetacentric pairs (6 and 8); three metacentric pairs (7,9 and 10) plus the largest of the metacentric chromosomes, the X chromosome. The mean TCL was 110.84μ, ranging from 88.64μ to 129.36μ. The fundamental number was 32. The ratio X/LA was 2.94 and the average length of each chromosome was 5.27μ (see Tables I,X, Figs. 8,19,78).

At diakinesis, the X chromosome still remained mass-structured and deep-stained as in the earlier prophase. Therefore, the chiasma frequency in this species was measured only from the autosomes and excluded the X chromosome. All chromosomes were homomorphic (Fig. 79). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

iii. Genus Gryllodes

G. sigillatus

The male diploid chromosome number was 21. Ten pairs of autosomes and a single metacentric X chromosome were observed. Pairs 1,2,5,8 and 10 were short to long acrocentrics; pairs 3,4,6,7 and 9 were subtelocentrics; no submetacentric or metacentric autosome occurred. The mean TCL was 100.56μ, ranging from 86.56μ to 113.36μ. The fundamental number was 32. The ratio X/LA was 3.10 and the average length of each chromosome was 4.78μ (see Tables I,XI, Figs. 9,19,80).

A single unequal bivalent occurred in metaphase I (Fig. 81), and achromatic gaps appeared in some cells (Fig. 81). An E-bridge

was observed in some anaphase cells (Fig. 82). The shape of the early spermatids was quite different from other species (Fig. 83), more or less semi-circular, half being deep-staining and half light-staining. Some early spermatids had a concave surface. The late spermatids were elongated with a small triangular or oval-shaped, deep staining, apical structure, which was separated from the main body and later disappeared (Figs. 84,85). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

iv. Genus Scapsipedus

S. marginatus

The male diploid chromosome number was 21. The karyotype consisted of three acrocentric pairs (1,3 and 4); two subtelocentric pairs (2 and 5); two submetacentric pairs (6 and 8); and four metacentric pairs (7,9,10 and the X chromosome). The mean TCL was 134.92μ, ranging from 108.88μ to 160.00μ. The fundamental number was 34. The ratio X/LA was 2.19 and the average length of each chromosome was 6.42μ (see Tables I,XII, Figs. 10,19,86).

The cells were mainly homomorphic (Fig. 87), but in a few, (about 6.1% from 20 individuals), single unequal bivalent occurred (Fig. 88). This was an asymmetric unequal bivalent, i.e., heteromorphic pair with different centromere positions. This might have been an occurrence of abnormal segregation of the bivalent. Achromatic gaps occurred occasionally (Fig. 89). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

v. Genus Melanogryllus

M. desertus

Only one male specimen was studied in order to confirm the chromosome number found by Brunelli (1909). The karyotype and the idiogram of this species were also studied. Brunelli (1909) reported only the spermatogonial number as 21; he neither described nor figured the shape and size of the chromosomes.

In the specimen examined, the karyotype consisted of three acrocentric pairs (1,2 and 6); one subtelocentric pair (3); five submetacentric pairs (4,5,7,8 and 9); and one metacentric pair (10). The X chromosome was metacentric with an arm ratio of 1.15. The mean TCL was 145.10μ, ranging from 135.60μ to 156.08μ. The fundamental number was 34. The ratio X/LA was 1.89 and the average length of each chromosome was 6.90μ (see Tables I,XIII, Figs. 11,19,90).

Because only a younger-instar nymph was studied, no meiotic division was observed.

vi. Genus Tartarogryllus

T. burdigalensis

The spermatogonial complement was found to be 19 in this species. The karyotype consisted of three acrocentric pairs (1,3 and 6); three subtelocentric pairs (2,4 and 5); one submetacentric pair (7); two metacentric pairs (8 and 9); and the largest, a metacentric X chromosome. The mean TCL was 124.98μ, ranging from 107.76μ to 137.84μ. The fundamental number was 30. The ratio X/LA was 1.71 and the average

length of each chromosome was 6.57μ (see Tables I,XIV, Figs. 12,19, 91).

The X chromosome formed a dense mass throughout meiotic prophase (Fig. 92). Therefore, no detail of chiasma frequency in the X chromosome was measured. A single unequal bivalent and achromatic gaps occurred in some metaphase I cells (Fig. 93). Three or four ring-formed chromosomes usually occurred in diakinesis (Fig. 94). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

b. Subfamily Nemobiinae

i. Genus Neonemobius

(1) N. palustris

The male diploid chromosome number was 19, and all autosomes were acrocentrics. The X chromosome was metacentric with a large light-staining heterochromatin region at the end of each arm. The mean TCL was 97.92μ, ranging from 80.76μ to 132.60μ. The fundamental number was 18. The ratio X/LA was 2.28 and the average length of each chromosome was 5.15μ (see Tables I,XV, Figs. 13,19,95).

During meiotic division, the two arms of the X chromosome were associated with each other to form a thick irregular mass, one part (2/3) showing heterochromatin and the other part (1/3) euchromatin (Fig. 96). A single or double bridge occurred at anaphase I and II (Fig. 97); bridges also occurred at telophase I, II (Fig. 98) and spermatogonial anaphase. The frequency of chromosomal bridges

was as follows:

Stages	% bridges		
	No bridge	One bridge	Two bridges
anaphase I	52.73	40.00	7.27
anaphase II	89.13	10.87	-
telophase I	79.91	19.16	0.93
telophase II	80.49	19.51	-

A single unequal bivalent occurred in many cells (about 58.41%) (Fig. 99) and achromatic gaps were observed in a few (9.77%) (Fig. 100). The shape of the testis (Figs. 131b,c) was quite different from that found in the genera Allonemobius and Eunemobius. Of 12 individuals studied, the testes of 10 individuals appeared as in Fig. 131c, and only 2 individuals as in Fig. 131b. The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(2) N. sp. near mormonius

In this species, the male diploid chromosome number was 19, the same as N. palustris. The karyotype could be distinguished from that of the latter species by the presence of a very large pair of V-shaped autosomes. The species showed the greatest chromosome mass among the species of Nemobiinae so far studied. The karyotype consisted of seven acrocentric pairs (1 to 7); one subtelocentric pair (8); and one metacentric pair (9). The X chromosome was metacentric with more than half of its length showing light-staining heterochromatin. The mean TCL was 120.76μ, ranging from 101.60μ to 138.10μ. The

fundamental number was 22. The ratio X/LA was 1.31 and the average length of each chromosome was 6.35μ (see Tables I,XVI, Figs. 14,19, 101).

The structure and behaviour of the X chromosome were similar to those of the X chromosome of N. palustris, i.e., it showed partly heterochromatin and partly euchromatin during meiotic division. A giant nucleolus, which was not observed in the previous species, occurred at early prophase I (Fig. 102). The two arms of the X chromosome were associated with each other to form an irregular mass at metaphase I (Fig. 103) and sometimes it formed a sticky bridge at anaphase II. Achromatic gaps occurred in some cells (about 20.7%) (Fig. 104) and chromosomal breaks (Fig. 105) were observed occasionally in others (6.02%). Chromosomal bridges were encounted at anaphase I and II (Fig. 106) and telophase I. The frequency of bridges was as follows:

Stages	% bridges			
	No bridge	One bridge	Two bridges	Three bridges
anaphase I	65.72	22.86	5.71	5.71
anaphase II	93.11	6.89	-	-
telophase I	92.31	7.69	-	-

The shape of the testis (Fig. 131d) was different from that found in N. palustris, being more or less bell-shaped and very small (approximately 1.0-1.5 mm in length), one testis being bigger than the other in each of two individuals studied. The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XVI,

XXII,XXIII, Fig. 194.

ii. Genus Allonemobius

(1) A. fasciatus

The male diploid chromosome number was 15. Seven pairs of acrocentric autosomes and a single metacentric X chromosome were observed. The mean TCL was 73.42μ, ranging from 67.32μ to 84.12μ. The fundamental number was 14. The ratio X/LA was 2.20 and the average length of each chromosome was 4.89μ (see Tables I,XVII, Figs. 15,19,107).

The X chromosome had two short segments of light-staining heterochromatin at the end of each arm (Fig. 107). During early meiotic prophase, the X chromosome appeared thicker and shorter, as compared with other species of Allonemobius, and took on a ring-form, or was J-shaped or broken into pieces (Fig. 108). Some individuals (2 out of 12 studied) had an extra small univalent in some cells, which stayed apart from the other bivalents at metaphase I (Fig. 109), and showed positive heteropycnosis similar to the X chromosome during early prophase I. Translocation bivalents occurred in some cells (Fig. 110). Sticky bridges occurred occasionally (Fig. 111). Each testis was in the form of a drawn-out and contorted S or might be described as having a mustache-like appearance (length approximately 4.5-5.0 mm) (Fig. 131e). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(2) A. allardi

The male diploid chromosome number was 15. The karyotype consisted of six rod-shaped pairs and one sphere-shaped pair of autosomes, and the X chromosome was metacentric with some light-staining heterochromatin regions at the end of each arm. The mean TCL was 74.40μ, ranging from 69.08μ to 83.48μ. The fundamental number was 14. The ratio X/LA was 2.33 and the average length of each chromosome was 4.96μ (see Tables I,XVIII, Figs. 16,19,112).

The X chromosome appeared as a long, slender thread, usually ring-formed in shape, at early meiotic prophase (Fig. 113). It always moved to the pole more slowly than the autosomes at anaphase I and sometimes formed a dicentric bridge at anaphase II (Fig. 114). The nucleolus was always associated with the largest autosome. One, two or three DNA bodies occurred in some cells (Figs. 115,116). A single translocation bivalent occurred in some metaphase I cells (Fig. 116) and achromatic gaps occurred occasionally (Fig. 117). The shape of the testis (Fig. 131f) was similar to that of A. fasciatus but smaller (approximately 2.5-3.0 mm in length, from 14 individuals). The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

(3) A. griseus griseus

The male diploid chromosome number was 15. All of the autosomes were acrocentrics, the largest autosome with an extra small dot-like piece attached to the minor arm as a satellite chromosome. The

X chromosome was metacentric with three short light-staining heterochromatin segments at the end of each arm. The mean TCL was 92.80μ, ranging from 82.48μ to 107.68μ. The fundamental number was 16. The ratio X/LA was 1.95 and the average length of each chromosome was 6.15μ (see Tables I,XIX, Figs. 17,19,118).

In early meiotic prophase, the X chromosome usually appeared ring-formed, as a figure-8, or as a U- or J-shaped body (Fig. 119). It formed a ring or a thick V-shaped body at metaphase I and II (Figs. 120a,b), and usually moved to the pole more slowly at anaphase II than did the autosomes (Fig. 121). The nucleolus usually stayed apart from the autosomes, but it sometimes became associated with one of the medium-size autosomes. A translocation bivalent (the largest autosome) was readily detected in most of the cells of metaphase I (Figs. 122a,b). The small translocation piece could also be observed in spermatogonial metaphase and other stages of meiotic division, but not so clearly as in metaphase I. Achromatic gaps occurred occasionally in some cells. Chromosomal bridges appeared in anaphase II (about 31.5% of the cells with chromosomal bridges, from 12 individuals) (Fig. 123). The testis (Fig. 131g) was of a shape similar to that found in the previous two species, and was approximately 3.5 mm in length. The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

iii. Genus Eunemobius

E. carolinus carolinus

This species has the lowest chromosome number reported in

Orthoptera, the male diploid chromosome number being only 7. All of the autosomes were metacentrics and the largest autosome had a secondary constriction on the proximal end of the long arm. The X chromosome was submetacentric with an arm ratio of 1.41, and there were some light-staining heterochromatin segments distributed over each arm. The total length of the X chromosome was shorter than that of the largest autosome. The mean TCL was 89.21μ, ranging from 84.56μ to 93.20μ. The fundamental number was 12. The ratio X/LA was 0.97 and the average length of each chromosome was 12.74μ (see Tables I, XX, Figs. 18,19,124).

The X chromosome differed from that observed in other nemobiine species studied and appeared as a dense mass at early meiotic prophase (Fig. 125). It was not possible, therefore, to measure chiasma frequency on the X chromosome at diplotene. Polyploid cells occurred (Fig. 126), and an unequal bivalent was observed in some cells at metaphase I (Fig. 127). The testes were elongated, and the acute end directed posteriorly (Fig. 131h); they were approximately 3.5mm long. Each testis consisted of 6 testicular follicles only. The frequencies of chiasmata and ring-formed chromosomes are summarized in Tables XXI,XXII,XXIII, Fig. 194.

iv. Genus '<u>Nemobius</u>'

'<u>N</u>. sp.? near <u>bivittatus</u>'

Three acetic-alcohol pre-fixed specimens collected at Kaikoura, South Island, New Zealand (two males and one female, penultimate-instar nymphs), were received from Dr. P.M. Johns, Christchurch, New Zealand.

Because of poor fixation, only some testis cells of one male individual could be studied cytologically. From these cells, the chromosome number of this undescribed species of 'Hemobius' (=Pteronemobius sp. of Johns (1970) — see footnote, p. 23) was established as being $2n\delta=21$; $n\delta=11$. All of the chromosomes were homozygous at metaphase I (Fig. 128). No further details of the chromosomes could be determined. The shape of the testis is shown in Fig. 131i. The result was, however, of great interest as the number of chromosomes is the highest known for Hemobiinae.

D. Discussion

1. Chromosome Numbers:

Harvey (1917,1920) suggested that the most frequently occurring chromosome number in a group might be called the "type number". This was considered to be the ancestral number for the group, the other numbers occurring in the same group being derived from it. White (1954), however, pointed out that there was no reason to believe that the commonest number was primitive or ancestral for a group, and he suggested substituting the term "model number", with no such special implication, as being a more suitable term. The model number for some Orthoptera is, for example, $2n\delta=23$ in Acrididae, s.str. (White,1954, 1957a), $2n\delta=19$ in the acridoid families Pyrgomorphidae and Pamphagidae (White,1954; Makino,1956), and $2n\delta=13$ in Tetrigidae (Robertson,1916, 1930; Rayburn,1917; Harman,1920; Nabours and Robertson,1933; Misra, 1937; White,1951a,1954). In Diptera, two examples are: $2n(\varphi\delta)=12$ in Scatophagidae (Boyes,1965) and $2n(\varphi\delta)=10$ in the genus Xylota (Syrphidae)

(Boyes and Van Brink, 1964). In Gryllidae, it is scarcely possible to consider a model number for the whole family because the chromosomes show wide variation in number between genera, although it is interesting to note that the commonest number in the Gryllinae, $2n\hat{\delta}$= 21, is also the highest number in the Nemobiinae. It is, however, possible to indicate generic model numbers, for most of the genera which have been studied are virtually homogeneous in this respect, with few exceptions (e.g., Pteronemobius, which, in any event appears to be polyphyletic, see pp. 10 and 11).

2. Cytotaxonomy:

a. Karyotypes

i. Gryllinae

In the genus Gryllus, the chromosome number shows great stability, all the species studied having a male diploid number of 29, except for some individuals of G. veletis having supernumerary chromosomes, in which it was found to be 30 or 31. Chromosome number alone thus throws little light on the taxonomy of this genus other than to support the current concept of its limits. There are, however, extensive differences between the species in karyotypic and other chromosomal characters, such as the occurrence of ring-formed chromosomes and chiasmata (see Tables XXI, XXII, XXIII, Fig. 194).

Gryllus veletis, G. bimaculatus (Azores population) and G. campestris all showed similarity in karyotype, in that most of the autosomes were acrocentrics and subtelocentrics; the fundamental

numbers in these three species, also, were the lowest in the genus. The karyotypes of G. assimilis, G. pennsylvanicus, G. bermudensis and G. rubens differred from those of the foregoing three species, but had certain features in common with each other: the chromosome mass consisted of a few acrocentrics, subtelocentrics, submetacentrics and metacentrics. The species studied thus fall into two cytologically distinguishable groups. However, in spite of similarities within groups, either no offspring or only sterile F_1 offspring were produced when crosses were made between species, even within one or the other group (Cousin, 1933, 1946, 1954a, b, 1955; Bigelow, 1960; Randell and Kevan, 1962; see also p. 36). It is thus clear that significant structural changes have taken place in the chromosomes during the evolution of these species, although the changes have not led to any alteration in the basic chromosome number.

The biological significance of any chromosomal rearrangement is reflected in its adaptative value and in the possible production of cytological isolating mechanisms between two karyotypically different populations of the same genus. Such isolating mechanisms are of great importance in the process of speciation. Thus, the northern spring cricket, G. veletis, and the fall cricket, G. pennsylvanicus, which are sympatric in their distribution over much of eastern and central North America, are reproductively isolated in spite of their almost identical external morphology and song patterns. The two species are karyotypically distinguishable (they belong to different groups, see above), and, in addition, the chromosome number sometimes

differs between them because of the occurrence in G. veletis of one or two supernumerary chromosomes, which have not been observed in G. pennsylvanicus (or in other species). The chromosome number of G. veletis (as in other Gryllus species) is basically $2n\delta=29$, as reported by Randell and Kevan (1962), but may be 30 or 31. The origin and function of these supernumerary chromosomes is not clear, but their occurrence may well have some adaptative significance. Under laboratory condition, no hybrid has ever been produced between the two species, nor is hybridization possible in the field because they mature at different times; they differ also in other aspects of their life-history, such as oviposition, behaviour and the stage at which diapause occurs (Alexander,1957; Alexander and Bigelow,1960).

The differences in chromosome number (in some instances) and in karyotype indicate that reproductive isolation between G. veletis and G. pennsylvanicus is largely genetically based and not necessarily due primarily to a seasonal isolation of adults, as believed by Alexander and Bigelow (1960). Cytological evidence thus weakens these authors' hypothesis of sympatric "allochronic speciation" in the two species. In this regard, it may also be noted that, although G. veletis and G. pennsylvanicus are virtually indistinguishable, either by their external morphology or by their song patterns, there are greater differences between their concealed male genitalia than there are between the phallic structures of either species and those of certain other members of the genus (R.L. Randell, unpublished). It is, therefore, quite possible that G. pennsylvanicus and G. veletis

evolved allopatrically in the more usual manner (Mayr,1966), their various reproductively isolating mechanisms becoming more strongly developed as a response to subsequent sympatry.

Present cytological studies have also indicated that the two populations of "G. bimaculatus" examined, one from Azores and one from Singapore, are quite different and should probably be considered as belonging to two different species, although they are very similar in their external features. This would seem to be a situation similar to that of the populations of "Acheta domesticus" studied by Ghouri and McFarlane (1957). In that case, although the Pakistani and Canadian populations were both assumed to be A. domesticus and were apparently similar in external features, they were reproductively isolated. They are now known to belong to two distinct species, the Pakistani population being referable to A. hispanicus (Dr. A.S.K. Ghouri, personal communication,1970).

The F_1 generation of the Singapore population of "G. bimaculatus" showed many chromosomal aberrations and produced no offspring. Unfortunately, it was not possible to attempt to cross the Singapore and Azores populations, so that the degree of biological divergence between them remains unknown. The loss of both fertility and ability to survive by the Singapore population was clearly a result of chromosomal abnormalities. The reason for these abnormalities is unknown. Changes in environmental conditions directly, as between the field and the laboratory, or an inherent inability to adapt to such changes, may have had some adverse effect on the chromosomes. As changes in

the environment (see Chapter III) can induce cytological abnormalities, it would not seem unreasonable to suppose that other less drastic changes could also have this effect.

Gryllus campestris was studied cytologically by Ohmachi (1929,1935). He reported no chromosomal abnormality, but the scanty material of this species investigated in the present work showed major abnormality of the chromosomes. The cytological study was conducted using only two male nymphs that had been collected in the field (these, and a female which died, were the only survivors of a small consignment sent from Hungary by Dr. B. Nagy of Budapest). The numerous chromosomal abnormalities, including breaks, stickiness, c-mitosis, polyploidy, lagging, unequal segregation and non-disjunction, were similar to those induced in other species by chemicals and radiation (see Chapters III and IV), but the degree and frequency of these aberrations were much greater in these field-collected G. campestris. The specimens were originally captured (as immature nymphs) in a rough pasture on Fót-Somlyó Hill, 15 km north-east of Budapest, and then transferred to the insect house of the Budapest zoological park. They were received at our laboratory in late September, 1970. The duration of their sojurnin the insect house in Budapest is not known but presumably was short.

Because the types of chromosomal aberrations found in G. campestris were very similar to those produced by phenolic compounds (see Chapter III), one may perhaps assume that materials containing phenols or similar chemicals were present in disinfectants used in

the zoo, and that the specimens may have been affected by these when they were kept in the insect house. However, as the specimens were collected very late in the year, the possibility of some other adverse ecological factors being involved cannot be ruled out. According to Dr. Nagy (in litt.,1970), the field from which the nymphs were originally collected has no known history of chemical treatment.

Although chromosome number has no taxonomic value between the following four genera: Acheta, Gryllodes, Scapsipedus and Melanogryllus, all having male diploid number of 21, the karyotypes and other cytological characters showed remarkable differences (see Tables I,XXI,XXII,XXIII, Figs. 19,194). S. marginatus showed more similarity, on the basisof karyotype, to A. domesticus and M. desertus than to G. sigillatus.

It is interesting to note that the male diploid chromosome number observed in the present study for Tartarogryllus burdigalensis was 19, but was reported by Leroy (1967) as being 21. Similarly, in Teleogryllus oceanicus, the chromosome number reported by Lim et al. (1969), Fontana and Hogan (1969) and Lim (1970) was $2n♂=27$, but $2n♂=29$ according to Leroy (op. cit.). It is difficult to suggest a reason for the discrepancy in the chromosome numbers reported by different workers for the same species, because Leroy (op. cit.) recorded the chromosome number only and no detail of the chromosome structure. Here might, however, conceivably have been situations similar to that found in G. veletis (see p. 50); i.e., the discrepancy might be accounted for by the occurrence of supernumerary chromosomes. Leroy's (1967) report of $2n♂=19$, rather than 25–29, for the type species of Teleogryllus (T. posticus), however, cannot be explained in these terms, and,

if correct, would alter the present concept of that genus (see p. 8).

ii. Nemobiinae

The three genera Neonemobius, Allonemobius and Eunemobius showed rather more uniform karyotypes than did genera of the subfamily Gryllinae. The first two genera, except for Neonemobius sp. near mormonius, all had acrocentric autosomes, the X chromosome being the largest metacentric with a light-staining heterochromatin region on each arm. All of the autosomes were metacentric and the X chromosome was a medium-sized submetacentric with, in Eunemobius, some light-staining heterochromatin regions distributed on each arm. The undescribed 'Nemobius' sp. from New Zealand had the highest chromosome number in the subfamily Nemobiinae, $2n♂=21$, and Eunemobius the lowest, $2n♂=7$, which is also the lowest chromosome number reported in Orthoptera.

The lesser chromosome numbers may be due to a past history of centric fusion in the group. This may be postulated because, at greater chromosome numbers, as in Neonemobius ($2n♂=19$), all of the autosomes (except in N. sp. near mormonius) are acrocentrics, whereas some metacentrics occur with somewhat decreased chromosome numbers, and all the autosomes are metacentrics in Eunemobius, in which the chromosome number is greatly reduced ($2n♂=7$). Davenport (unpublished, 1960) also pointed out that "the acrocentrics probably went through a confusion-pericentric inversion-fusion cycle to produce the metacentric autosome of the Eunemobius". Since few species of Nemobiinae have so far been studied cytologically, intermediate forms of karyotypes (includings chromosome numbers completing the, at present,

incomplete alternating series) may be expected to occur. According to the theory of downward evolutionary change of chromosome numbers for the Nemobiinae (Davenport, unpublished, 1960), the undescribed 'Nemobius' sp. would have the most primitive chromosome number for this subfamily. This would not be out of keeping with the occurrence of the species in New Zealand, where many primitive representatives of different animal groups are found. The species is clearly not a true Nemobius, as the chromosome number for that genus is $2n\delta=17$ (Lim, 1971).

Karyotypic characters, chromosome number, differing structure of the X chromosome and other chromosome structures give added weight to the morphological characters indicating that Neonemobius, Allonemobius and Eunemobius must be regarded as belonging to different genera (Vickery and Johnstone, 1970), not subgenera of the genus Nemobius as proposed by Hebard (1913) and accepted by Davenport (unpublished, 1960).

In Neonemobius, the karyotypes of N. palustris and N. sp. near mormonius, were distinct from each other, the former species having all acrocentric autosomes, whereas, in the latter, there were a large metacentric and a subtelocentric in addition to the remaining acrocentric autosomes. The shape and size of the testes and the body size were also different between these two species. The chromosome number, structure and behaviour of the X chromosome, however, indicated that these two species probably indeed belong to the same genus. It is expected that the taxonomic position of N. sp. near mormonius will

be confirmed shortly by the combined study of morphological, acoustical and other characters by Dr. T.J. Walker, University of Florida.

In other Nemobiinae, the literature reports widely differing chromosome numbers in Pteronemobius and Homonemobius (Ohmachi,1935, 1958; Bhattacharjee and Manna,1967), clearly indicating that these two genera, as at present constituted, are heterogeneous. It is,unfortunately, not yet possible to assign a chromosome number to the genus Pteronemobius, s.str., as the type species, P. tartarus Saussure, 1874 (a junior synonym of P. concolor (Walker,1871)), has not yet been cytolgoically investigated. However, according to Dr. V.R. Vickery (personal communication,1970), this species, on morphological grounds, is definitely not congeneric with "Pteronemobius" fascipes (Walker), of which the male diploid chromosome number is 17 (Ohmachi,1927,1935, 1958; Tateishi,1932; Bhattacharjee and Manna,1967). It would therefore seem unlikely that Pteronemobius, s.str., has the same number.

b. Other characters

The sex-determining mechanism is not identical throughout the Grylloidea, but in all the species of Gryllidae presently studied it was found to be of the X0♂-XX♀ type. The structure, behaviour and morphology of the X chromosome are very uniform throughout the subfamily Gryllinae (Figs. 130a,b), but remarkable differences were found among the three genera of the subfamily Nemobiinae (Figs. 125,130c,d, e,f,g,h) (see pp. 40 to 46).

The shape of the testis shows a similar situation. The testes are heart-shaped with the acute end directed posteriorly in

all species of Gryllinae studied (Fig. 131a), but they vary in shape and size between different genera, and, in Neonemobius even between species of the same genus (Figs. 131b,c,d,e,f,g,h,i).

Thus, in addition to chromosome number and other karyotypic characters, the structure of the X chromosome and the shape of the testis have taxonomic significance. Members of the subfamily Nemobiinae, in all these respects, seem to have been more divergent than those of the subfamily Gryllinae during the process of evolution, although karyotypic analyses present a converse picture (i.e. uniform karyotypes were observed in the subfamily Nemobiinae compared with variable karyotypes occurring in the subfamily Gryllinae). On the basis of cytological, morphological and ecological evidence, it is clear that these two subfamilies have moved along quite different evolutionary pathways. No straight phylogenetic parallels can be drawn between them.

3. Supernumerary Chromosomes:

The chromosome complements of some plant and animal nuclei contain, in addition to the normal chromosome sets, one or more supernumerary, or accessory, or 'B' chromosomes, and these have been found in Gryllus veletis(see pp. 28 and 29). The origin and nature of supernumerary chromosomes are entirely unknown, except in a few species. Such chromosomes are not homologous with any of the normal chromosomes. They are often smaller and may be present in some individuals of a species or population but not in others. They often vary in number among individuals of a population in which they occur, or even among

cells of a single organism. The usual number of supernumeraries in a nucleus is one or two, although greater numbers are known. Supernumerary chromosomes are much more common in plants than among animals, but White (1954) reported their occurrence in 52 species of invertebrates: 2 species of flatworm and 50 insect species, of which nearly 60 per cent. (29 species) were short-horned grasshoppers (Acridoidea).

It is usually impossible to tell from its external appearance (phenotype) whether or not a particular individual carries supernumerary chromosomes, or their presence may be expressed only in various subtle ways which are difficult to detect, although there are some exceptions. Nevertheless, an increase in the number of chromosomes seems often to be accompanied by a decrease in viability, survival or fertility of the organism concerned. The 'B' chromosomes occurring in a species of mealy-bug (Pseudococcus obscurus Essig), for example, are harmful to the development of these insects, especially the males (Nur, 1962, 1966a, b, 1969). In this regard, Östergren (1947) postulated that supernumerary chromosomes might be, in effect, parasites possessing genes for their own survival. White (1954), however, believed that they were adaptative for the natural conditions under which they developed and that they might play a part in evolution.

During the present study, supernumerary chromosomes were demonstrated for the first time in a grylline cricket (Gryllus veletis) and a supernumerary-like chromosome was also found in some cells of

a few individuals of the nemobiine Allonemobius fasciatus. Their presence or absence, however, did not seem to affect the appearance of the individuals in any noticable manner. Some individuals of G. veletis possessing supernumerary chromosomes were, indeed, larger than those without such chromosomes, but the differences were not constant. Jobin (unpublished,1961), in a study of the development of the nymphs of four Gryllus species, showed, in fact, that individuals of southern populations of G. veletis moulted more frequently and were larger than those of northern populations, but there is, as yet, no evidence that the former are more prone to possess supernumeraries. The presence of supernumerary chromosomes in G. veletis seemed to have no special effect on the morphology of the organisms or the cells in which they occurred, although it might be postulated (White,1954) that they could have some adaptative value. The genetic adaptation of species and populations to their environment has presumably been a very general biological phenomenon, and changes of this nature might be regarded as a basis of biological evolution (White,1963).

In G. veletis, during anaphase I, when cells possessed a single supernumerary chromosome, the latter either stayed on the spindle near one of the poles or lagged behind on the equator plate; where two supernumeraries were present, each went either to the same or to different poles, neither lagging on the equator. Melander (1950) suggested that the basic cause of such differential behaviour was a change in strength and rhythm of division of the centromere.

Supernumerary chromosomes commonly occur in Acrididae (Carroll,1920; Kings,1923; Corey,1933; Minouchi,1934; Powers,1942; Helwig,1942; White,1949,1951a,b,c,d,1954; Rothfel,1950; Ray-Chaudhuri and Manna,1951; Sharman,1952; John and Hewitt,1965,1966,1968,1969; Hewitt,1967; Hewitt and John,1967,1968,1970; Bhunya and Manna,1968; Westerman,1969 and others), but have seldom been reported in Grylloidea, although they have been recorded in Cyrtoxiphus ritsemae (Saussure) (=Homoeoxipha lycoides (Walker)) (Ohmachi,1935), Trigonidiinae, and in a Euscyrtus species, Gryllidae, Phalangopsinae (Smith,1953). Supernumerary chromosomes were also found by Makino et al. (1938), Steopoe (1939) and Asana et al. (1940) in mole-crickets (Gryllotalpidae); either one or two supernumerary chromosomes occurred in some individuals.

The occurrence of supernumerary chromosomes in Gryllus veletis and supernumerary-like chromosomes in Allonemobius fasciatus was previously unknown. In some individuals one was found, in others two. As northern populations of G. veletis differ slightly from southern populations (Jobin,unpublished,1961), some kind of geographical divergence seems to have occurred between them, and further study of the occurrence of supernumeraries in different geographical populations of the species might well be enlightening.

4. Polymorphism:

Chromosomal polymorphism is common in Orthoptera, and four different types are found in the family Gryllidae: (1) as in Euscyrtus hemelytrus in which the chromosome number and the shape of the

chromosomes can both be variable (Ohmachi and Ueshima,1957); (2) the chromosome number, but not the shape, may vary within the same species, as reported for Loxoblemmus arietulus, $2n\delta$=11 to 17 (Honda,1926; Ohmachi,1927,1932b; Suzuki,1933; Ohmachi and Ueshima,1955), and for Brachytrupes portentosus, $2n\delta$=13 to 20 (Tateishi,1932; Komma in 1942 (as cited by Makino,1951,1956); Ohmachi,1932a,1935); (3) the chromosome number is not variable, but one, two, or more particular chromosomes occur in different forms, as in various Gryllidae; the heteromorphic bivalent is usually a hook-shaped structure consisting of a J-shaped and a rod-shaped chromosome, which can be clearly observed at metaphase I; this is the most common type (Ohmachi,1935; Manna and Bhattacharjee,1964,1966; Bhattacharjee and Manna,1969; Fontana and Hogan,1969; Lim et al.,1969; Lim,1970,1971); (4) similar to type (3) but the heteromorphic pair does not include a hook-shaped structure, having only a small dot-like element attached to one end or on the side of the bivalent (Figs. 122a,b); this type has been observed only in Allonemobius, it is regarded as a "translocation bivalent" instead of as an "unequal bivalent" by Lim (1971).

The chromosomal polymorphisms observed in Gryllinae, in Neonemobius and in Eunemobius all belong to the third type ("unequal bivalent"). Chromosomal polymorphism from variation in the chromosome structure was due either to interchromosomal rearrangements or to the unequal pairing of chromosomes.

The frequency of the translocation bivalent, type (4) polymorphism, varied among three Allonemobius species. In A. fasciatus

and A. allardi, it occurred in some cells in every individual, but in A. griseus it was found in almost every cell. Davenport (unpublished, 1960) reported a contrary situation. He found "hook autosomes" (=translocation bivalent of the present text) in all species of Allonemobius that he had studied, except in A. griseus, but only in certain populations of any one species and not in others. In the present study, the occurrence of translocation bivalents was, in addition to being observed in metaphase I, also detected in A. griseus at the spermatogonial metaphase, in which one of the members of the largest pair of autosomes usually had an extra small element attached to the end of the minor (short) arm (Fig. 129). Although the populations of A. griseus involved came from different sources, it is difficult to explain why the results of different authors working on the same species should show such a completely reversed situation. Since translocation bivalents were observed only in Allonemobius, which has an intermediate chromosome number, translocation (interchange) may have occurred during the evolution of the karyotypes of Allonemobius from a Neonemobius-like form.

5. Chiasma Frequency:

Chiasma frequency was found, in the present study, to be relatively high during the diplotene stage. The number of chiasmata in Gryllus species ($2n\delta=29$) varied from one to four per bivalent, although one chiasma per bivalent was the most common number in different bivalents in most species of that genus (see Table XXI). In Gryllus, in most of the acrocentric chromosomes, a single chiasma

occurred quite close to the centromere. The distal region of such chromosome seldom formed chiasmata.

With a decrease in chromosome number, the chiasma frequency increased regardless of taxonomic position. In the species having $2n\delta=21$ (Acheta, Gryllodes etc.) two to three chiasmata per bivalent were quite commonly encountered. In Tartarogryllus burdigalensis ($2n\delta=19$), however, the number of chiasmata varied from one to as many as six per bivalent, although, in Neonemobius palustris (also $2n\delta=19$), most of the bivalents had only one chiasma. In Allonemobius ($2n\delta=15$), A. griseus had the highest chiasma frequency (average of 13.07 chiasmata per cell) when compared with the other two species of the same genus, A. fasciatus (average of 11.82 chiasmata per cell) and A. allardi (average of 11.42 chiasmata per cell). This was presumably because the chromosome length is relatively greater in A. griseus than in either A. fasciatus or A. allardi. Eunemobius carolinus, having the longest chromosomes, also had, as a rule, the highest chiasma frequency per bivalent (from two to seven) of all the species of Gryllidae utilized in the present study.

There was a considerable reduction in the occurrence of chiasmata by the time metaphase I was reached, and, in the majority of genera, most of the bivalents showed only a single chiasma, except in some ring-formed bivalents which had two chiasmata. The species with greater chromosome numbers, however, usually had a higher frequency of terminal chiasmata — again with a few exceptions. This was presumably because the number of very small acrocentric chromosomes increased in species having greater chromosome numbers. Thus,

the frequency of terminal chiasmata was also higher in the species having more than in those having fewer acrocentrics when the chromosome numbers were the same (see Table XXIII, Fig. 194).

6. Chromosomal Bridges:

Chromosomal bridges occurred occasionally in some species. In most cases, these were merely sticky bridges rather than 'true' dicentric bridges; or they were terminal associations between two non-homologous chromosomes, for the two members of a bridge would separate again later under the stress action of the spindle fibre at the end of telophase. In Neonemobius palustris, for example, an X chromosome bridge occurred quite commonly at anaphase II. This was because the heterochromatin ends of the X chromosomes were associated together during meiotic division and remained so during anaphase. The movement of the spindle fibre of two daughter X chromosomes would also, sometimes, result in the formation of a sticky bridge.

Terminal associations have also been found in other Orthoptera (Acridoidea) by White (1957b,1961), John and Lewis (1965), Nankivell (1967), Southern (1967), John and Hewitt (1968). White (1961) and Nankivell (1967) postulated that these were chiasmate in origin; when a chiasma formed very close to the end of a chromosome it might terminalize as the bivalent separated and contract so that a terminal association occurred between the ends of homologous chromatids. These authors did not, however, present any evidence for the chiasmate nature of these terminal associations. The association would be expected to break down under the stress action of the spindle fibre (Nankivell,

1967). John and Lewis (1965) found that at least some of the terminal associations must be non-chiasmate.

7. Chromosome Evolution within the Family Gryllidae:

a. General

The evolution of chromosome systems must necessarily be connected with the evolution of organic systems because the chromosomes constitute the most important substrate for the genes. In other words, if the understanding of evolution remains a central problem of biology, chromosome evolution, too, must be understood. Indeed, the number, structure and behaviour of chromosomes do furnish criteria for the understanding of the evolutionary aspects of taxonomy.

Evolutionary changes in chromosomes involve two basic, and often interrelated, types of variation: numerical and structural. Numerical changes are often accompanied by structural changes. The latter, however, are always very difficult to identify and to measure because the small size of chromosomes presents a formidable barrier to their analysis, except in unusual cases, such as the salivary-gland chromosomes of some Diptera, such as Drosophila.

b. Numerical changes

Some 2000 species of Gryllidae, sens.lat., have been described, estimating from the catalogues of Chopard (1967), and many more await description. Some 6 per cent. of those described (about 121 species) have been studied cytologically (see Makino,1951,1956; Ohmachi,1958; Randell and Kevan,1962; Sharma,1963; Bhattacharjee and

Hanna,1967; Leroy,1967), so that, although this proportion is small, the crickets may be included among the cytologically reasonably well known groups of animals. Table XXIV and Fig. 195 summarize the species of Grylloidea (excluding Gryllotalpidae) hitherto studied. From the table it may be seen that the male diploid chromosome numbers range widely, from the lowest, seven, to the highest, thirty-one, forming a continuous, alternating series. Within this range, $2n\delta$=19 is the most frequently found among the 121 species of Gryllidae whose chromosome numbers have been determined. However, $2n\delta$=15 and 21 are almost equally common, so that it is impossible to consider any one number as being typical of the family. No standard, basic, or model, number is found in Gryllidae as it is in the case of Acrididae, Pyrgomorphidae, Pamphagidae and Tetrigidae.

It may also be observed that gryllid groups in which the chromosome number is high always show more variation in number than do groups with fewer chromosomes. Thus, members of the subfamily Gryllinae, which, on the average, have the highest chromosome numbers as compared with species of other subfamilies, also show a greater numerical range ($2n\delta$=11 up to 31, with a peak at 21). Most of the species in this subfamily have chromosome numbers ranging from 19 to 29, so that it would seem probable that other species are derived from those whose chromosome numbers lay within these limits. The highest and lowest chromosome numbers among the Gryllinae probably represent the end-products of evolutionary processes involving increases or decreases, in chromosome number, respectively. The subfamily Nemobiinae can be

differentiated cytologically from Gryllinae, not only by the structure and size of the X chromosome and by the nucleolus usually being demonstrable in prophase I, but also by the spermatogonial ($2n\delta$) number (averaging lower), ranging between 7 and 21 with a peak at 15 chromosomes. In this subfamily it may be that most, if not all, change in chromosome number has been by decrease. Thus, although there is currently no model chromosome number, for the Gryllidae, it may originally have been in the vicinity of $2n\delta=21$.

Karyotype changes of an evolutionary nature are known within families, genera and species. The most common and basic changes in animals occur at the diploid level by alterations in chromosome morphology and/or number. Changes in the basic chromosome number within a genus or family may be either upward or downward. The most common examples are downward changes which are caused by a process of centric fusion (White,1954,1969; Davenport, unpublished,1960). This process is most clearly demonstrated by 'species' having multiple chromosome numbers, such as Loxoblemmus arietulus and Brachytrupes portentosus. In the former, the chromosome number ranges from 11 to 17 (Honda,1926; Ohmachi,1927,1932b,1935; Suzuki,1933; Ohmachi and Ueshima,1955); in the latter from 13 to 20 (Tateishi,1932; Ohmachi,1932a,1935; Homma in 1942, as cited by Makino,1951,1956). The variation in chromosome number in these species seems to depend on the occurrence and number of V-shaped autosomes. In Loxoblemmus arietulus, for example, individuals with a chromosome number of $2n\delta=13$ exhibited, in addition to the X chromosome, 6 V-shaped and 6 rod-shaped autosomes; those with $2n\delta=15$ had 4 V-shaped and 10 rod-shaped autosomes plus the X chromosome; and

those with $2n\delta$=14 had 5 V-shaped and 8 rod-shaped autosomes plus the X chromosome (Ohmachi,1935). The greater frequency of V-shaped in individuals with lower total chromosome numbers is accounted for by the centric fusion of pairs of rod-shaped autosomes to form V-shaped autosomes (Honda,1926; Suzuki,1933; Ohmachi,1935; Ohmachi and Ueshima, 1955).

Increase in chromosome number is rather difficult to observe and to prove, and its occurrence is supported only by circumstantial evidence. The persistence of supernumerary chromosomes, such as are known in some Grylloidea, has been proposed as such a method whereby the basic chromosome number may be increased. In Gryllus veletis, the basic chromosome number is presumed to be $2n\delta$=29, as reported by Randell and Kevan (1962), but one or two supernumerary chromosomes have been observed in some individuals, so that the complement may occasionally be $2n\delta$=30 or 31 in this species. A comparable situation has also been noted in Homoeoxipha lycoides (as Cyrtoxiphus ritsemae) by Ohmachi (1935) and in Euscyrtus sp. by Smith (1953).

As previously mentioned (p. 67), White (1954,1967,1969), Davenport (unpublished,1960) and Saez (1968) suggested that reduction in chromosome number is due to centric fusion. On the other hand, White (1957a) maintained that centric fission (misdivision) has played no significant role in chromosome evolution in animals. Nevertheless, John and Hewitt (1968) pointed out that misdivision has certainly been a factor in plants, e.g., in Triticum aestivum (Steinitz-Sears,1966) and that its possible operation in animals would merit serious

consideration. For example, considerable centric fission may have occurred in the evolutionary change in chromosome number between that of European wild swine and the (European) domesticated pig (McFee et al.,1966). This, however, would assume that the latter are directly descended from the former; but the mixed origin of modern domesticated swine (Zeuner,1963) might explain the difference in chromosome number without implying centric fission.

That misdivision has operated in the chromosome evolution of Grylloidea was suggested long ago by Ohmachi (1935): "As for the Gryllodea, I am inclined to consider that it has taken the course of fragmentation, but these problems are highly speculative in their nature so that we cannot speak decidedly about them." It is, however, my own opinion that it is still quite premature to attempt to decide in which direction the evolution of chromosome complements in Gryllidae has really moved, for insufficient species of Gryllidae have been studied cytologically, and those that have been so studied do not include the most primitive living Gryllinae, such as Turanogryllus Tarbinskiĭ (cf. Randell,1964). At the present time, one can only presume that the evolution of chromosome complements in Gryllidae has probably progressed in both directions, centric fusion playing a more important part than centric fission (fragmentation) or the appearance of supernumerary chromosomes.

In discussing reduction of chromosome number, processes other than centric fusion should be considered. Certain species of Gryllidae possess an unusually low number of chromosomes, due to the apparent

loss of one or more members of the primitive chromosome complement. In such cases it seems unlikely that whole chromosome pairs have actually been lost in the course of evolution. It is much more probable that the greater part of a 'lost' chromosome has been transferred to another member of the chromosome complement, only the centromere and small heterochromatin regions being indeed lost. The translocation bivalents found in Allonemobius provide some evidence for the occurrence of such transference during evolutionary changes from a Neonemobius-like condition to that found in Allonemobius.

c. Structural changes

In the genus Gryllus, the differences in karyotype between species may be due to centromere shifts which have converted a varying number of the originally acrocentric chromosomes into metacentric or submetacentric elements without changing the chromosome number.

Evolutionary changes in total chromosome length (TCL) are also known in Gryllidae, especially in the genus Gryllus. The highest TCL in this genus is 156.01μ, in G. assimilis, and the lowest is 104.44μ, in G. bimaculatus. The lower TCL may be due to a decrease in polyteny or in the amount of heterochromatin or matrix, or to gene duplications or to a combination of these factors. Any one factor could cause tighter coiling or other changes that might result in a shortening of the chromosomes.

Almost all species of Gryllidae have an XO-XX type of sex-determination mechanism, the male representing the digametic sex and

the female the homogametic. The X chromosome is always the largest, or one of the largest, in the chromosome mass and it takes a peripheral position at spermatogonial metaphase. The shape of the X chromosome is important in the cytological classification of Grylloidea, and it also shows evolutionary significance. It is usually V-shaped in Gryllinae, Eneopterinae and in some Trigonidiinae and Mogoplistinae; somewhat U-shaped, with some light-staining heterochromatic regions either at the end of each arm or distributed on the two arms, in Nemobiinae; and rod-shaped in Oecanthidae, Phalangopsinae and a species (Homoeoxipha lycoides) of Trigonidiinae (Ohmachi,1935). The V-shaped X chromosome seems to be more primitive than the others, the U-shaped and rod-shaped X chromosome probably being derived from it during the course of evolution.

In addition to XO-XX type of sex-determination mechanism, multiple sex chromosomes are reported in a few species of Grylloidea: Oecanthus longicauda (XY-XX type) (Ohmachi,1927,1935; Makino,1932); Euscyrtus concinnus, Euscyrtus sp., Seychellesia sp. and Eneoptera surinamensis (X_1X_2Y-$X_1X_1X_2X_2$ type) (Ray-Chaudhuri and Manna,1950; Claus,1956; Manna and Ray-Chaudhuri,1965; Bhattacharjee and Manna,1967). Since multiple sex chromosomes are unusual in Grylloidea, they may possibly be regarded as having been derived from a primitive XO-XX type.

Considering all of the cytological evidence together, we may assume that, in crickets, there was presumably a prototype chromosome mass which has changed from one type to another, and that some of these changes are no longer evident, having been present only in species which have since become extinct.

III. EFFECTS OF CHEMICALS

A. Literature Review

Much has been published, particularly in recent years, regarding the effects on chromosomes of a variety of chemical treatments, but studies of such effects with respect to crickets have been virtually nil.

Colchicine is a substance long known to induce veritable changes in chromosomes and spindle apparatus, and it is much used by plant cytologists to induce polyploidy (see Eigsti and Dustin,1957). Östergren (1950) regarded colchicine action as narcosis, and suggested a relationship between spindle poisoning and lipoid solubility. Manna and Parida (1965a) studied the effects of colchicine on the testis cells of grasshoppers and found that the treatment produced various kinds of changes in cells and on chromosomes, such as c-mitotic metaphase, multinucleate cells, failure of synapsis, multipolar spindle, sticky chromosomes, etc.

Although various chemical substances other than colchicine have been known to induce genetic and chromosomal changes in both plants and animals (see, for example, Mangenot and Carpentier,1944; Hadron and Niggli,1946; Rapoport,1946), it would seem that the discovery by Auerbach and Robson (1947) of the mutagenic effects of nitrogen mustard on *Drosophila* stimulated various workers to attempt to induce chromosomal aberrations by different chemical treatments.

Following earlier, limited work by Yosida (1950), Gaulden

and Carlson (1951) and Sarkar (1956) on the cytological effects of chemicals other than colchicine, Manna and his collaborators undertook a series of investigations on the effects of various such chemicals upon the spermatocyte chromosomes of grasshoppers (Manna and Mazumder,1964; Manna and Roy,1964; Manna and Parida,1965b,1966,1967, 1968; Manna and Lahiri,1966; Manna and Mukherjee,1966; Mazumder and Manna,1966; Parida and Manna,1967; Manna,1967,1969; Bhunya and Manna, 1969). The chemicals they used included the chelating agents ethylene-diamine-tetra-acetic acid and cupferron; formalin; ethyl alcohol; the nuclei acid analogues maleic hydrazide, 5-bromodeoxyuridine and iodo-deoxyuridine; the antibiotics tetracycline, nanovobiocin, grisovin, chloranphenical and streptomycin; the hormones insulin, testoveron, ovocycline and corline; and metallic salts such as aluminium chloride, mercuric nitrate, potassium cyanide, etc. Aberrations, such as chromosome, chromatid and subchromatid breaks, sticky bridges, lagging, failure of synapsis, reduction of chiasmata, c-mitosis, chromosome and chromatid type gaps, dumping and misdivision of chromosomes, etc. at different meiotic stages, were observed.

Some information also exists for substances other than those mentioned above. For example, the narcotic ethyl urethane was discovered by Rapoport (1946) and Vogot (1948,1950) to produce lethal gene-mutations and chromosome changes in Drosophila; and urethane was found to induce chromosomal aberrations, both in mitosis and in meiosis, as well as cytoplasmic changes, in the pyrgomorphid grasshopper Poekilocerus pictus (F.) by Nambiar (1955).

Saxena and Aditya (1969a,b) studied the effect of apholate on the reproductive tissues of the same grasshopper species, Poekilocerus pictus. Spermatogonia, spermatocytes and spermatids showed pycnotic nuclei, fragmentation of chromatin and vacuolization after 15 days of treatment; apholate also affected the DNA content of the germ cells. Connective tissue cells and mature sperms, however, showed no histological damage. Apholate also induced chromosomal breaks, exchange and chromosomal gaps in the acridid grasshopper Melanoplus differentialis. The proportion of abnormal cells reached a maximum of 85 per cent on the eighth day following treatment and then fell to about half this maximum value at 21 days (Klassen et al.,1969).

Actinomycin-D, an antimetabolite which prevents RNA synthesis, has been found to produce chromosome breakages in the Desert locust, Schistocerca gregaria (Forsk.) (Jain and Singh,1967). The effects on both chromosomal aberrations and on the development of spermatocytes resulted from disorganization of the synthetic apparatus of the cells. Actinomycin-D was also found to increase the chiasma frequency in an inbreed stock of Schistocerca gregaria, but it produced no effect in a heterozygous stock (Craig-Cameron,1970). The author suggested that this chemical might cause the induction of enzymes involved in crossing-over and suppress the action of certain genes concerned with chiasma formation.

Some substances used in cytological technique may also produce chromosomal abnormalities. Caffeine can be used as a pretreatment agent at low concentration; it enlarges and disperses the chromatic

materials, making the chromosomes clearly visible (Reiss,1969). Caffeine, however, has also been found to provoke chromosomal ruptures and to inhibit cytokinesis, producing binucleate cells in plants (Magenot and Carpentier,1944; Kihlman and Levan,1949; López-Sáez et al.,1966; Gimenez-Martín et al.,1969). It also has a lethal effect when applied in stronger concentration (1 and 2%) and it has a suppressive action on the frequency of mitosis, although it was not shown to induce full c-mitosis except at very strong concentrations (Kihlman and Levan,1949).

Similarly, phenolic compounds can be employed for the study of chromosome morphology if applied at concentrations below about 10^{-3}M; but above this, they can cause chromosomal abnormalities, lethality ensuing when they are applied at high concentration (Sharma and Sharma, 1965). Phenols have been applied in the case of many groups of plants, but very rarely for animals. A few studies on the genetical and cytological effects of phenols have been carried out, e.g. by Hadron and Niggli (1946), Levan and Tjio (1948a,b) and Amer and Ali (1968,1969). Phenols decreased the mitotic index and disturbed the normal mitotic and meiotic division; they also induced the lagging of chromosomes, stickiness, fragmentation and cytomixis.

The possible cytological and genetic effects of the widespread use of herbicides, fugicides and insecticides are currently giving rise to some concern (Varaana,1947; Levan and Tjio,1948a,b; Muhling et al.,1960; Sawamura,1964; Huu and Grant,1966,1967; Amer and Ali,1968,1969; Amer and Farah,1968; Grant,1970). There is some evidence

that chromosomal abnormalities are produced by them, at high concentrations, at least in plants (Varaama,1947; Levan and Tjio,1948a,b; Levan,1949; Kihlman and Levan,1949; Kuhling et al.,1960; Sawamura, 1964; Amer,1965; Wuu and Grant,1966,1967; Amer and Ali,1968,1969; Amer and Farah,1968; Reiss,1969; Grant,1970), but there have been few studies of the effects of such substances on animal (including insect) chromosomes, and none hitherto on crickets. However, some insecticides (parathion, dieldrin and sevin) have been found by Young and Stephen (1970) to effect the acoustical and sexual behaviour of Acheta domesticus. The crickets fed with dieldrin and sevin stopped singing for 3 to 6 hours, and there was an increase in chirp rate and pulse rate of the calling song once singing was resumed. Crickets treated with parathion were unable to produce pure calling songs. The authors believed that parathion acted on the peripheral neuromuscular system and the thoracic gland, whereas both dieldrin and sevin effected the brain, first as an inhibitant and then as an excitant. Thus the physiological upsets produced by insecticides can clearly affect the reproduction of crickets through their behaviour, but cytological effects have not hitherto been considered. Water loss following treatment with several insecticides in Gryllus bimaculatus was also recorded by Srivastava (1969).

B. Materials and Methods

1. Materials:

Male nymphs of the last two instars of the following species (from the sources indicated previously) were used:

Gryllus assimilis (Fabricius)

G. bermudensis Caudell

G. bimaculatus De Geer

G. pennsylvanicus Burmeister

Acheta domesticus Linnaeus

Gryllodes sigillatus (Walker)

Scapsipedus marginatus (Afzelius et Brannius)

2. Methods:

a. Injection-administered series

The test insects were injected *via* the abdominal pleura with 0.02-0.05 ml of chemical prepared in insect saline (Baker, 1950) using a 27-gauge hypodermic needle with 1 cc tuberculin syringe (both supplied by Fisher Scientific Co.). They were sacrificed at various times after injection. The insects were anaesthetized by ethyl acetate and a mid-dorsal slit was then cut from the posterior end of the thorax to the end of the abdomen and the testes were dissected out in insect saline. The concentrations of chemicals used, the intervals between injection and fixation, and the survival rate after 24 hours are listed in the following table:

chemicals	concentrations (%)	hours between treatment and fixation	survival rate after 24 hours
colchicine	0.1	18,24	40%
colcemid	0.05,0.1	18,24	100%
caffeine	0.5	24	100%
ethyl acetate	100	0.5	0%

chemicals	concentrations (%)	hours between treatment and fixation	survival rate after 24 hours
glacial acetic acid	100	1.0	0%
phenol	0.05,0.1	12,24,72	100%

After injection, the insects always showed effects of poisoning by the chemicals, i.e. there was less movement, they remained still, or they turned upside-down after a short period of time, especially in the case of those injected with colchicine, ethyl acetate, or glacial acetic acid.

b. Feeding-administered series

i. Food:

Last-instar nymphs of G. bermudensis were fed on a diet containing 8 grams of crushed "baby rabbit pellets" (Ogilvie Four Mills, Montreal — the regular food for the crickets reared in the McGill University, Department of Entomology laboratory) mixed with 6 ml of 0.5% cupferron or 0.5% caffeine. Fresh food containing the chemical was supplied everyday. Drinking water (tap water) was supplied from a vial by means of a cotton-batten 'wick'. The test insects were starved for 48 hours prior to administration of food. They were sacrificed at 3 or 10 days after feeding. The following table lists the percentage of survival and attainment of adulthood after treatment in the case of crickets given the opportunity of surviving 10 or more days after treatment:

chemicals	no. of specimens	% surviving after treatment 3D	6D	10D	% attaining adulthood after treatment 3D	6D	7D	10D
cupferron	10	90	80	10	-	-	-	-
caffeine	10	100	100	100	-	-	10	10
control	14	100	100	100	64.3	100	100	100

D=days

ii. Drinking water:

Third-instar nymphs of G. assimilis were fed on a standard diet of untreated "baby rabbit pellets" and supplied with a 0.01% or 0.001% aqueous solution of colchicine instead of tap water supplied to the control series. The percentage of survival is recorded in the following table:

series	no. of specimens	% survival after treatment 10D	15D	20D	25D	30D	35D	45D
0.01% colchicine	10	100	100	40	10	0	0	0
0.001% colchicine	10	100	100	100	100	90	90	50
control	10	100	100	100	100	100	100	90

D=days

c. Cytological technique

Squash preparations only were used. The procedure is described in Chapter II.

C. Results

The cytological behaviour of all control series was similar

to that of 'normal' individuals, as described in Chapter II, and no abnormality showed itself in the chromosomes. Treated series showed the following results.

1. Caffeine:

Two different treatments, injection and food-adulteration, were tried. Specimens of various species injected with 0.5% caffeine were sacrificed at 5 and 24 hours after injection. Specimens fed with 0.5% caffeine mixed with standard food (G. bermudensis only) were sacrificed 3 days and 10 days after adminstration. The frequencies of chromosomal aberrations are recorded in Tables XXV, XXVI, XXXVI, Fig. 196.

Various types of abnormality, such as breakages (Fig. 132), stickiness (Fig. 133), clumped conditions (Fig. 134), chromosome gaps (Fig. 135), lagging chromosomes (Fig. 136) and sticky bridges (Fig. 137) were observed. Some second-division metaphase cells were found to be in a polyploid condition which could have been due to the destruction of the spindle. The most common effect observed at the late prophase I and metaphase I was the stickiness of the chromosomes. In most cases, interbivalent connections in the form of thin chromatin threads connecting the bivalents were observed (Fig. 138). In metaphase I, the bivalents were always clumped into groups (Fig. 139); no detail could be studied.

The quantitative data for the abnormalities are recorded in Tables XXV, XXVI. The frequency of occurrence was scored from more than 300 cells examined at any particular stage at a particular hour

after fixation. In the food-administered series, the percentage of breakage increased directly with the increase in time of fixation after treatment (Table XXV). Caffeine seemed to have some inhibitory action on the maturation of the last-instar nymphs. Only 10 per cent., as compared with 100 per cent. of the control series, became adult at 10 days after treatment.

An analysis of the percentage values of the different types of abnormality (Table XXVI, Fig. 196) indicated that the frequency of damage was relatively higher in Scapsipedus marginatus than in the other two species studied. However, when the percentages of total abnormal cells were compared (S. marginatus:20.94%; A. domesticus: 20.78%; G. bermudensis: 20.72%), the differences between species were negligible.

2. Colchicine:

Third-instar nymphs of G. assimilis provided with 0.01% colchicine solution in their water supply showed certain somatic effects of colchicine. The body size was smaller and the coloration darker than in control individuals. All treated individuals died within 30 days. These phenomena were less apparent in individuals given 0.001% colchicine solution, and only about 10 per cent. died within 30 days (see table on p. 79). Thus, colchicine had some lethal effect at higher concentrations, the lower concentrations producing lesser effects.

Last-instar nymphs of G. assimilis injected with 0.1% colchicine were unable to survive beyond two days after injection. Various changes in the chromosomes and spindle apparatus in the testis

cells of the experimental individuals were observed. The most frequent types of chromosomal aberration were fragmentation and stickiness (Figs. 140a,b; Table XXXVI). Sometimes, instead of having a clear break in the chromosome, a constriction was found. The production of polyploid cells (Fig. 141), chromosomal bridges and disorganization of the spindle also occurred. Further, colchicine arrested the process of meiosis, as most of the cell were found to be in a resting stage. Beside the abnormalities mentioned, the chromosomes became swollen, shortened (supercontraction of chromosomes) and stained only lightly.

3. Colcemid:

The chromosomal aberrations induced by colcemid resembled those produced by colchicine, but the degree of damage was less. The most significant aberrations were breakage (Fig. 142) and stickiness (Fig. 143). Colcemid seemed to affect the spindle, for unequal segregation was detected at late meiotic division (Fig. 144) and some chromosomes sometimes lagged behind at the equatorial plate (Fig. 145). Sticky bridges (Fig. 146) and c-mitosis (Fig. 147) occurred occasionally. Supercontraction of chromosomes in mitosis was also encounted. The spermatids increased in size and the sperms sometimes curved into a ring shape.

Tables XXVII,XXXVI show the quantitative data for abnormalities. An analysis of these data indicates that the effect of colcemid was quantitatively and qualitatively different as between G. pennsylvanicus and G. assimilis. Some chromosomal aberrations, such as lagging and

unequal segregation, occurred only in the former species but not in the latter. The total proportion of abnormal cells was 20.85 per cent. in the former species, but only 10.96 per cent. in the latter.

4. Cupferron:

Only the food-administered method was used in testing this substance. The effects on the chromosomes were similar to those produced by caffeine on the food-administered series. From table on page 79, cupferron seemed to have an inhibitory effect on the maturation of the last-instar nymphs and caused high mortality among the treated specimens; only 10 per cent. of the specimens survived for as long as 10 days, and no individual became adult after 10 days, while all of the control series survived.

The most common types of chromosomal abnormality were breaks (Fig. 148) and stickiness (Fig. 149). The presence of extra fragments was also observed. This was not only due to breaks, but also to the failure of bivalent formation by some chromosomes -- in metaphase I, all of the chromosomes were clumped into a sticky-mass and bivalents were not produced. One to four fragments were observed (Figs. 150, 151) spread throughout the cells, remaining apart from the main chromatin mass.

The quantitative data for the occurrence of abnormalities are recorded in Tables XXVIII, XXXVI. The frequency of abnormalities increased directly with the time before fixation after treatment.

5. Ethyl acetate:

No individual of G. assimilis survived beyond one hour after being injected with 0.02 ml of ethyl acetate into the abdomen. The insects became inactive and turned upside-down immediately after injection. The data were obtained from individuals sacrificed half an hour after injection. The chromosomal abnormalities were similar to those produced by glacial acetic acid. Breakage and stickiness were the most common abnormalities produced by ethyl acetate (Table XXXVI). At metaphase I, the bivalents of a cell clumped into a dense mass, but the X chromosome usually stayed apart from the mass (Fig. 152). Chromosome breaks occurred at first and second meiotic divisions, but were much more obvious at second division.

6. Glacial acetic acid:

No individual survived beyond two hours after injection of 0.02 ml of glacial acetic acid into the abdomen. All of the data were obtained from individuals sacrificed one hour after injection. Among the limited number of cells available for study, second division stages were not observed in detail, but it is believed that they were not qualitatively different from those of the first meiotic division. Chromosome breaks, stickiness (Fig. 153) and clumping of chromosomes were observed (Table XXXVI). Quantitative data were not obtained because the specimens did not survive for long after treatment. Less stain was picked up by chromosomes treated with glacial acetic acid than by those treated with other substances. All such chromosomes were very faint in appearance when compared with those of the control individuals.

7. Phenol:

Treated specimens of G. bimaculatus were injected with 0.05 ml of 0.05% and 0.1% phenol prepared in insect saline (Baker,1950). They were sacrificed at 12, 24 and 72 hours after injection. The occurrence of spermatogonial metaphase was more frequent than in normal and control individuals, especially in those injected with 0.05% phenol. This is in agreement with previous findings. Phenol can have an effect on the arrest of spermatogonial metaphase, and some workers have used phenol as a pretreatment agent for the study of mitotic chromosomes (Sharma and Sharma,1965).

The most noticeable effects of phenol were failure in the formation of the spindle, breakage (Fig. 154) and stickiness (Figs. 155a,b). In some cells, the bivalents were found widely distributed throughout cells as a result of the destruction of the spindle (Figs. 156a,b). Non-disjunction (Fig. 157), numerous univalents (Fig. 158) and unequal segregation (Fig. 159) were observed in individuals injected with 0.1% phenol and fixed at 72 hours. Some chromosomes lagged behind at anaphase I (Fig. 160), and dicentric bridges (Fig. 161) or sticky bridges (Fig. 162) were also observed. Some telophase nuclei were found to contain pycnotic masses. Breakage in the X chromosome was observed in mitotic metaphase, but it was very rarely found in meiotic divisions. C-mitosis occurred in the testis sheath cells, too.

The quantitative data for the abnormalities are recorded in Tables XXIX to XXXVI, Figs. 197,198. An analysis of these data indicate

that chromosomal aberrations increased gradually with increased time before fixation following treatment. The frequency of breaks at metaphase I and II was relatively low compared with occurrence at other stages of division. The spiralized and over-condensed state of the chromosomes, however, may have made the detection of this abnormality more difficult in these two stages. The frequency of bridges produced by 0.05% phenol reached its peak at 12 hours after injection and dropped back somewhat with increase of the period before fixation. The frequency of polyploidy produced by 0.1% phenol showed a similar result.

In almost all cases, the frequency of chromosomal aberrations was relatively greater in individuals of the 0.1%-concentration series than in those of 0.05%-concentration series (Table XXXV). Not only was the sum total of the abnormalities found to be greater but the types of aberration were more varied.

D. Discussion

The cytological abnormalities produced by different chemicals were mainly stickiness, breakage, bridges, lagging, c-mitosis, polyploidy, non-disjunction and unequal segregation. The first two or three of these were general effects produced by all of the chemicals used, but the remainder were noticed only for certain chemicals.

Two types of fragments were found: free fragments and attached fragments. The latter remained attached to the parent chromosomes by a faintly-staining thread. Since both types of fragment

occurred as a result of all treatments, they are considered to represent different aspects of the same reaction. Perhaps a stronger attack on the chromosome by a chemical would result in one or more free fragments, while a less severe attack would produce a constriction or an incomplete break in a chromosome (Levan and Tjio,1948b). The free fragments were of variable size, ranging from a very small dot to a rod or even an entire chromosome arm.

The chromatid fragments were mainly found in the prophase and usually remained paired with their sister segments. In a few cases, half-chromatid breaks were observed in prophase I. Kaufmann (1954) suggested that, under certain conditions, chemicals might act selectively on the component units of a multiple-strand chromosome. At anaphase, free fragments usually remained at the equator, whereas the attached fragments were pulled by their parent chromosomes towards the poles.

The principle of chromosomal breakage induced by various chemicals is not fully understood. Auerbach (1949) suggested that chemicals produced hazards in protein reduplication which were ultimately responsible for chromosomal breaks. After a series of experiments, Sharma and Sharma (1962) concluded that a disturbance in the metabolism of RNA was responsible for chromosomal breaks. This disturbance affected the protein synthesis and finally, indirectly, the DNA synthesis in the chromosomes, resulting in chromosomal breaks. They also pointed out that the way in which this type of disturbance arose, whether the same or different for different chemicals, was

unknown. Manna and Parida (1967) stated that formalin produced breakages, behaving as an anti-metabolite; it reacted on protein rather than on nucleic acid. Levan and Tjio (1948b) found that the production of breakages by phenolic compounds was due to an induced intercalary stickiness of the chromosomes which led to the observed formation of anaphase bridges and fragments.

The fragmentation reaction induced by chemicals in the present work was found to be similar in many features to that resulting from irradiation effects, but considerable differences were also observed. Thus, the percentage and degree of fragmentation were higher for the gamma rays treatment (see Chapter IV) than for the chemical treatments. This may have been due to the chemically induced chromosomal breaks being spread over a reasonably long period, whilst the gamma rays breaks appeared virtually simultaneously with treatment.

Stickiness of chromosomes is a common physiological phenomenon effected by many chemicals and by irradiation. It has been observed by Östergren (1944a), Varaama (1947), Kihlman and Levan (1949), Koller (1952), Cornman (1954), Sharma and Mukherji (1955), Nambiar (1955), Ohno (1960), Ohno and Tanihuzi (1960), Manna and Roy (1964), Manna and Parida (1965a,b,1967,1968), Amer (1965), Hakeem and Amer (1966), Amer and Ali (1968,1969), Amer and Farah (1968) and others. In the present study, it seemed to be but a temporary effect since the percentage of stickiness decreased gradually from the early to the later stages of prophase and metaphase. In metaphase I, the degree of stickiness varied from multivalent formation to the clumping of all bivalents into a single mass.

Some workers (Darlington,1942; Darlington and La Cour,1945) suggested that stickiness was due to a depolymerization and cross-linking of the DNA of the chromosomes. This suggestion was later supported by physiochemical studies on DNA solutions (Sparrow and Rosenfield,1946; Taylor et al.,1947,1948). However, Kaufmann et al. (1955) stated that stickiness was not due to the depolymerization of DNA, but rather to a partial dissociation of the nucleoproteins and an alteration in their pattern of organization. Yaraama (1947) thought that it was caused by a reduction in viscosity of the matrix rendering the chromosome surface more fluid. Nambiar (1955) believed that a change took place on the chromosome surface in which its discreteness and individuality were lost so that the chromosomes became irregularly shaped masses from which a few thin threads projected.

In the present study, dicentric chromosomal bridges were observed in cupferron, caffeine and phenol treatments. Chromosomal bridges may originate in one of the following ways: (1) a chromosome may break before replication and form an anaphase bridge and an acentric fragment after the proper fusion of the broken ends (Lea,1947a); (2) heterozygous paracentric inversion may occur in interphase chromosomes, which will result in a similar configuration (Rai,1964); or (3) a chromosomal bridge may occur as a result of stickiness, especially when no fragment accompanies the bridge. Most of the chromosomal bridges observed in the present study were merely of the sticky bridge type; 'true' bridges occurred at a very low frequency.

Colchicine and colcemid caused the contraction of chromosomes

at mitosis. Apart from shortening and condensation, the chromosomes showed no other abnormality. Urethane (Nambiar,1955) and methyl-naphtho hydroquinone diacetate (Nybom and Knutsson,1947) were found to produce similar effects. The contraction was due to an inherent change in the form and shape of protein molecules of the chromosomes (Östergren,1944b). Nambiar (1955) suggested that the contraction might be an expression of spiralization. She added that the reason for different behaviour between mitotic and meiotic chromosomes might be because the meiotic chromosomes usually have an additional spiral over the mitotic chromosomes, and therefore no room for further spiralization would exist. Colchicine was found not only to produce chromosomal abnormality in crickets, but also to have a lethal effect, particularly when applied to the earlier instars.

Phenolic compounds were found, in the present study, to suppress spindle activity and to inhibit the onset of mitosis in a manner similar to colchicine and colcemid. Wilson (1960) found that 2,4-dinitrophenol at 10^{-5}M markedly inhibited the glucose-stimulated rise in mitotic activity in excised pea roots. The nature of this inhibition was unknown, but it was probably associated with the ability of this compound to uncouple oxygen from phosphorylation.

Of all the treatments, phenol produced the highest degree of chromosomal abnormality of any of the chemicals tested (see Table XXXVI). The cytological damage to plant cells caused by phenol has been demonstrated by many workers (Levan and Tjio,1948a,b; Levan,1949; Muhling et al.,1960; Wilson,1960; Amer and Ali,1968,1969) who have

observed abnormalities similar to those recorded in the present study, such as breakage, stickiness, c-mitosis, lagging, bridge formation, etc. Although Sharma and Bhattacharyya (1956) have demonstrated advantages in the application of phenol for the study of karyotype, it is not, in general, safe to apply this substance as a pretreatment agent, even at a low concentration, as it may result in chromosomal abnormality.

In the current study, glacial acetic acid, ethyl acetate and cupferron affected mainly the chromosomes having a lesser or no effect upon the spindle apparatus. Abnormalities such as c-mitosis, polyploid cells, anaphase with destroyed spindle, unequal segregation, etc., were not observed. From this, it may be presumed that these chemicals have very little effect on the proteins which are largely present in the spindle apparatus. Manna and Mukherjee (1966) also stated that acetic acid treatment did not produce a significant effect on spindle structure.

Sensitivity to most of the different chemicals tested in the present study varied between different species, although the response to caffeine treatment was the same even in species belonging to different genera. It is particularly notable that Gryllus pennsylvanicus and G. assimilis, although they both belong to the same genus, showed remarkable differences in the degree of sensitivity to colcemid. Cytological responses may be correlated with interference with biochemical processes at different sites and in somewhat different ways. The chemicals caffeine and colcemid both produced generally similar effects (in spite of interspecific differences in the case of

the latter), but the former was more effective in causing damage to the spindle structure. Therefore, caffeine should be considered less safe than colcemid for use as a pretreatment agent for karyotypic analysis.

It should further be noted that there appears to be some variation between the results obtained by different workers dealing with the same chemicals. For example, phenols have been found by Levan and Tjio (1948a,b) to produce chromosomal breaks in Allium cepa, whereas Loveless and Revell (1949) failed to obtain any significant fragmentation in Vicia faba with a similar chemical. On the other hand, phenol did induce chromosomal breakage in crickets in the present study. Nothing is to be gained by assuming that one set of workers is right and the other is wrong. The differing results are more likely to reflect differences in the purity of chemical used, in the test organisms, in the sensitivities of different parts of the mitotic and meiotic cycle, etc. In some cases, if scoring is not carried out at the right time, breakage potential of the chemicals may be overlooked (Wilson, 1960).

IV. EFFECTS OF RADIATION

A. Literature Review

1. General:

That ionizing radiations can induce chromosomal aberrations had been realized since the fundamental discoveries by Mohr (1919) and Müller (1927,1928) in animals, and by Stadler (1928) in plants, that X-rays produced mutation in the organisms. Subsequently, a considerable literature has accumulated describing the cytogenetic effects of ionizing radiations, viz. X-rays and gamma and beta rays (both directly and by the use of various radioisotopes) and neutrons. Most of the studies agree that the degree of chromosome damage due to radiation is directly correlated with dosage (Kaufmann,1954; Evans, 1962). Radiation interferes with a number of biochemical processes, especially those concerned with protein and nucleic acid synthesis. The effects may be temporary and reversible, or permanent and usually lethal.

2. X-rays:

The study of X-ray-induced chromosomal aberrations in Orthoptera has been quite extensive, particularly in grasshoppers. Most of the earlier workers (Mohr,1919; White,1932,1937; Helwig,1933,1938; Carothers,1940; Creighton,1941; Creighton and Evans,1941; Bishop,1942) employed testis cells of various species for the investigation of the effects on meiotic chromosomes. Carlson (1938a,b,1940,1941a,b,1954), however, examined the mitotic chromosomes of neuroblast culture cells.

Chromosomal aberrations such as breakage, anaphase bridges, stickiness and reciprocal translocation were observed in both mitotic and meiotic chromosomes.

Helwig (1938), using X-rays, irradiated partially developed embryos of the grasshopper Circotettix verruculalus (Kirby) at very low dosages (200 rad to 350 rad) and studied the effects of this radiation on the meiotic chromosomes of the resultant last-instar nymphs. Reciprocal translocation and breakage occurred. Translocation occurred more frequently (in 76 or 78% vs. 22 to 24% of the occurrences) between the large elements (the twelve largest chromosomes) than between the small ones (the four smallest chromosomes). The frequency of breakage was greatest immediately after exposure and became less as time elapsed. The fragments always became reattached to their respective parent chromosomes at the loci of breakage. Carlson (1938a,b,1940,1941a,b, 1954) studied the neuroblasts in the embryos of Chortophaga viridifasciata (De Geer) developing in eggs which had been irradiated with X-rays. Two phenomena, side-arm bridges and 'stickiness', occurred at anaphase shortly after irradiation. Carlson (1954) pointed out that a dose as low as 25 rad was capable of inducing meiotic delay in Chortophaga. Fox (1966a,b) obtained similar results with Schistocerca gregaria (Foskål), but added that acentric fragments were rare and that non-chromatid breaks were found.

Ray-Chaudhuri and Sarkar (1952), Ray-Chaudhuri et al. (1957) and Ray-Chaudhuri (1961) proposed the "target hypothesis" in their studies of the effects of X-ray-induced chromosomal aberrations in

grasshoppers, and used the dicentric bridge of anaphase I as an indicator of chromosome damage. Manna and his co-workers (Manna and Mazumder,1962,1967; Mazumder and Manna,1966,1967,1968; Manna,1967) used the occurrence of X-ray induced X chromosome aberrations as an indicator of chromosome damage. They found that X-ray treatment, combined with chemical pre- or post-treatment, would increase the percentage of damage (Mazumder and Manna,1966). Similar results had previously been reported in plants by Merz et al. (1961) for the broad bean, Vicia faba L. Besides the X-ray treatment, Manna and his collaborators (Manna and Roy,1964; Manna and Mukherjee,1966) also studied the effects of other ionic radiations (pH dependence) on grasshopper chromosomes. Anomalies, in the forms of breakage, fragmentation, constriction, anaphase bridges and multipolar spindles, were discovered.

Much less attention has been paid to the cytological effects of ionizing radiations on crickets. Similar work to that of Carlson (1954) and Fox (1966a,b) has, however, been carried out on the house cricket, Acheta domesticus L., by Bluzat (1964). Developed embryos were X-irradiated at dosages of 300 and 500 rad and neuroblasts of the embryos were studied cytologically. Fragmented chromosomes and double bridges were observed at different stages of meiotic division; the sensitivity to X-rays varied between different stages of embryogenesis. Radiosensitivity of eggs of Gryllus bimaculatus was also examined by Sereno (1960). An exposure of 350 rad reduced the hatch of 0-, 1- or 2-day-old eggs to about 50 per cent and 3-day-old eggs to 11 per cent of the controls.

3. Beta and Gamma Radiation:

In addition to the above study of the cytogical effects of radiation, four additional works concerning the effects of radiation on crickets have been published. In the first of these, treatment with the radioactive chemical L-Methionine-Methyl-^{14}C was shown to cause sterility of males of Gryllus assimilis (F.), and to inhibit oviposition by normal females when these mate with treated males (Abdel-Malek and Kevan,1961). The inhibited females resumed oviposition after isolation for about two weeks and mating with normal males. The authors presumed that some inhibiting factors were passed to the females from the treated males by way of the spermatophores. The chemical had no direct effect upon the females.

Recently, Jobin et al. (1970) studied the sensitivity to gamma rays of the house cricket, Acheta domesticus. The maximum lethal effects were manifested after 100 hours of development; subsequently they declined rapidly. Radiosensitivity of adults increased with age; females were more sensitive than males. Adults developed from irradiated nymphs showed some abnormality in their morphology, especially of the wings. Gamma radiation was also found to affect life expectancy and reproduction in the same species (Menhinick and Crossley,1968; Hunter and Krithayakiern,1971). Both adults and nymphs were tested. In each experiment it was found that the life expectancy was reduced with increased dosages when the insects were irradiated at 4000 rad or more. The life expectancy of females was increased, however, when they were irradiated with 500 rad, 1000 rad and 2000 rad;

no significant increase was found in males irradiated at the same dosages. Only small nymphs showed an increase in life expectancy when irradiated at 1000 rad. Hunter and Krithayakiern (1971) also reported that the number of eggs laid was greatly reduced after irradiation, and that eggs were not laid by females treated with more than 4000 rad.

4. Ultraviolet:

Earlier investigations have shown that ultraviolet radiation can induce chromosomal breaks (Swanson,1940,1942,1944; Slizynski,1942; Kaufmann and Hollaender,1946) and sterility in male Drosophila (Mackenzie and Müller,1940; Demerec et al.,1942; Kaufmann and Demerec, 1942). Recently, most of the information on the effects of ultraviolet radiation has been obtained by the irradiation of delimited areas within cells in culture. Several studies have shown that irradiating a chromosome bring about a loss of DNA and histone at the site of irradiation (Takeda,1964; Bloom and Czarslan,1965) and that the spindle diminishes in size or disappears temporarily following the irradiation at any part of a cell; it was also found that irradiated cells later reconstructed a new small spindle (Uretz et al.,1954,1955; Izutsu,1959,1961a,b; Takeda and Izutsu,1961; Wada and Izutsu,1961; Yashima,1962). Takeda et al. (1967) found that irradiation at a nuclear or extra-nucleolar nuclear site rapidly caused the inhibition of DNA and RNA synthesis and that the protein synthesis was resistant to the irradiation of any cellular area.

Ultraviolet radiation also affects the behaviour of

chromosomes. Daughter chromosome groups move rapidly from the irradiated pole towards the non-irradiated opposite pole after the cell is treated at telophase with an ultraviolet microbeam in a restricted part (Nakanishi and Kato,1965). According to Blum (1959) a churning or cyclic movement rapid occurs in the cytoplasm within a few minutes after exposure of cells to ultraviolet rays. Therefore, Nakanishi and Kato (1965) believed that a prompt change in viscosity might occur at the irradiated area which would cause cytoplasmic streaming in the cytoplasm around the irradiated area. This resultant streaming might push the chromosome groups towards the equator of the cell.

B. Materials and Methods

1. Materials:

Nymphs and adults of the following species (from the sources indicated previously) were used:

Gryllus assimilis (Fabricius)

G. bimaculatus De Geer

G. pennsylvanicus Burmeister

Acheta domesticus Linnaeus

Scapsipedus marginatus (Afzelius et Brannius)

Allonemobius allardi (Alexander & Thomas)

All of the various species of cricket listed above were exposed to gamma rays, but only Gryllus assimilis was used for ultraviolet treatment.

2. Methods:

Ten to twelve individuals were used for each treatment. The majority were penultimate-instar male nymphs, although some third- and last-instar male nymphs and adult males and females were also used.

Gamma irradiation was carried out using an A.C.E. 'Gammacell 220' cobalt 'bomb'. An aluminium 'filter', which eliminated 70 per cent. of the gamma and all beta radiation, was inserted between the radioactive source and the material to be irradiated. Each insect to be irradiated was put in a 22mm X 35mm glass vial, closed by a plastic ('Neoprene') stopper, and placed at a distance about 8.2cm above the bottom of the operating tube (i.e., directly in line with the radioactive source). Four vials were irradiated simultaneously on the same horizontal level. The exposure rate was kept constant at 54.35 r/sec, but the exposure time varied in different treatments. After treatment, the specimens were reared for varying times at a temperature of 21.5±1°C under standard laboratory conditions. Individuals of the control series were reared under similar laboratory conditions, but received no radiation treatment.

Individuals treated with ultraviolet radiation (Gryllus assimilis only) were reared from the penultimate nymphal instar in standard one-gallon candy jars placed in an incubator illuminated from above by ultraviolet light. The exposure rate was kept constant at 65 mμ/cm^2/sec.

At intervals after irradiation, the testes of each insect

were dissected out in insect saline (Baker,1950) and fixed in acetic-alcohol (1:3) for 24 hours. They were then stained in alcoholic HCl-carmine (Snow,1963) and squash preparations in 45% acetic acid were made. Two to three individuals were fixed for each treatment. Most of the data were secured by examination of the first meiotic division. Figures were drawn at a magnification of 1250X using a camera lucida.

Some gamma-irradiated nymphs of different species were not dissected, but were maintained under standard laboratory culture conditions in order to observe the effects of radiation on subsequent development.

C. Results

1. Effects on Survival, Development and Reproduction:

The effect of gamma rays on survival was more or less similar for all species, except Gryllus bimaculatus which showed a very high mortality rate (Table XXXVII). Gamma rays also inhibited the development, especially of the younger-instar nymphs. Of the third-instar nymphs of Gryllus assimilis, Acheta domesticus and Scapsipedus marginatus, which were irradiated with 100 rad and reared under standard conditions after treatment, almost all showed arrested development. No further moulting occurred in these nymphs, i.e., they remained in the third-instar until they died (about two months after treatment). A few irradiated nymphs of G. assimilis, G. pennsylvanicus, Acheta domesticus and Scapsipedus marginatus, however, developed to the adult state, but showed abnormal wing development.

Crossing experiments were attempted between irradiated females and normal males, and vice versa. Mating occurred and some eggs were laid in both cases but not a single egg hatched. No egg was produced when irradiated females were mated with irradiated males.

Some nymphs of G. assimilis, irradiated in their penultimate-instar with 1000 rad, were sacrificed (as last-instar nymphs) 21 days after treatment. These were smaller in body size than normal and the gonads were only about 1/4 to 1/3 of the size of those occurring in normal last-instar nymphs. Further, the gonads were abnormal, being made up largely of degenerated connective tissues, and were covered with large amounts of fat.

Not all of the above effects which occurred in the individuals treated with gamma rays were observed on individuals treated with ultraviolet rays. The latter developed normally to the adult stage and behaved like the control series.

2. Cytological Effects:

a. Gamma rays

The most significant of the chromosomal abnormalities induced by gamma rays was fragmentation, chromosomal breakages being observed at any stage of division. Therefore, in the present study, attention was focused largely on the occurrence of fragments, especially from a quantitative viewpoint. Other abnormalities, such as the regular occurrence of anaphase bridges (Figs. 163,164), stickiness (Figs. 165,166), gaps (Figs. 167,168), lagging chromosomes (Figs.

169,170,171), unequal segregation (Figs. 172,173), multipolar configuration (Figs. 174,175,176), giant spermatids (Fig. 177) and meiotic delay, were, however, also observed. The fragments varied in appearance, size and number in different cells, but no difference was recorded with regard to the configurations observed as a result of different dosages or in different species.

Although the fragments varied in size, they usually were very small, appearing as dots, tiny spheres, or small to large rods (Figs. 178,179,180,181). They were found scattered throughout the cells, outside or inside the nuclei. This distribution of fragments through the cells (especially outside the spindle areas) indicated a lack of power in poleward movement, and most of them could be expected to be eliminated. The fragments were also observed to lie, either in the vicinity of their respective parent chromosomes or as separate scattered entities. They ranged from one to many in a single cell (Figs. 182,183,184), the number, increasing, in general, with increase in dosage and duration of treatment. Formation of micronuclei, probably from a few of the fragments, was also observed. Ring fragments, though infrequent, were found at both metaphase (Fig. 185) and anaphase (Figs. 186,187). The fragments may have resulted from simple deletion (chromatid and chromosome breaks), which might be terminal or interstitial, or they may have been derived during the formation of chromosome dicentrics.

In the present study, multiple breaks, particularly affecting the chromatids, were found to be quite frequent. Chromosomal gaps

were usually observed in the cells containing free fragments, but the frequency of the gaps was less than that of the free fragments occurring in the same cell. Among the different species studied, the frequency of free fragments was higher in those species with higher chromosome numbers (Figs. 178,188), but the frequency of breaks was higher in the species with lower chromosome numbers (see Table XXXIX).

Chromosomal bridges occurred very commonly in irradiated cells. Like the fragments, anaphase bridges appeared in various configurations, the most common being sticky bridges (Fig. 164) and bridges due to delayed separation of chromatids (Fig. 163). Interchange bridges (Fig. 189) occurred only occasionally. Most of the bridges ultimately broke up due to the mechanical pulling of the spindle fibres.

Interbivalent connections occurred frequently. During the diplotene and diakinesis, usually more than half the bivalents were connected, while, in some cells, all bivalents were involved. At metaphase I, some cells clumped into a mass (Fig. 190) or into a few groups (Fig. 191). At diakinesis, different combinations of quadrivalents, bivalents and fragments were observed. The formation of quadrivalents was probably due either to the reciprocal translocation of broken chromosome ends or to the stickiness of the chromosomes.

Quantitative data for fragmentations are recorded in Tables XXXVIII and XXXIX. The frequency of occurrence was scored from more than 600 cells examined after different dosages and at specific stages at particular hours after treatment. Because of the limited occurrence

of second meiotic division cells, a quantitative study for this stage could not be made. The results indicated that anaphase I and telophase I were the most sensitive stages and that the percentage of damage increased with increase in dosage and/or duration of treatment. A graphical representation of the percentage of damage (Fig. 199) takes the form of an exponential curve. No significant restitution of breakage occurred in the cells within 10 days after radiation.

b. Ultraviolet

Penultimate-instar nymphs of only one species, Gryllus assimilis, were used to study the effects of ultraviolet radiation. The development and survival rates of individuals treated with 65 $m\mu/cm^2/sec$ ultraviolet showed no difference from those of the control series. No chromosomal abnormality occurred after 20 days of continuous treatment. Abnormalities, such as breaks (Fig. 192) and stickiness (Fig. 193), were, however, observed after 25 days of continuous treatment. The quantitative data are as follows:

duration of treatment(days)	% cells showing stickiness	% cells showing breaks PI	MI	MII
20	-	-	-	-
25	22.7	2.4	4.7	3.9
30	59.3	9.1	11.4	11.2
0 (control)	-	-	-	-

PI = prophase I
MI = metaphase I
MII = metaphase II

D. Discussion

The present study has shown that gamma rays not only induce chromosomal abnormalities, but also have an effect on survival, development and reproduction. The percentage mortality increased with an increase in dosage and either eggs were not produced, or only sterile eggs were laid by the treated females. Similar results were also observed by Menhinick and Crossley (1968), Jobin et al. (1970) and Hunter and Krithayakiern (1971). Physiological changes caused by gamma radiation have not been adequately explained. However, from cytological evidence, the high mortality and sterility among test insects are shown to be due to serious chromosomal damage.

After radiation treatment, most of the cells in the testis, especially those of the earlier-instar nymphs, were found to be in interphase, because the most significant effect of radiation, besides breakage, is inhibition of both mitosis and meiosis. If a cell were approaching prophase at the time of treatment, it would be inhibited from entering this stage, or if it were in early prophase, it might appear to regress in phase (Müller, 1954). On the other hand, if a cell were already in late prophase, metaphase or anaphase when radiation was applied, it would complete its division without interruption.

Two types of fragmentation usually occurred after irradiation in a tissue containing dividing cells: chromosome type and chromatid type. The structural change occurring within or between chromosomes and chromatids is one of simple deletion, which results in an acrocentric fragment and the exchange of material. An exchange of

the chromosome type may either be an intrachange, resulting in one or two fragments, sometimes accompanied by the formation of a ring bivalent, or one which usually results in the formation of a dicentric bridge plus one or two fragments. Chromatid type aberrations are essentially similar to those of the chromosome type, but show more variety of change, such as translocation, duplication, etc.

Three hypotheses have been put forward to explain the mechanism of chromosomal breakage due to radiation. The "breakage first" hypothesis, proposed by Stadler (1928), is that a single deletion is caused by a single break either in the chromatid or in the chromosome. The "contact hypothesis", suggested by Serebrovsky (1929), is that breakage is produced in a chromosome following a single 'hit' by X-rays at a place where the parts previously remained in close association. Investigations on the chromosomes of the plant, Tradescantia, supported these two hypotheses (Sax,1938,1939,1940,1941). A third hypothesis known as the "exchange hypothesis", however, was proposed by Revell (1959). According to this, all chromatid and chromosome breaks result from exchanges of the intra-chromosomal type. Certain cases of fragmentation in the present study can be explained better by the exchange hypothesis than by the two previous hypotheses. The occurrence of some types of fragmentation, however, do not fit well with any of the three above hypotheses, and a different explanation is necessary.

Kihlman (1961) believed that at least one type of break, extreme fragmentation of some or all chromosomes in a cell, does not

arise by an exchange mechanism. Such extreme fragmentation has been described under different names, such as chromosome "shattering" by Lovelace (1954), "pulverization" by D'Amato (1950) and "total Zusammenbruch" by Marquardt (1950). The present study supports Kihlman's belief. The occurrence of numerous fragments in a cell must be a result of multiple breaks caused by radiation and is not explicable on the basis of exchange.

Evans (1962) pointed out that radiation induced large numbers of breaks in chromosomes. In some instances there may be restitution of a fragmented chromosome from its several parts, in some cases structural rearrangement may be involved; and in others, free fragments appear and remain as such. That is to say, in some cases rejoining occurs to give rise either to the original configuration or to the formation of exchange aberrations, but in other cases, no such rejoining occurs. The evidence from the experiments on intensity of radiation and fracturation by Sax (1939,1940,1941) and Fabergi (1940) indicate that a break remains available for rejoining for only a limited period of time (up to one hour). Thoday (1954) found that when breaks are induced during the presynthesis period of DNA, i.e., a "chromosome break", about 40 to 80 per cent showed no evidence of sister-chromatid union, whereas when breaks are induced during the postsynthesis period, i.e., a "chromatid break", more than 90 per cent. showed sister-chromatid union. When breakage ends are capable of rejoining, the probability of restitution of the original chromosome appears to depend, not on a difference in the breakage process, but mainly on whether or not other breaks are available with which

interchange can occur (Lea,1946). In some cases, chance circumstances will prevent rejoining (Lea,1947b).

Bacq (1951) and Mazumder and Manna (1967) believed that radiation produced indirect effects on the production of chromosomal aberrations or gene mutations, and that ionizing radiations acted in the same manner as some organic peroxides whose action can be modified. Kaufmann (1954) stated that the process of induced chromosomal breakage cannot at present be described either as a direct or an indirect effect, for, whether the chemical reactions originate for the most part from molecules in nucleic acids and proteins, or are mediated through associated aqueous solutions, is not clear. However, the protection afforded by dissolved substances, such as cysteamine, versene, sodium cyanide, cystein, etc. (Bacq,1951; Bacq et al.,1951; Mikaelson,1954; Riley,1957; Ray-Chaudhuri,1961; Brahma et al.,1961, 1962) strongly support the contention that the effects of radiation are indirect.

Sensitivity to radiation, in the present study, varied between different types of cells and division stages. Savahager (1960) indicated that metaphase-anaphase I might be the most sensitive of the division stages. Bozeman and Metz (1949) suggested that the highest frequency of aberrations occurred following irradiation at anaphase I. Newcombe (1942), Whiting (1945) and Cahberg and DiGinno (1960), however, believed that meiotic metaphase was the most sensitive stage for the production of aberrations. This may be partly because of the increase in the number of strands when the chromosome splits (Sax,1940),

or to the strand breaking more readily at this stage (Marshak,1937), or it may be because reduced restitution occurs at metaphase (Sax, 1940).

As the testicular follicles of the crickets studied in the present work included different divisional stages at the same developmental time, it is difficult to indicate the exact stages involved at the time radiation was applied. From the fact that the highest damage occurred at anaphase I and telophase I, however, one might assume that cells approaching metaphase, or already in metaphase, are the most sensitive. It has also been reported that cells with short meiotic cycles and intermitotic periods are more sensitive to radiation and suffer greater damage than those with longer cycles (Koller, 1947; Knowlton and Widner,1950).

In the present study, some giant spermatids were formed after irradiation. These sometimes incorporated more than two sets of chromosomes. The formation of giant spermatids may have been as a result of normal meiotic division being inhibited on account of irradiation by gamma rays. Similar results after X-rays treatment have been reported for some Acrididae (White,1932; Makino,1939; Creighton and Evans,1941; Carlson,1941b). Kaufmann (1954), however, suggested that giant spermatids might originate in prophase cells that revert in phase at the time of treatment and those chromosomes undergo a second doubling as they progress toward metaphase for a second time.

Early investigations suggested that a single 'hit' by X-rays could induce only a single chromatid break at any given locus

on a chromosome. Later, many studies indicated that an X-ray 'hit' could break one or two chromatids and that secondary effects of a single 'hit' could cause breaks simultaneously at the same locus (Patterson,1933; Moore,1934; Carlson,1937; Kaufmann,1937; Sax,1938). In the present study, large numbers of both chromatid and chromosome breaks occurred after gamma ray treatment, clearly showing that a single 'hit' can, indeed, break more than one chromatid at the same locus, and/or, that secondary effects of a single 'hit' may produce further breaks on the chromosomes. Single hitsapart, however, multiple hits of gamma rays were presumably the main cause producing the numerous breaks and fragments occurring in individual cells.

In Fig. 199 the number of breaks are plotted against radiation dose and show an exponential increase in breakage with increased dosage. This is in agreement with Zimmer (1941) who indicated that the curves for multiple-hit events would be of the powered exponential type, rather than of the straight-line type for single-hit events (Sax,1938,1940). Zimmer (op. cit.) added that, under certain conditions, such an exponential curve could have an almost linear middle range.

In the crickets here studied, there was some variation in radiosensitivity between different species. Differences in the response of chromosomes of different species to ionizing radiation would depend upon a large number of factors, one of the most important being the total volume of the chromosomes in the nuclei (Östergren et al., 1958; Sparrow et al.,1961; Evans,1961,1962). The increased effects

which accompanied the increase in chromosome volume was interpreted by these authors as being due to an increased target size. This, therefore, might be the reason why, in the cricket species studied, those having higher chromosome numbers also showed greater damage (more fragments) in a given cell than did species with lower chromosome numbers. The latter group (e.g., Acheta domesticus), however, showed higher frequency of total breakage than did the former group. This might be explained on the premise that "the long chromosomes have been found much more sensitive to radiation than the short chromosomes" (Sharma and Chatterji,1962).

The present studies have shown that ultraviolet radiation produces some structural changes in the chromosomes, but the frequency of aberration induced by a given dose of ultraviolet rays was found to be much lower than that resulting from gamma radiation given in a similar dose.

V. CONCLUSIONS

Cytology has greatly influenced the systematics of many groups by offering a new approach to research on phylogenetic relationships, for it supplies additional evidence and new concepts leading to a better understanding of a particular group. The study of systematics, therefore, may be greatly improved by the development of cytological investigations.

In Gryllidae, the chromosome number is not constant (i.e. there is no 'model' number) throughout the whole family, nor even within any one subfamily. This implies, either that the family is polyphyletic, for which there is little or no other evidence, or that considerable evolutionary change has occurred within the groups and that the family is thus one of great antiquity, which the fossil record indeed shows (Zeuner,1939; Sharov,1968). Evidence so far available suggests that,in the course of evolution, various groups of crickets have been involved in both upward and downward changes in chromosome number from a possible ancestral complement in the vicinity of $2n\delta=21$.

Thus, the chromosome number alone is a valuable character which may be used in the classification of the Gryllidae. Karyotypes and other cytological characters, however, are also of value in this respect since different genera, such as Acheta, Scapsipedus, Gryllodes and Melanogryllus, may have the same chromosome number but show marked differences in ~~karyotype and~~ those other ~~cytological~~ characters. Karyotypic differences are also useful at the species level and serve especially

well to distinguish between Gryllus species.

Chromosome number, the structure of the X chromosome and other cytological characters, the form of the testes, combined with morphology and acoustic behaviour, set the subfamily Gryllinae apart from the Nemobiinae. Further, studies of many species may perhaps reveal not only comparable differences between other subfamilies and families of Grylloidea but also the desirability of further generic differentiation in certain groups.

With respect to the cytogenetic effects of radiation, the present work indicates, in a limited way, for crickets, that radiosensitivity increases with increase in chromosome number and chromosome length, and that there are variations among different species. However, the configurations resulting from the damage caused indicate no great difference as a result of different dosages or in different species.

Chromosomal abnormalities are also produced by chemical treatments. Some chemicals, such as colchicine, caffeine, phenol, have been used as a pretreatment substance for studying the chromosome morphology when applied at low concentrations. The present study shows, however, that these chemicals, especially phenol and caffeine, are not safe to employ as pretreatment agents, even when applied at low concentrations.

The cytogenetic abnormalities caused by strong, artifically induced, environmental factors, such as unnatural amounts of ionizing radiations or concentrations of toxic chemicals, may be very great.

Pollution of the environment by such agencies may therefore have very serious long-term consequences. However, it should be borne in mind that, even in the absence of such agencies, similar abnormalities occur to a lesser degree (or even to a comparable degree, as was possibly the case with the Gryllus campestris studied). Further investigations on the relative effects of chemicals and radiation on chromosomes are clearly necessary in order to solve the problems concerning the degree of cytological damage directly attributable to various forms of environmental contamination.

VI. SUMMARY

1. Thirteen species of the subfamily Gryllinae and seven species of the subfamily Nemobiinae have been studied cytologically. The spermatogonial numbers range from eleven to thirty-one in the former group and from seven to twenty-one in the latter.

2. The chromosomes of Gryllinae assume various shapes and sizes; they may be spheres, short to long rods, J-shaped or V-shaped. The distribution of these various types of chromosomes among different species differs. The subfamily shows uniformity of the form of the sex chromosomes and of the testes.

3. The male diploid chromosome number is 29 in all species of Gryllus examined, except for some individuals of G. veletis possessing supernumerary chromosomes. Analysis of karyotypes showed that acrocentric chromosomes were very common in G. veletis, G. bimaculatus and G. campestris but rather rare in G. assimilis, G. bermudensis, G. pennsylvanicus and G. rubens. The variation in karyotype and the complete incompatibility between certain species of Gryllus indicated that some important structural changes have occurred during evolution, even although these changes have so far led to no change in the basic chromosome number.

4. Two populations of "G. bimaculatus", one from the Azores and the other from Singapore, probably belong to different species. Chromosomal aberrations occurred in the F_1 generation of the Singapore population; they produced no offspring.

5. Two male individuals of G. campestris, from Hungary, were studied and they showed many chromosomal abnormalities which were similar to those induced by chemicals and radiation. The reason for the abnormalities is unknown, but a possible cause is discussed.

6. The uniformity of karyotype throughout those members of the subfamily Nemobiinae studied is very remarkable. All of the autosomes were acrocentrics in Neonemobius, except in N. sp. near mormonius, and in Allonemobius, while the autosomes were all metacentrics in Eunemobius. However, the structure and size of the X chromosome and the testes varied from genus to genus.

7. One or two supernumerary chromosomes occurred in some individuals of Gryllus veletis, the chromosome number of this species thus varied between $2n\hat{\sigma}=29$ and 31; no supernumerary chromosome was observed in the sympatric species G. pennsylvanicus. The presence or absence of supernumerary chromosomes had no noticeable effect on the outward appearance of individuals of G. veletis.

8. Chromosomal polymorphism was quite common in both Gryllinae (except in the genus Gryllus), and in Nemobiinae; it usually occurred in the form of a single heteromorphic pair. Translocation bivalents, instead of the heteromorphic bivalents occurring in other genera, were observed in Allonemobius.

9. Chromosomal bridges occasionally appeared in G. veletis, G. pennsylvanicus, G. rubens, Gryllodes sigillatus, Neonemobius palustris, N. sp. near mormonius, Allonemobius griseus and A. fasciatus. They were mainly sticky bridges and would separate again at late

telophase under the influence of the spindle fibres.

10. An analysis of chiasma frequency within diplotene cells was made. There was a positive correlation between chromosome length and chiasma frequency, but this relationship was not strictly linear throughout the chromosome complement, either within or between species.

11. It is suggested that the evolution of the chromosome complement in the Gryllidae has probably progressed by both increase and decrease in number (possibly from an ancestral number in the vicinity of $2n\delta=21$), centric fusion playing a more important part than centric fission.

12. Various chemicals, caffeine, colcemid, colchicine, cupferron, ethyl acetate, glacial acetic acid and phenol, were used to induce chromosomal abnormality in some species.

13. Two methods of administration, injection and feeding, were used. In the injection-administered series, 0.02-0.05 ml of chemicals were introduced via the abdominal pleura and the insects were sacrificed at various times after injection. In the feeding-administered series, the aqueous solutions of chemicals were either mixed with the standard food or supplied in drinking water.

14. Chromosomal abnormalities, such as breakage, stickiness, bridges, lagging, c-mitosis, polyploidy, non-disjunction and unequal segregation were observed as a result of chemical treatment. Of all the treatments, phenol produced the highest degree of abnormality.

15. In addition to the production of chromosomal abnormalities, some chemicals, such as colchicine and cupferron, were found to have a lethal effect; cupferron and caffeine also had an inhibitory effect on the maturation of the last-instar nymphs.

16. Nymphs of various species were exposed to gamma radiation using a cobalt 'bomb'. The dosages applied were kept constant at 54.35 r/sec but the exposure time varied in different treatments. The irradiated insects were studied at different intervals. Gamma radiation was found to have an effect on oviposition, reproduction and survival of the tested insects.

17. Comparative radiosensitivity in different species was scored particularly from the frequency of chromosome fragmentations, although other aberrations such as stickiness, bridges, lagging, multipolar, unequal segregation, gaps, etc. were also observed. With regard to chromosomal breakage, the species having higher chromosome numbers were much more sensitive than those with lower numbers; cells approaching metaphase appeared to be in the most sensitive stage.

18. The occurrence of numerous breaks and fragments in a single cell might be a result of multiple 'hits' by gamma rays.

19. The frequency of aberration induced by ultraviolet radiation was found to be much lower than that produced by gamma rays, given in a similar dose.

20. The sensitivity to different chemicals and radiations varied between different species.

21. Changes in chromosome number would appear to have occurred within the Gryllidae during the course of evolution. Chromosome number, as well as other cytological features, thus provide valuable taxonomic characters in this family.

22. Further investigations on the relative effects of chemicals and radiation on chromosomes are necessary in order to solve problem concerning the degree of cytological damage attributable to various forms of environmental contamination.

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Tables and Figures

Table I Frequency of four different types of chromosomes in Gryllidae.

Species	A	ST	SM	M	Total chromosome pairs
Gryllus veletis	10	5	-	1	15 + X
G. pennsylvanicus	3	7	2	3	14 + X
G. assimilis	4	7	1	3	14 + X
G. bimaculatus	9	5	-	1	14 + X
G. bermudensis	4	7	3	1	14 + X
G. rubens	7	2	4	2	14 + X
G. campestris	9	3	1	2	14 + X
Acheta domesticus	4	1	2	4	10 + X
Gryllodes sigillatus	5	5	-	1	10 + X
Scapsipedus marginatus	3	2	2	4	10 + X
Melanogryllus desertus	3	1	5	2	10 + X
Tartarogryllus burdigalensis	3	3	1	3	9 + X
Neonemobius palustris	9	-	-	1	9 + X
N. sp. near mormonius	7	1	-	2	9 + X
Allonemobius fasciatus	7	-	-	1	7 + X
A. allardi	7	-	-	1	7 + X
A. f. griseus	7	-	-	1	7 + X
Dunemobius c. carolinus	-	-	1	3	3 + X

Note: A = acrocentric : arm ratio = 7.01–∞
ST = subtelocentric : arm ratio = 1.71–7.00
SM = submetacentric : arm ratio = 1.31–1.70
M = metacentric : arm ratio = 1.00–1.30

Table II Karyotype of Gryllus veletis (2n♂ = 31).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.75	-	A	5.80	0
2	3.01	-	A	5.30	0
3	3.14	-	A	5.08	0
4	3.26	-	A	4.89	0
5	3.35	2.44	ST	4.76	28.90
6	3.43	-	A	4.65	0
7	3.56	-	A	4.48	0
8	3.65	2.00	ST	4.37	33.15
9	3.72	-	A	4.29	0
10	3.84	-	A	4.15	0
11	3.95	-	A	4.04	0
12	4.14	2.06	ST	3.85	32.60
13	4.36	-	A	3.66	0
14	4.60	2.01	ST	3.47	33.04
15	4.93	2.02	ST	3.23	33.06
X	15.97	1.15	M		46.39
TCL	127.62				

Table III Karyotype of Gryllus pennsylvanicus ($2n\delta=29$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.86	-	A	7.02	0
2	3.24	-	A	6.20	0
3	3.54	1.26	M	5.67	44.06
4	3.87	1.47	SM	5.19	40.31
5	4.11	1.76	ST	4.89	36.00
6	4.41	1.95	ST	4.55	33.78
7	4.54	2.10	ST	4.42	32.15
8	4.85	2.53	ST	4.14	28.24
9	5.05	2.50	ST	3.98	24.95
10	5.09	-	A	3.94	0
11	5.73	1.35	SM	3.50	42.58
12	6.12	2.31	ST	3.28	30.06
13	6.46	2.71	ST	3.11	27.24
14	7.64	1.23	M	2.63	44.76
X	20.10	1.13	M		46.76
TCL	147.45				

Table IV Karyotype of Gryllus assimilis ($2n\delta=29$)(Antigua population).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.57	-	A	7.76	0
2	3.07	1.98	ST	6.50	33.55
3	3.49	2.12	ST	5.71	32.09
4	3.57	-	A	5.59	0
5	4.04	-	A	4.94	0
6	4.19	2.36	ST	4.76	29.59
7	4.50	2.16	ST	4.43	31.55
8	4.71	2.18	ST	4.23	31.42
9	5.05	2.34	ST	3.95	29.90
10	5.28	1.99	ST	3.78	33.33
11	5.56	-	A	3.58	0
12	6.05	1.69	SM	3.29	37.02
13	6.63	1.22	M	3.01	44.91
14	8.53	1.21	M	2.33	45.13
X	19.96	1.12	M		47.09
TCL	156.01				

Table V Karyotype of Gryllus bimaculatus ($2n\hat{\delta}=29$)(Azores population).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.48	-	A	4.79	0
2	2.74	-	A	4.33	0
3	2.89	-	A	4.11	0
4	3.02	-	A	3.93	0
5	3.07	1.89	ST	3.86	34.52
6	3.19	-	A	3.72	0
7	3.27	-	A	3.63	0
8	3.36	-	A	3.53	0
9	3.41	1.91	ST	3.48	34.31
10	3.49	-	A	3.40	0
11	3.58	2.31	ST	3.31	30.16
12	3.73	1.79	ST	3.18	35.65
13	3.94	-	A	3.01	0
14	4.18	2.54	ST	2.84	28.22
X	11.88	1.18	M		45.79
TCL	104.97				

Table VI Karyotype of Gryllus bermudensis ($2n\hat{\sigma}=29$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.65	-	A	7.55	0
2	2.97	1.62	SM	6.74	38.04
3	3.37	1.93	ST	5.94	34.12
4	3.53	-	A	5.67	0
5	3.69	1.85	ST	5.42	34.68
6	4.24	2.02	ST	4.72	33.01
7	4.30	2.09	ST	4.65	32.32
8	4.64	1.90	ST	4.31	34.48
9	4.78	2.09	ST	4.18	32.21
10	4.97	-	A	4.02	0
11	5.13	1.82	ST	3.90	35.28
12	5.30	1.62	SM	3.77	38.11
13	5.83	-	A	3.43	0
14	6.45	1.57	SM	3.10	38.75
X	20.02	1.16	M		46.20
TCL	145.44				

Table VII Karyotype of *Gryllus rubens* ($2n\delta=29$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.41	-	A	7.03	0
2	2.69	-	A	6.30	0
3	2.80	1.49	SM	6.05	40.00
4	2.97	1.67	SM	5.70	37.37
5	3.12	-	A	5.43	0
6	3.28	-	A	5.16	0
7	3.36	-	A	5.04	0
8	3.48	1.99	ST	4.87	33.33
9	3.76	-	A	4.50	0
10	3.89	1.66	SM	4.35	37.53
11	4.13	-	A	4.10	0
12	4.53	2.06	ST	3.74	32.67
13	5.02	1.43	SM	3.37	41.03
14	6.39	1.12	M	2.65	47.10
X	16.95	1.19	M		45.48
TCL	120.17				

Table VIII Karyotype of Gryllus campestris ($2n\delta=29$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.41	-	A	6.35	0
2	2.63	-	A	5.82	0
3	2.84	-	A	5.39	0
4	3.08	-	A	4.97	0
5	3.24	-	A	4.72	0
6	3.51	-	A	4.36	0
7	3.62	-	A	4.23	0
8	3.69	2.06	ST	4.15	32.52
9	3.88	-	A	3.94	0
10	3.97	2.00	ST	3.85	33.24
11	4.17	1.90	ST	3.67	34.53
12	4.43	-	A	3.45	0
13	4.75	1.68	SM	3.22	37.26
14	5.80	1.19	M	2.64	45.51
X	15.32	1.10	M		47.58
TCL	119.33				

Table IX Frequency of chromosomal abnormalities of Gryllus campestris.

types \ stages	% abnormalities				
	PI	MI	AI	TI	MII
c-mitosis	-	60.60	-	-	76.20
polyploidy	26.12	-	-	-	-
chromosomal breaks	15.18	25.80	21.62	-	-
stickiness	48.14	52.55	-	-	-
clumping	-	15.07	-	-	12.43
non-disjunction	-	5.53	-	-	-
lagging	-	-	24.86	41.66	-
bridges	-	-	8.10	-	-
unequal segregation	-	-	11.35	8.33	-

PI : Prophase I
MI : Metaphase I
AI : Anaphase I
TI : Telophase I
MII : Metaphase II

Table X Karyotype of *Acheta domesticus* ($2n\hat{\sigma}=21$)

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.00	-	A	6.32	0
2	3.29	-	A	5.76	0
3	3.50	2.15	ST	5.42	31.71
4	3.65	-	A	5.19	0
5	4.19	-	A	4.52	0
6	4.90	1.45	SM	3.87	40.81
7	5.17	1.13	M	3.60	46.80
8	5.59	1.31	SM	3.39	43.11
9	6.11	1.26	M	3.10	44.11
10	6.45	1.17	M	2.94	45.89
X	18.97	1.16	M		46.23
TCL	110.84				

Table XI Karyotype of *Gryllodes sigillatus* ($2n\delta=21$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.08	-	A	5.71	0
2	3.54	-	A	4.96	0
3	3.57	1.79	ST	4.92	40.05
4	3.64	2.08	ST	4.83	32.41
5	3.96	-	A	4.44	0
6	4.07	2.86	ST	4.32	25.79
7	4.37	2.99	ST	4.02	24.94
8	4.64	-	A	3.79	0
9	5.03	4.03	ST	3.49	19.88
10	5.67	-	A	3.10	0
X	17.59	1.15	M		46.33
TCL	100.56				

Table XII Karyotype of *Scapsipedus marginatus* (2n♂=21).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.90	-	A	4.58	0
2	4.38	3.03	ST	4.08	24.65
3	4.75	-	A	3.76	0
4	5.20	-	A	3.44	0
5	5.51	1.71	ST	3.24	36.84
6	5.72	1.66	SM	3.12	37.58
7	6.36	1.30	M	2.81	43.39
8	6.82	1.31	SM	2.62	43.25
9	7.33	1.26	M	2.44	44.20
10	8.14	1.20	M	2.19	45.45
X	17.89	1.12	M		47.12
TCL	134.92				

Table XIII Karyotype of Melanogryllus desertus ($2n\delta=21$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	4.14	-	A	4.10	0
2	4.69	-	A	3.62	0
3	5.11	1.81	ST	3.32	35.42
4	5.70	1.49	SM	2.98	40.00
5	6.38	1.62	SM	2.66	38.08
6	6.58	-	A	2.58	0
7	7.03	1.37	SM	2.41	42.10
8	7.30	1.34	SM	2.32	42.60
9	8.01	1.46	SM	2.12	40.57
10	8.99	1.18	M	1.89	45.71
X	17.00	1.15	M		46.35
TCL	145.10				

Table XIV Karyotype of *Tartarogryllus burdigalensis* ($2n\delta=19$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.48	-	A	5.40	0
2	3.96	2.75	ST	4.75	26.51
3	4.24	-	A	4.43	0
4	4.56	3.07	ST	4.12	24.56
5	5.21	2.58	ST	3.61	27.83
6	5.72	-	A	3.28	0
7	7.02	1.31	SM	2.67	43.16
8	7.85	1.29	M	2.39	43.56
9	10.94	1.09	M	1.71	47.80
X	18.81	1.12	M		47.10
TCL	124.92				

Table XV Karyotype of Neonemobius palustris ($2n\delta=19$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.95	-	A	4.01	0
2	4.12	-	A	3.85	0
3	4.40	-	A	3.60	0
4	4.64	-	A	3.42	0
5	4.93	-	A	3.21	0
6	5.20	-	A	3.05	0
7	5.42	-	A	2.92	0
8	5.92	-	A	2.68	0
9	6.96	-	A	2.28	0
X	15.87	1.10	M		47.58
TCL	97.92				

Table XVI Karyotype of Neonemobius sp. near mormonius ($2n\delta=19$).

chronosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	2.77	-	A	5.90	0
2	3.46	-	A	4.72	0
3	3.96	-	A	4.13	0
4	4.12	-	A	3.97	0
5	4.45	-	A	3.67	0
6	4.96	-	A	3.29	0
7	5.18	-	A	3.15	0
8	5.46	4.99	ST	2.99	16.66
9	12.44	1.09	M	1.31	47.74
X	16.36	1.13	M		46.94
TCL	120.76				

Table XVII Karyotype of Allonemobius fasciatus ($2n\delta=15$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.14	-	A	4.52	0
2	3.16	-	A	4.50	0
3	4.32	-	A	3.29	0
4	4.52	-	A	3.14	0
5	4.93	-	A	2.88	0
6	6.00	-	A	2.37	0
7	6.44	-	A	2.20	0
X	14.22	1.07	M		48.28
TCL	73.42				

Table XVIII Karyotype of Allonemobius allardi ($2n\delta=15$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.16	-	A	4.74	0
2	3.57	-	A	4.20	0
3	3.76	-	A	3.98	0
4	4.12	-	A	3.64	0
5	4.57	-	A	3.28	0
6	6.04	-	A	2.48	0
7	6.42	-	A	2.33	0
X	15.00	1.16	M		46.15
TCL	74.40				

Table XIX Karyotype of Allonemobius griseus ($2n\delta=15$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	3.55	-	A	4.39	0
2	4.05	-	A	3.85	0
3	4.74	-	A	3.29	0
4	5.10	-	A	3.05	0
5	5.65	-	A	2.76	0
6	7.91	7.05	A	1.97	12.38
7	8.01	7.57	A	1.94	11.61
X	15.60	1.09	M		47.94
TCL	93.80				

Table XX Karyotype of Eunemobius carolinus carolinus ($2n\hat{\delta}=7$).

chromosome number	length in μ	arm ratio	chromosome designation	X/A	centromeric index
1	10.67	1.15	M	1.26	47.70
2	12.27	1.24	M	1.10	44.58
3	13.84	1.10	M	0.97	47.54
X	13.52	1.41	SM		41.42
TCL	89.21				

Table XXI The percentage chiasma frequency of Gryllidae (scored at diplotene).

Species	% chiasma frequency								
	7Xta	6Xta	5Xta	4Xta	3Xta	2Xta	1Xta	Xta/cell	Xta/bivalent
Gryllus veletis	-	-	-	-	5.52	30.62	63.96	21.37	1.42
G. pennsylvanicus	-	-	-	-	10.25	46.50	43.25	27.20	1.70
G. assimilis (Antigua population)	-	-	-	-	10.97	36.87	52.16	24.46	1.63
G. assimilis (Jamaica population)	-	-	-	-	10.85	38.37	50.78	24.78	1.65
G. bimaculatus (Azores population)	-	-	-	-	6.94	37.10	55.44	22.59	1.50
G. bermudensis	-	-	-	1.95	11.19	42.39	44.47	25.60	1.68
G. rubens	-	-	-	0.44	6.00	38.22	55.33	23.23	1.55
Acheta domesticus	-	-	1.06	5.56	20.44	45.50	27.44	20.95	2.09
Gryllodes sigillatus	-	-	-	0.82	10.05	46.13	43.00	18.63	1.68

Table XXI - continued.

Species	% chiasma frequency								
	7Xta	6Xta	5Xta	4Xta	3Xta	2Xta	1Xta	Xta/cell	Xta/bivalent
Scapsipedus marginatus	-	-	1.09	5.39	21.37	45.79	26.36	23.25	2.10
Tartarogryllus burdigalensis	-	0.31	1.74	5.37	15.95	46.98	29.75	19.40	2.15
Neonemobius palustris	-	-	-	-	0.33	42.86	56.81	14.35	1.43
N. sp. near mormonius	-	-	2.00	6.00	4.00	32.00	56.00	16.60	1.66
Allonemobius fasciatus	-	-	-	0.25	2.87	41.26	55.62	11.82	1.47
A. allardi	-	-	-	0.18	2.25	37.76	59.81	11.42	1.42
A. g. griseus	-	-	-	3.38	16.30	34.44	45.88	13.07	1.63
Eunemobius c. carolinus	2.90	10.94	25.14	29.02	20.00	12.00	-	12.17	3.04

Table XXII The percentage frequency of the ring-formed chromosomes of Gryllidae (scored at diakinesis).

Species	number of ring-formed chromosomes						
	0	1	2	3	4	5	6
Gryllus veletis	-	13.00 ±2.17	34.00 ±2.27	34.50 ±2.09	15.50 ±2.17	2.50 ±0.25	-
G. pennsylvanicus	27.70 ±0.96	42.00 ±0.76	26.32 ±1.05	2.40 ±0.47	-	-	-
G. assimilis (Antigua population)	30.30 ±2.41	46.60 ±2.11	21.50 ±1.47	1.50 ±0.50	-	-	-
G. assimilis (Jamaica population)	27.50 ±1.03	47.32 ±0.97	22.50 ±0.92	2.66 ±0.35	-	-	-
G. bimaculatus (Azores population)	11.75 ±1.09	38.50 ±2.07	33.87 ±1.49	12.75 ±1.27	1.87 ±0.51	-	-
G. bermudensis	20.33 ±1.94	44.50 ±3.04	26.08 ±2.43	7.41 ±1.42	1.33 ±0.39	0.33 ±0.14	-
G. rubens	24.50 ±1.03	47.32 ±0.97	22.50 ±0.92	4.00 ±0.35	1.00 ±0.19	-	-
G. campestris	20.68 ±1.10	54.31 ±0.78	21.55 ±1.02	3.44 ±0.56	-	-	-
Acheta domesticus	11.50 ±0.84	35.80 ±0.66	38.20 ±1.06	12.60 ±0.68	1.30 ±0.36	0.30 ±0.21	-

Table XXII - continued.

Species	number of ring-formed chromosomes						
	0	1	2	3	4	5	6
Gryllodes sigillatus	27.14 ±1.05	44.29 ±0.79	24.29 ±0.91	4.29 ±0.44	-	-	-
Scapsipedus marginatus	21.75 ±1.90	39.00 ±0.87	27.75 ±1.16	9.16 ±1.11	1.91 ±0.57	0.41 ±0.14	-
Tartarogryllus burdigalensis	-	-	12.37 ±0.82	40.37 ±1.33	32.62 ±1.37	13.25 ±0.97	1.25 ±0.36
Neonemobius palustris	49.83 ±4.48	43.83 ±2.78	6.08 ±1.84	0.26 ±0.18	-	-	-
N. sp. near mormonius	-	-	38.80 ±0.78	33.40 ±0.42	27.78 ±0.54	-	-
Allonemobius fasciatus	4.16 ±0.78	21.00 ±2.91	29.32 ±2.25	26.00 ±1.83	14.66 ±2.43	3.98 ±1.36	-
A. allardi	-	25.40 ±1.77	47.00 ±0.99	24.40 ±1.31	3.20 ±0.49	-	-
A. g. griseus	4.54 ±0.42	38.72 ±1.21	40.90 ±1.39	15.44 ±0.91	0.36 ±0.18	-	-
Eunemobius c. carolinus	-	3.08 ±0.41	35.38 ±0.97	61.54 ±0.84	-	-	-

Table XXIII The percentage frequency of interstitial chiasmata and terminal chiasmata of Gryllidae (scored at metaphase I).

Species	Interstitial chiasmata		Terminal chiasmata	
Gryllus veletis	76.55	0.60	23.45	0.60
G. pennsylvanicus	86.93	1.55	13.07	1.55
G. assimilis (Antigua population)	89.44	0.37	10.56	0.37
G. assimilis (Jamaica population)	87.20	0.87	12.80	0.87
G. bimaculatus (Azores population)	69.34	1.06	30.66	1.06
G. bermudensis	88.25	0.50	11.75	0.50
G. rubens	90.40	1.00	9.60	1.00
G. campestris	79.93	0.14	20.07	0.14
Acheta domesticus	97.24	0.29	2.76	0.29
Gryllodes sigillatus	92.53	0.94	7.47	0.94
Scapsipedus marginatus	98.96	0.10	1.04	0.10
Tartarogryllus burdigalensis	97.32	0.39	2.68	0.39
Neonemobius palustris	96.32	0.52	3.68	0.52
N. sp. near mormonius	96.08	0.76	3.92	0.76
Allonemobius fasciatus	85.38	1.11	14.62	1.11
A. allardi	83.93	1.09	16.07	1.09
A. f. griseus	89.32	0.82	10.68	0.82
Eunemobius c. carolinus	100.00		0.00	

Table XXIV Number of species having the same chromosome number in Grylloidea*.

Groups \ 2N♂	7	9	11	13	14	15	17	18	19	20	21	23	25	27	29	31	Total
Gryllinae	-	-	5	2	-	2	3	-	6	-	15	1	5	7	13	1	60
Nemobiinae	3	-	3	-	-	9	6	-	5	-	1	-	-	-	-	-	27
Mogoplistinae	-	-	1	-	1	-	-	-	2	-	-	-	-	-	-	-	4
Eneopterinae	-	1	2	2	-	1	1	-	4	-	-	-	-	-	-	-	11
Trigonidiinae	-	-	2	-	-	4	-	-	2	-	-	-	-	-	-	-	8
Phalangopsinae	-	-	1	-	-	-	-	-	2	-	1	-	-	-	-	-	4
Scleropterinae	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Oecanthidae	-	-	-	-	-	-	-	1	4	1	-	-	-	-	-	-	6
Total	3	1	14	4	1	17	10	1	25	1	17	1	5	7	13	1	121

* From Makino (1951,1956), Ohmachi (1958), Randell and Kevan (1962), Bhattacharjee and Manna (1967), Leroy (1967), Lim (1971) and the present work.

Table XXV Frequency of abnormalities produced by different methods of administration of 0.5% caffeine in Gryllus bermudensis.

mode of administration	duration of treatment (days)	% abnormalities					
		breakage				stickiness	
		PI	MI	AI	TI	Dipl.	Diak.
Injection	1	6.79	4.92	11.30	10.00	92.59	11.19
Food	3	5.63	5.09	11.36	7.25	83.89	9.56
	10	15.90	10.10	29.07	19.00	98.08	20.27

PI : Prophase I
MI : Metaphase I
AI : Anaphase I
TI : Telophase I
Dipl. : Diplotene
Diak. : Diakinesis

Table XXVI Frequency of abnormalities produced by 0.5% caffeine administered by injection.

species	duration of treatment (hours)	% abnormalities							
		breakage				stickiness		bridges	c-mitosis
		PI	MI	AI	TI	Dipl.	Diak.	AI	MI
Gryllus bermudensis	5	3.05	1.57	4.35	3.13	89.29	10.46	-	-
	24	6.74	4.92	11.30	10.00	92.59	11.19	-	-
Acheta domesticus	5	1.70	2.13	4.76	3.03	78.48	3.75	10.81	-
	24	2.50	3.15	11.11	6.77	89.34	15.91	62.86	-
Scapsipedus marginatus	5	2.54	2.76	8.70	10.46	66.67	8.39	3.60	23.08
	24	6.74	5.23	11.90	16.85	93.07	11.11	37.93	23.55

PI : Prophase I
MI : Metaphase I
AI : Anaphase I
TI : Telophase I
Dipl. : Diplotene
Diak. : Diakinesis

Table XXVII Frequency of abnormalities produced by 0.05% colcemid after 20 hours of treatment.

Species	% abnormalities					
	breakage				stickiness	lagging
	PI	MI	AI	TI	PI	AI
Gryllus assimilis	2.99	2.52	2.74	2.99	42.70	-
G. pennsylvanicus	3.88	5.95	14.81	13.25	69.01	9.28

PI : Prophase I
MI : Metaphase I
AI : Anaphase I
TI : Telophase I

Table XXVIII Frequency of chromosomal abnormalities produced by 1% cupferron in Gryllus burmudensis.

Duration of treatment	% abnormalities						
	breakage				bridges	stickiness	
	PI	MI	AI	TI	AI	Dipl.	Diak.
3 days	13.71	4.43	11.86	5.5[illegible]	6.78	83.27	10.02
10 days	20.40	13.48	22.05	17.65	10.21	96.86	17.66

PI : Prophase I
MI : Metaphase I
AI : Anaphase I
TI : Telophase I
Dipl. : Diplotene
Diak. : Diakinesis

Table XXIX Frequency of chromosomal abnormalities produced by 0.05% phenol after 12 hours of treatment in Gryllus bimaculatus.

Stages \ Types	% abnormalities				
	breaks	lagging	bridges	polyploidy	stickiness
prophase I	4.63	-	-	-	28.20
metaphase I	5.29	-	-	-	15.36
anaphase I	9.76	1.22	7.32	-	16.13
telophase I	7.41	-	-	-	-
prophase II	3.57	-	-	-	37.50
metaphase II	1.30	-	-	0.87	20.11
anaphase II	4.35	-	-	-	7.69
telophase II	-	-	-	-	-
interkinesis	-	4.65	-	-	-

Table XXX Frequency of chromosomal abnormalities produced by 0.1% phenol after 12 hours of treatment in Gryllus bimaculatus.

Stages \ Types	% abnormalities				
	breaks	lagging	bridges	polyploidy	stickiness
prophase I	10.36	-	-	-	55.31
metaphase I	5.98	-	-	-	26.71
anaphase I	18.94	2.27	5.30	-	20.83
telophase I	18.18	-	-	-	-
prophase II	15.29	-	-	5.88	52.69
metaphase II	4.04	-	-	2.02	20.85
anaphase II	7.97	2.79	7.97	3.98	12.27
telophase II	15.91	13.64	-	-	-
interkinesis	-	25.37	-	-	-

Table XXXI Frequency of chromosomal abnormalities produced by 0.05% phenol after 24 hours of treatment in Gryllus bimaculatus.

Stages \ Types	% abnormalities					
	breaks	lagging	bridges	polyploidy	stickiness	c-mitosis
prophase I	8.93	-	-	-	60.07	-
metaphase I	7.25	-	-	0.14	22.39	-
anaphase I	17.42	5.16	10.97	-	24.05	-
telophase I	14.55	14.55	7.27	-	-	-
prophase II	16.93	-	-	2.12	55.87	-
metaphase II	5.13	-	-	-	28.25	1.92
anaphase II	9.38	-	-	-	20.00	-
telophase II	6.45	9.68	3.23	-	-	-
interkinesis	-	25.23	-	-	-	-

Table XXXII Frequency of chromosomal abnormalities produced by 0.1% phenol after 24 hours of treatment in Gryllus bimaculatus.

Stages \ Types	% abnormalities					
	breaks	lagging	bridges	polyploidy	tickiness	c-mitosis
prophase I	9.56	-	-	-	62.08	-
metaphase I	7.76	-	-	0.12	27.35	-
anaphase I	27.87	14.08	12.68	-	39.02	-
telophase I	22.58	22.58	3.23	-	-	-
prophase II	26.67	-	-	-	63.64	-
metaphase II	5.88	-	-	3.53	29.17	2.35
anaphase II	12.82	-	2.56	-	22.58	-
telophase II	16.67	8.33	-	-	-	-
interkinesis	-	36.96	-	-	-	-

Table XXXIII Frequency of chromosomal abnormalities produced by 0.05% phenol after 72 hours of treatment in Gryllus bimaculatus.

Stages \ Types	% abnormalities				
	breaks	lagging	bridges	polyploidy	stickiness
prophase I	12.69	-	-	-	49.56
metaphase I	8.34	-	-	0.10	28.83
anaphase I	20.00	3.41	3.90	-	16.67
telophase I	9.46	21.79	-	-	-
prophase II	27.03	-	-	-	61.29
metaphase II	5.80	-	-	0.89	30.21
anaphase II	11.11	4.04	1.01	-	26.92
telophase II	7.58	4.55	-	-	-
interkinesis	-	38.71	-	-	-

Table XXXIV Frequency of chromosomal abnormalities produced by 0.1% phenol after 72 hours of treatment in Gryllus bimaculatus.

Stages \ Types	% abnormalities						
	breaks	lagging	bridges	polyploidy	stickiness	non-disjunction	abnormal segregation
prophase I	22.09	-	-	1.84	63.30	-	-
metaphase I	32.58	-	-	-	29.28	5.88	-
anaphase I	28.79	27.27	10.61	-	39.58	-	7.58
telophase I	46.67	20.00	13.33	-	-	-	-
prophase II	28.30	-	-	0.63	65.13	-	-
metaphase II	9.56	-	-	1.17	39.35	-	-
anaphase II	15.19	8.86	2.53	2.53	30.36	-	5.06
telophase II	14.71	5.88	-	-	-	-	-
interkinesis	-	54.55	-	-	-	-	-

Table XXXV Mean frequency of chromosomal abnormalities produced by 0.05% and 0.1% phenol in Gryllus bimaculatus.

Types of abnormalities	conc.(%)	% frequency of abnormal cells at different fixation hours		
		12	24	72
breaks	0.05	5.16	10.75	12.75
	0.10	12.08	16.22	24.73
lagging	0.05	2.93	13.66	14.50
	0.10	11.01	20.48	23.31
bridges	0.05	7.32	7.15	2.45
	0.10	6.63	6.15	8.82
polyploidy	0.05	0.87	1.13	0.49
	0.10	3.96	1.82	1.54
stickiness	0.05	20.83	35.10	35.58
	0.10	31.44	40.63	44.50
non-disjunction	0.05	-	-	-
	0.10	-	-	5.88
abnormal segregation	0.05	-	-	-
	0.10	-	-	6.32
c-mitosis	0.05	-	1.92	-
	0.10	-	2.35	-

Table XXXVI Frequency of chromosomal aberrations produced by different chemicals in Gryllidae.

Chemicals	% chromosomal aberrations							
	breaks	stickiness	lagging	bridges	c-mitosis	polyploidy	non-disjunction	abnormal segregation
Colchicine	8.16	83.80	-	-	-	3.15	-	-
Colcemid	6.14	52.99	4.64	-	-	1.02	-	-
Caffeine	12.92	84.90	-	28.80	23.31	-	-	-
Cupferron	13.64	90.06	-	8.49	-	-	-	-
Ethyl acetate	7.69	93.16	-	-	-	-	-	-
Glacial acetic acid	6.16	94.59	-	-	-	-	-	-
Phenol	13.61	34.68	14.31	6.42	2.13	1.63	2.94	3.16

Table XXXVII Dosage-mortality relationship produced by gamma rays.

Species	Dosage	% survival					
		10D	15D	20D	25D	30D	35D
Gryllus assimilis	1467r	100	100	67	67	30	0
	1630r	100	100	100	50	0	
	1848r	100	100	50	25	0	
	2174r	100	50	25	0		
	2283r	100	50	25	0		
	2446r	100	50	25	0		
G. pennsylvanicus	1630r	100	50	0			
	2174r	100	50	0			
G. bimaculatus	2174r	34	34	0			
Acheta domesticus	1467r	100	100	100	67	30	0
	1630r	100	100	100	67	0	
	2174r	100	100	100	50	0	
	2446r	100	100	50	0		
Scapsipedus marginatus	1630r	100	100	100	67	0	
	2174r	100	100	67	50	0	
Allonemobius allardi	1087r	100	100	100	100	50	0

D : days

Table XXXVIII Dosage-duration-frequency relationship of the fragmentation produced by gamma rays in Gryllus assimilis.

dose	duration of treatment	% fragmentation			
		PI	MI	AI	TI
1467 r	48 hours	25.30	40.69	96.23	97.06
1630 r	24 hours	30.07	31.78	96.69	98.27
	48 hours	31.40	39.83	97.06	97.30
	67 hours	52.29	54.98	100.00	100.00
	80 hours	71.11	65.11	100.00	100.00
	96 hours	78.22	84.14	100.00	100.00
	10 days	94.78	93.02	100.00	100.00
1848 r	24 hours	26.34	20.44	96.96	95.60
	48 hours	39.02	34.92	97.37	98.90
	67 hours	76.40	58.94	100.00	100.00
	96 hours	86.22	79.93	100.00	100.00
2283 r	24 hours	45.79	54.56	100.00	100.00
	96 hours	88.78	93.07	100.00	100.00
2446 r	48 hours	58.93	62.92	100.00	100.00

PI : Prophase I
MI : Metaphase I
AI : Anaphase I
TI : Telophase I

Table XXXIX Frequency of fragmentation produced by gamma rays in Gryllidae.

Species	Dose	duration of treatment	% fragmentation			
			PI	II	AI	TI
Gryllus assimilis	2174 r	67 hours	37.89	46.72	98.27	98.74
G. bimaculatus	2174 r	67 hours	33.23	43.37	71.43	82.30
G. pennsylvanicus	2174 r	67 hours	34.00	37.92	89.24	94.30
Acheta domesticus	2174 r	67 hours	54.48	64.67	100.00	100.00
Scapsipedus marginatus	2174 r	67 hours	53.62	73.91	70.35	78.67
Allonemobius allardi	1087 r	67 hours	48.88	65.23	100.00	100.00

Fig. 1 Idiogram of *Gryllus veletis*.

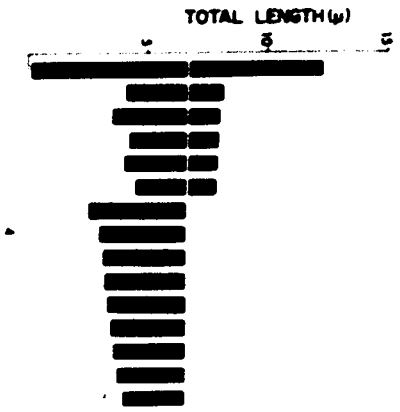
Fig. 2 Idiogram of *Gryllus pennsylvanicus*.

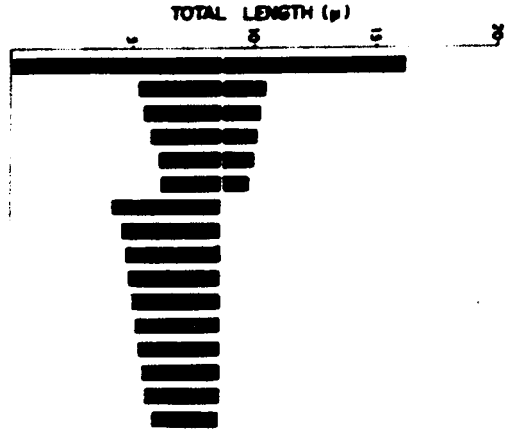
Fig. 3 Idiogram of *Gryllus assimilis*.

Fig. 4 Idiogram of *Gryllus bimaculatus*.

Fig. 5 Idiogram of *Gryllus bermudensis*.

Fig. 6 Idiogram of *Gryllus rubens*.


TOTAL LENGTH (μ)
5
10
15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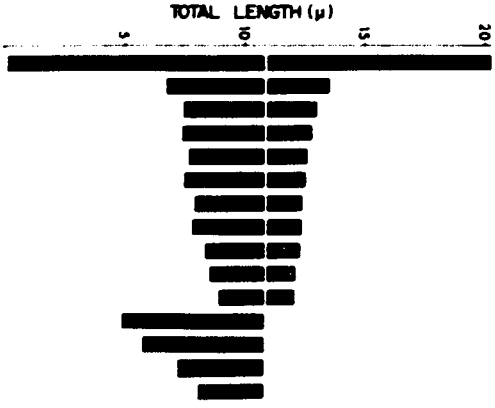
15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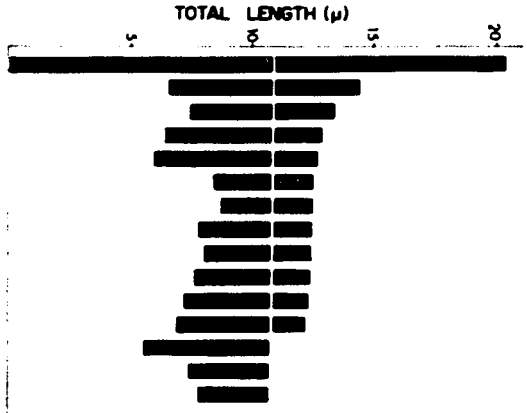
TOTAL LENGTH (μ)
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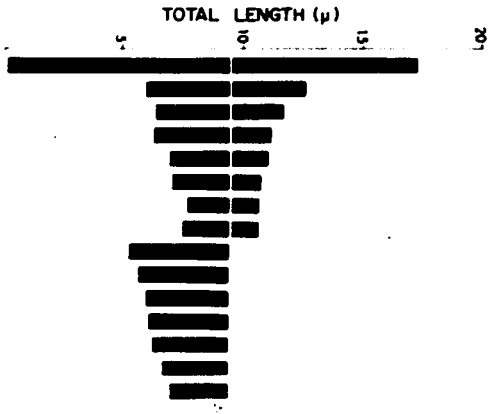
10
15
20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15
20

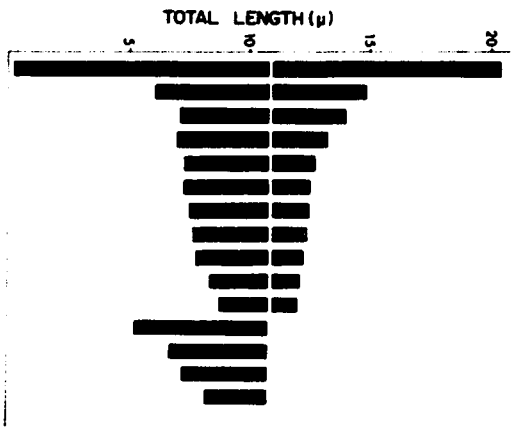

TOTAL LENGTH (μ)
5
10
15
20

Fig. 7 Idiogram of *Gryllus campestris*.

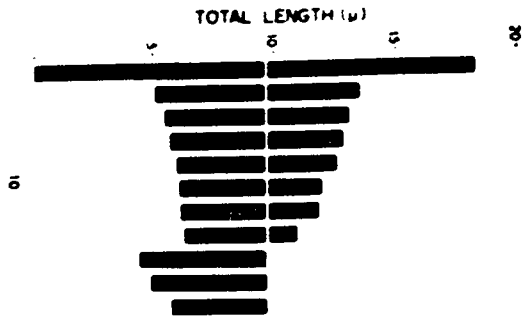
Fig. 8 Idiogram of *Acheta domesticus*.

Fig. 9 Idiogram of *Gryllodes sigillatus*.

Fig.10 Idiogram of *Scapsipedus marginatus*.

Fig.11 Idiogram of *Melanogryllus desertus*.

Fig.12 Idiogram of *Tartarogryllus burdigalensis*.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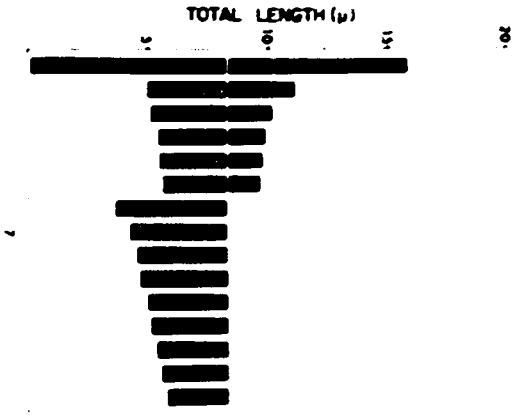
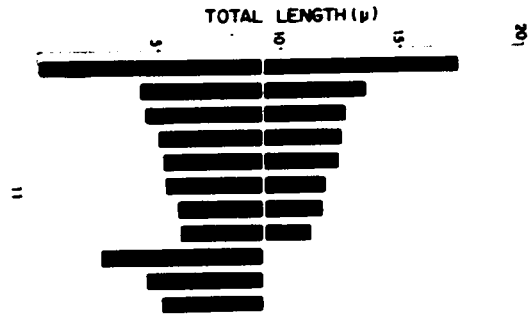

TOTAL LENGTH (μ)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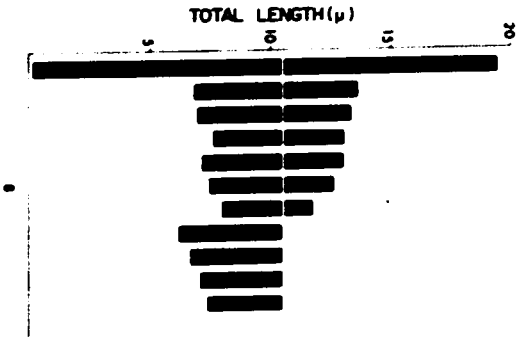
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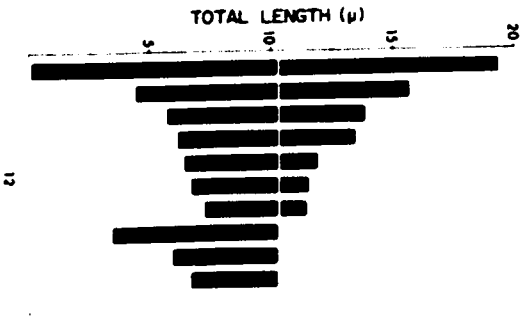
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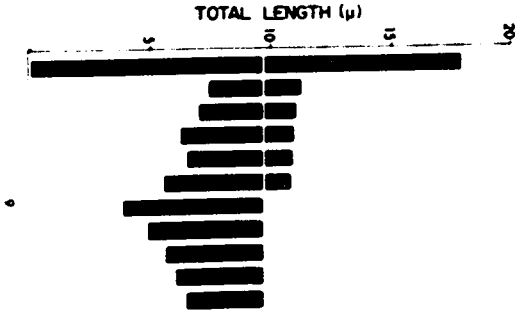

TOTAL LENGTH (μ)

Fig.13 Idiogram of Neonemobius palustris.

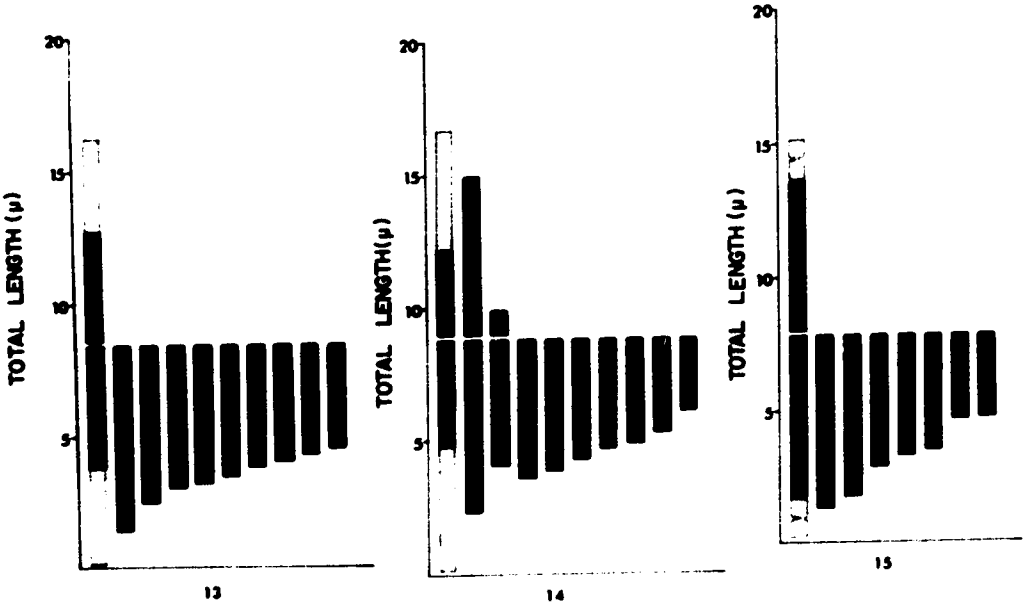
Fig.14 Idiogram of Neonemobius sp. near mormonius.

Fig.15 Idiogram of Allonemobius fasciatus.

Fig.16 Idiogram of Allonemobius allardi.

Fig.17 Idiogram of Allonemobius griseus griseus.

Fig.18 Idiogram of Eunemobius carolinus carolinus.


TOTAL LENGTH (μ)
20
15
10
5
13
TOTAL LENGTH(μ)
14
TOTAL LENGTH (μ)
15

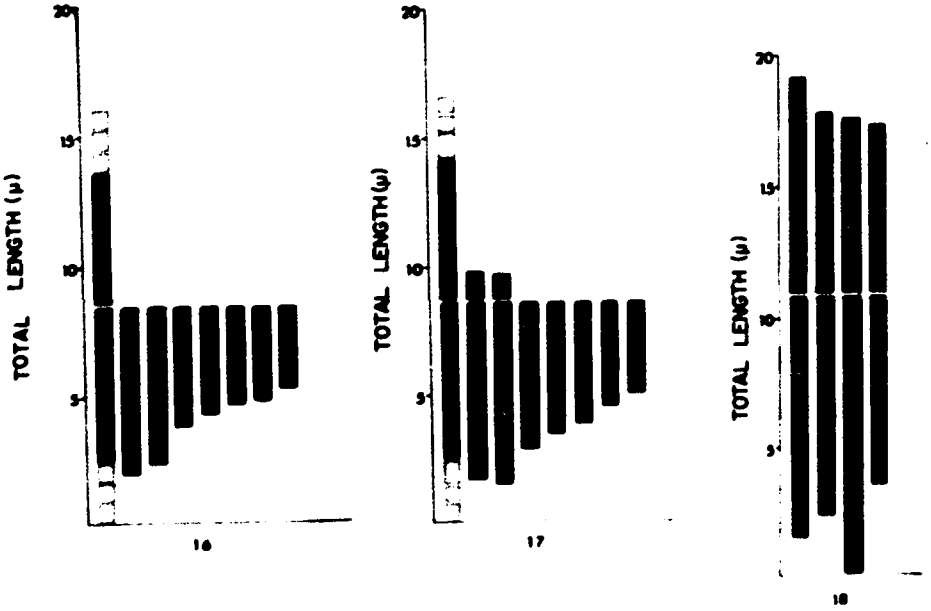

TOTAL LENGTH (μ)
16
TOTAL LENGTH(μ)
17
TOTAL LENGTH (μ)
18

Fig. 19 Comparison of karyotypes of grylloid species: (a) G. veletis; (b) G. pennsylvanicus; (c) G. assimilis (Antigua population); (d) G. bimaculatus (Azores population); (e) G. bermudensis; (f) G. rubens; (g) G. campestris; (h) A. domesticus; (i) G. sigillatus; (j) S. marginatus; (k) M. desertus; (l) T. burdigalensis; (m) N. palustris; (n) M. sp. near mormonius; (o) A. fasciatus; (p) A. allardi; (q) A. g. griseus; (r) E. c. carolinus.

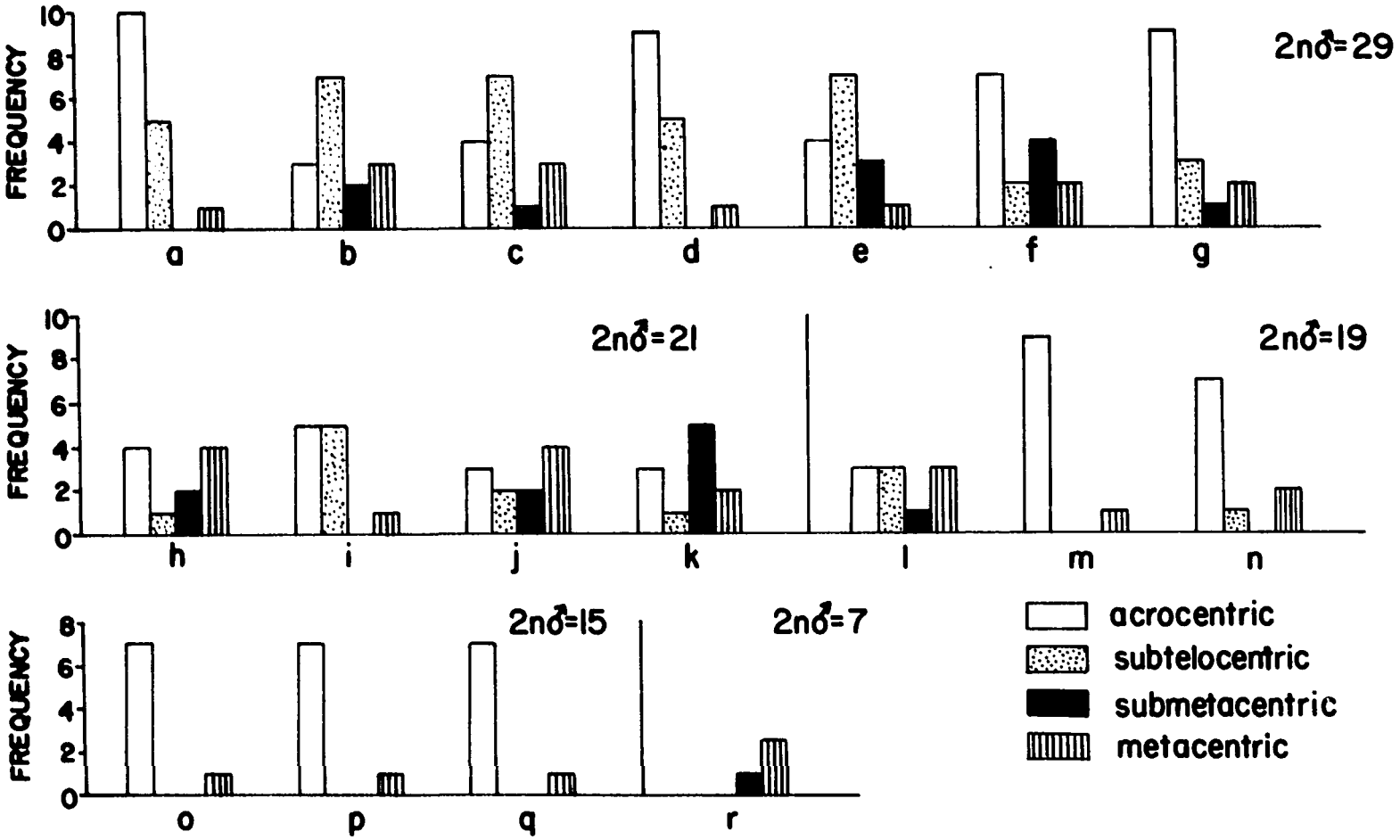

FREQUENCY
2nδ=29
a
b
c
d
e
f
g
2nδ=21
2nδ=19
h
i
j
k
l
m
n
2nδ=15
2nδ=7
o
p
q
r
acrocentric
subtelocentric
submetacentric
metacentric

Fig. 19

All the figures are 1000X, unless stated otherwise.

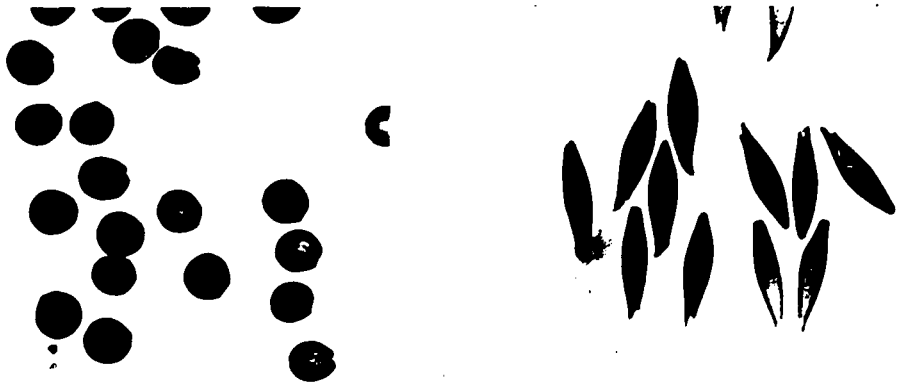
Fig. 20 Spermatids of Gryllinae.
a. early stage
b. later stage

Fig. 21 Karyotype of *Gryllus veletis*.

Fig. 22 Metaphase I of *Gryllus veletis*, a single supernumerary chromosome at the same pole as the X chromosome.

Fig. 23 Metaphase I of *G. veletis*, a single supernumerary chromosome at the opposite pole to the X chromosome.

Fig. 24 Metaphase I of *G. veletis*, a single supernumerary remaining at the equatorial plate.



a b

Fig. 20

Fig. 21

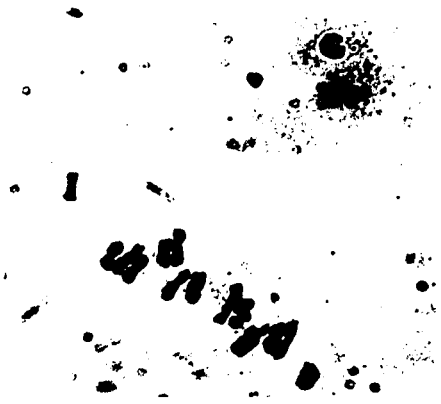


Fig. 22

Fig. 23

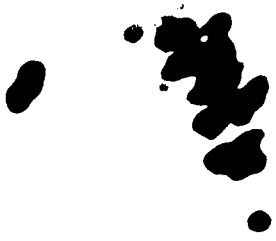
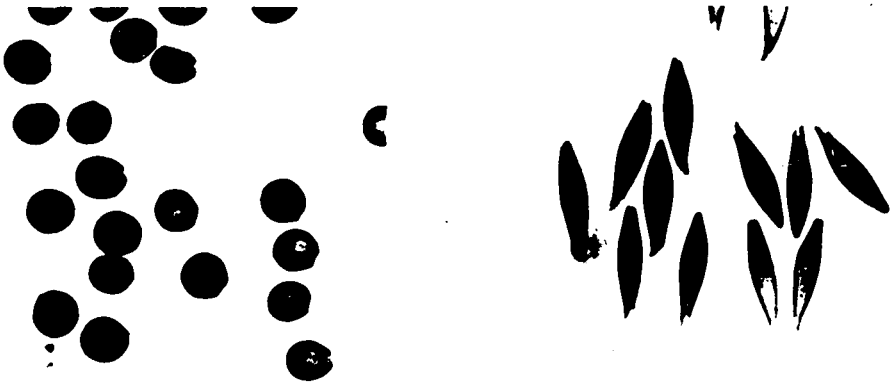


Fig. 24



a b

Fig. 20

Fig. 21

Fig. 22

Fig. 23

Fig. 24

Fig. 25 Metaphase I of G. veletis, two supernumerary chromosomes at the same pole as the X chromosome.

Fig. 26 Metaphase I of G. veletis, showing two supernumerary chromosomes, one at the opposite pole and one at the same pole to the X chromosome.

Fig. 27 a. Mitotic metaphase of G. veletis ($2n\delta=29$).
b. Diakinesis of G. veletis, showing 15 chromosomes.

Fig. 28 a. Anaphase I of G. veletis, two supernumerary chromosomes moved to opposite pole.
b. Late anaphase I of G. veletis, showing one supernumerary chromosome lagged behind on equator area.

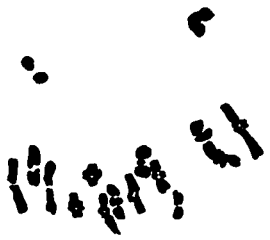
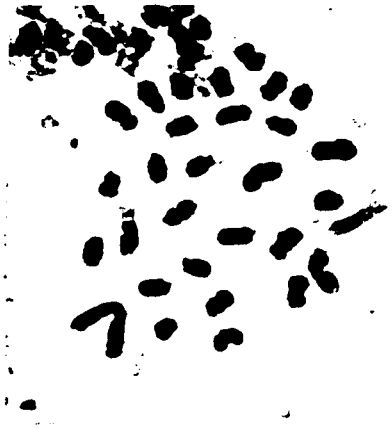


Fig. 25

Fig. 26



a

b

Fig. 27

a

b

Fig. 28

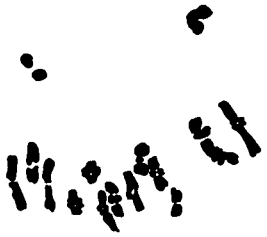


Fig. 25

Fig. 26

a

b

Fig. 27

a

b

Fig. 28

Fig. 29 Interkinesis of G. veletis, supernumerary chromosome formed a small vesicle (arrow) apart from the dividing nucleus.

Fig. 30 Polyploid cell of G. veletis (800X).

Fig. 31 Anaphase I of G. veletis, showing a sticky bridge.

Fig. 32 Metaphase I of G. veletis, all of the chromosomes are homomorphic.

Fig. 33 Karyotype of Gryllus pennsylvanicus.

Fig. 34 Early meiotic prophase of G. pennsylvanicus, all of the chromosomes are connected to each other and closely associated with the nucleolus.

Fig. 29

Fig. 30

Fig. 31

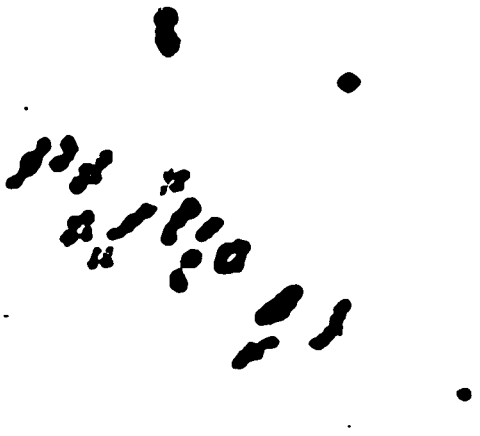


Fig. 32

Fig. 33

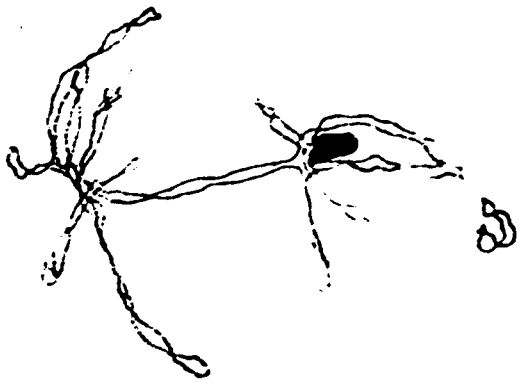


Fig. 34

Fig. 29

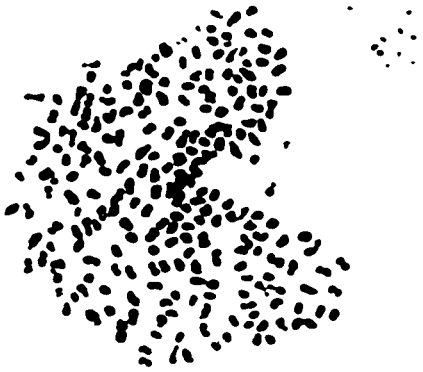


Fig. 30

Fig. 31

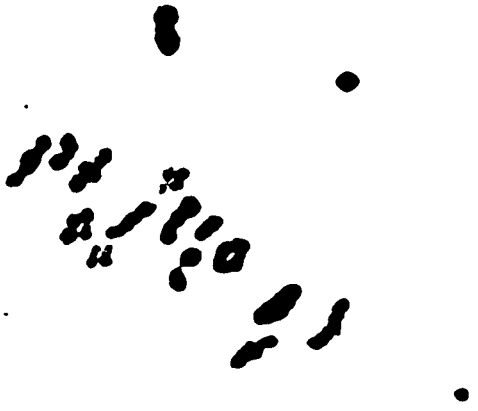


Fig. 32

Fig. 33

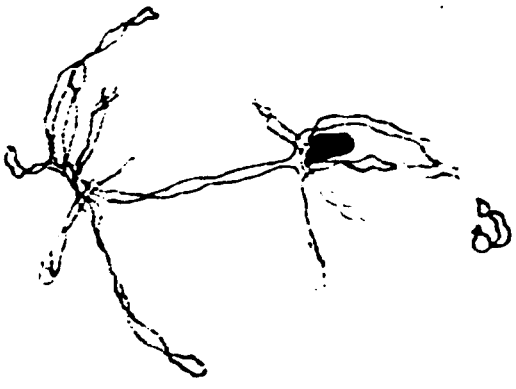


Fig. 34

Fig. 35 Metaphase I of G. pennsylvanicus, showing a single unequal bivalent.

Fig. 36 Anaphase I of G. pennsylvanicus, showing a sticky bridge.

Fig. 37 Karyotype of Gryllus assimilis (Antigua population).

Fig. 38 Spermatids of G. assimilis (Antigua population)
a. Early stage
b. Later stage

Fig. 39 Early mature sperms of G. assimilis (Antigua population).

Fig. 35

Fig. 36

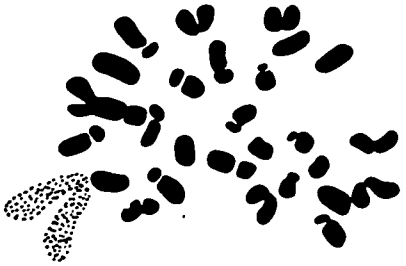


Fig. 37

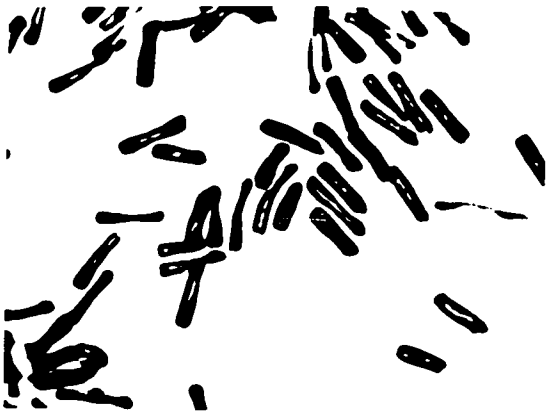


Fig. 39

a b

Fig. 38

Fig. 35

Fig. 36

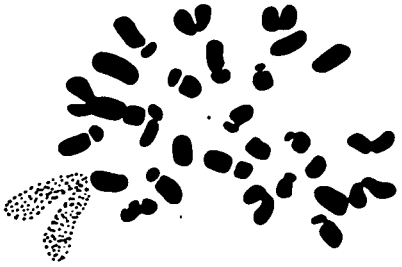


Fig. 37

Fig. 39

a b

Fig. 38

Fig. 40 Metaphase I of G. assimilis (Antigua population), the X chromosome appears as cross-shaped.

Fig. 41 Metaphase I of G. assimilis (Antigua population), all of the chromosomes are homomorphic.

Fig. 42 Metaphase I of G. assimilis (Jamaica population), all of the chromosomes are homomorphic.

Fig. 43 Karyotype of Gryllus bimaculatus (Azores population).

Fig. 44 Metaphase I of G. bimaculatus (Azores population), all of the chromosomes are homomorphic.

Fig. 45 Spermatids of G. bimaculatus (Azores population).

Fig. 40

Fig. 41

Fig. 42

Fig. 43

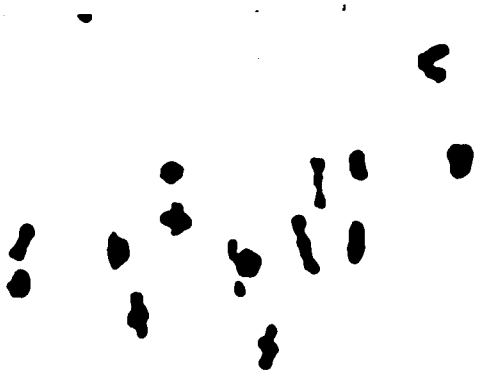


Fig. 44

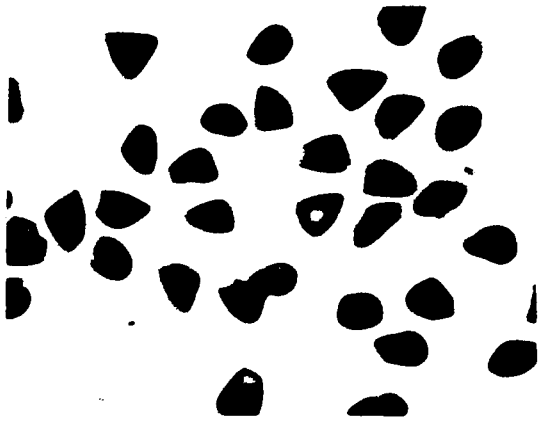


Fig. 45

Fig. 40

Fig. 41

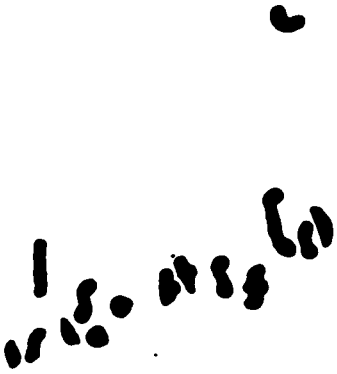


Fig. 42

Fig. 43

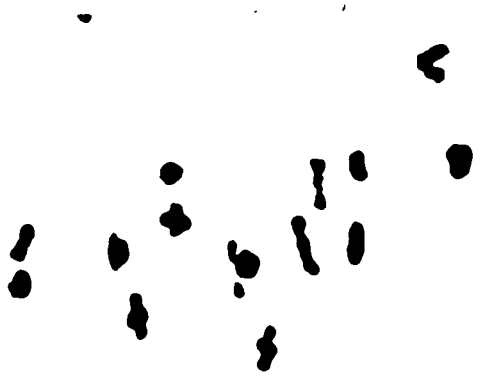


Fig. 44

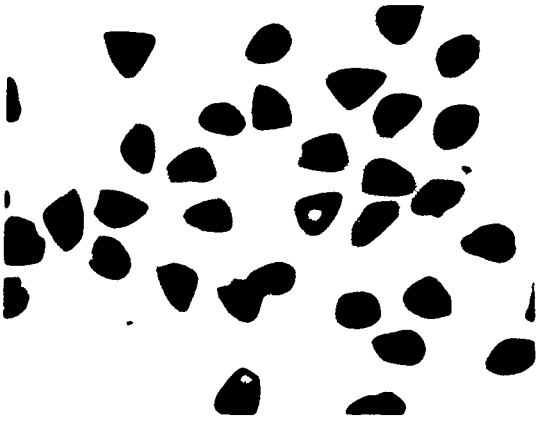


Fig. 45

Fig. 46 Spermatogonial metaphase of '*G. bimaculatus*' (Singapore population), most of the chromosomes are sticky connected together.

Fig. 47 Late anaphase I of '*G. bimaculatus*' (Singapore population), showing unequal segregation of the chromosomes.

Fig. 48 Metaphase-anaphase I of '*G. bimaculatus*' (Singapore population), showing numerous fragmentations.

Fig. 49 Polyploid cell of '*G. bimaculatus*' (Singapore population). (800X)

Fig. 50 Anaphase I of '*G. bimaculatus*' (Singapore population), showing chromosomal bridge.

Fig. 51 Telophase I of '*G. bimaculatus*' (Singapore population), chromosomal bridge occurs.

Fig. 46

Fig. 47

Fig. 48

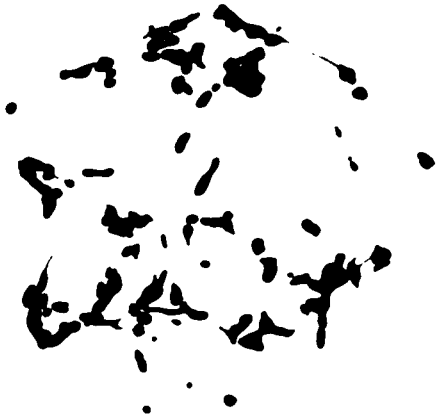


Fig. 49

Fig. 50

Fig. 51

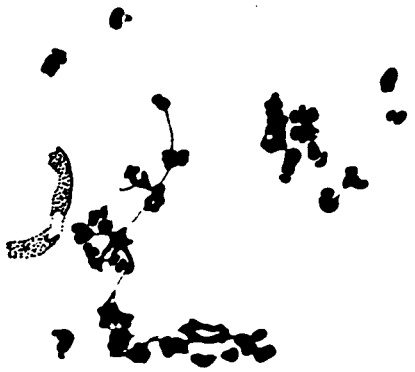


Fig. 46

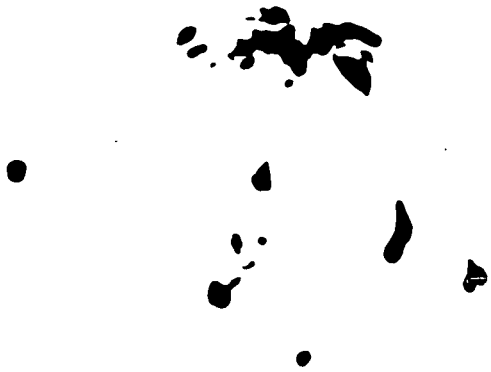


Fig. 47

Fig. 48

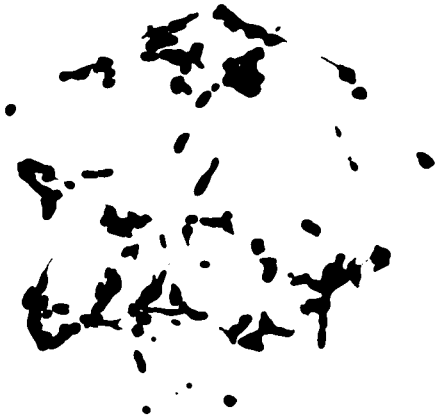


Fig. 49

Fig. 50

Fig. 51

Fig. 52 Multinuclei of '*G. bimaculatus*' (Singapore population) at interkinesis.

Fig. 53 Telophase I of '*G. bimaculatus*' (Singapore population), some chromosomes lagging behind.

Fig. 54 Metaphase I of '*G. bimaculatus*' (Singapore population), achromatic gap occurs.

Fig. 55 Karyotype of *Gryllus bermudensis*.

Fig. 56 Anaphase I of *G. bermudensis*, the X chromosome appears as cross-shaped and it moves to the pole more slowly than the autosomes.

Fig. 57 Metaphase I of *G. bermudensis*, all the chromosomes are homomorphic.

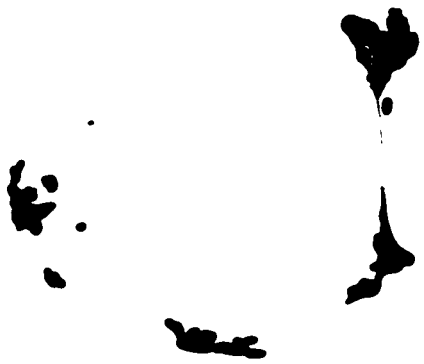


Fig. 52

Fig. 53

Fig. 54

Fig. 55

Fig. 56

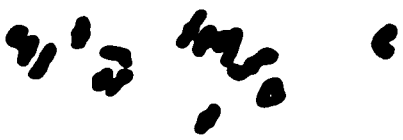


Fig. 57

Fig. 52

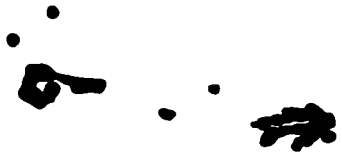


Fig. 53

Fig. 54

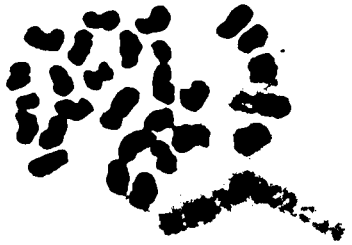


Fig. 55

Fig. 56

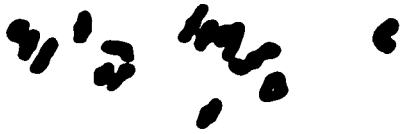


Fig. 57

Fig. 58 Polyploid cell of G. bermudensis (800X).

Fig. 59 Karyotype of Gryllus rubens.

Fig. 60 Metaphase I of G. rubens, showing stickiness bivalents.

Fig. 61 Metaphase I of G. rubens, a non-homologous association occur (arrow).

Fig. 62 Metaphase I of G. rubens, an unequal bivalent, achromatic gaps and chromosomal break (arrow) occur.

Fig. 63 Anaphase I of G. rubens, showing a sticky bridge.

Fig. 58

Fig. 59

Fig. 60

Fig. 61

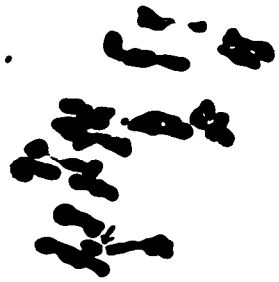


Fig. 62

Fig. 63

Fig. 58

Fig. 59

Fig. 60

Fig. 61

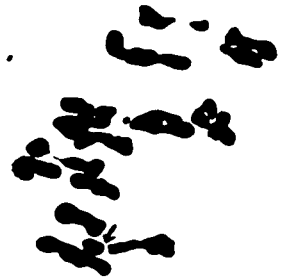


Fig. 62

Fig. 63

Fig. 64 Karyotype of Gryllus campestris.

Fig. 65 Metaphase I of G. campestris, showing chromosomal break.

Fig. 66 Anaphase I of G. campestris, a chromosomal bridge occurs.

Fig. 67 Late prophase I of G. campestris, showing the heavy stickiness chromosomes.

Fig. 68 Metaphase I of G. campestris, showing c-mitotic effect.

Fig. 69 Polyploid cells of G. campestris (400X).

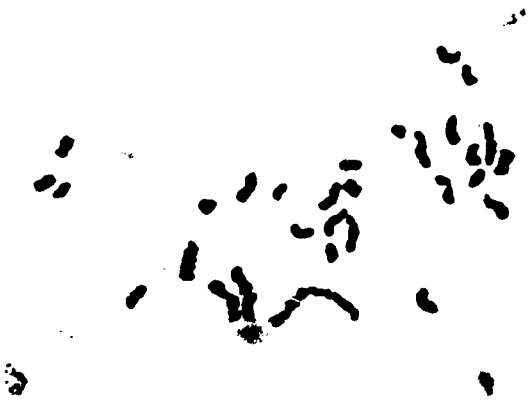


Fig. 64

Fig. 65

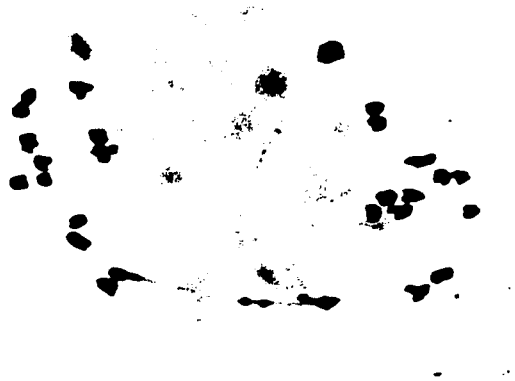


Fig. 66

Fig. 67

Fig. 68

Fig. 69

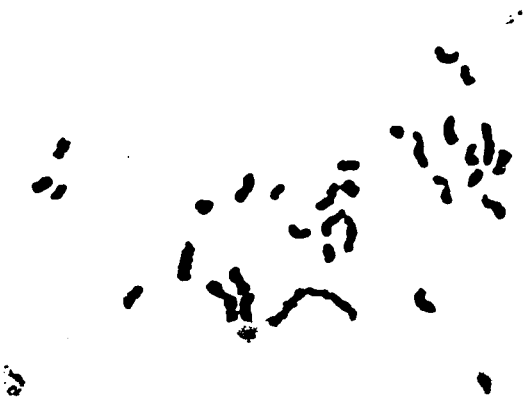


Fig. 64

Fig. 65

Fig. 66

Fig. 67

Fig. 68

Fig. 69

Fig. 70 Metaphase I of G. campestris, showing numerous univalents.

Fig. 71 Anaphase I of G. campestris, a few chromosomes lagging behind.

Fig. 72 Late metaphase I of G. campestris, showing non-disjunction effect.

Fig. 73 Late anaphase I of G. campestris, unequal segregation occur.

Fig. 74 Metaphase I of G. campestris, some bivalents connect together forming a pseudomultivalent.

Fig. 75 Metaphase I of G. campestris, all bivalents are clumped into a mass.

Fig. 70

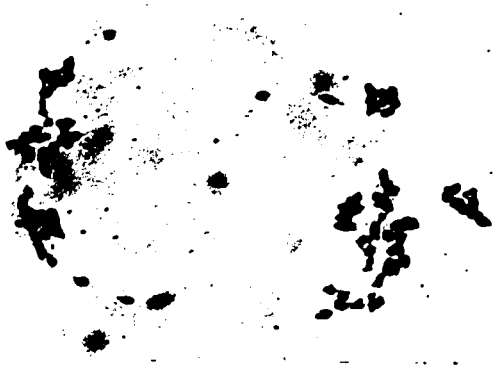


Fig. 71

Fig. 72

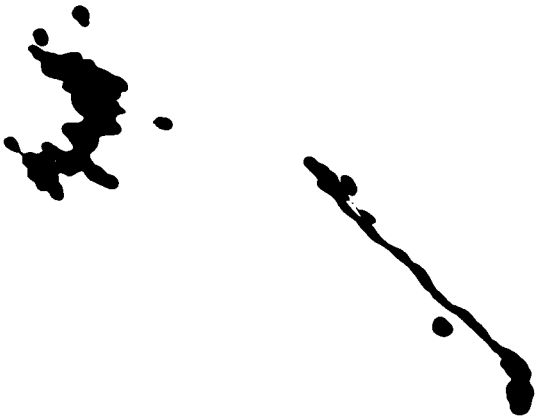


Fig. 73

Fig. 74

Fig. 75

Fig. 70

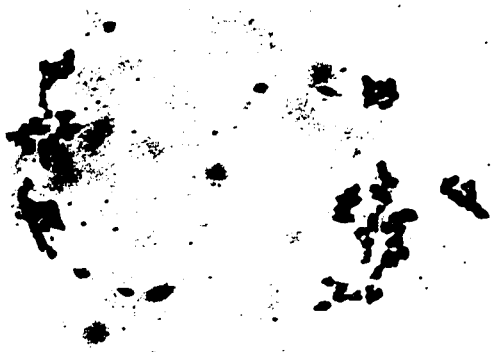


Fig. 71

Fig. 72

Fig. 73

Fig. 74

Fig. 75

Fig. 76 Metaphase I of G. campestris, all bivalents are clumped into a few small mass groups.

Fig. 77 Testicular follicle of G. campestris, most of the cells were polyploidy.

Fig. 78 Karyotype of Acheta domesticus.

Fig. 79 Metaphase I of A. domesticus, all of the chromosomes are homomorphic.

Fig. 80 Karyotype of Gryllodes sigillatus.

Fig. 81 Metaphase I of G. sigillatus, showing an unequal bivalent and achromatic gap.

Fig. 76

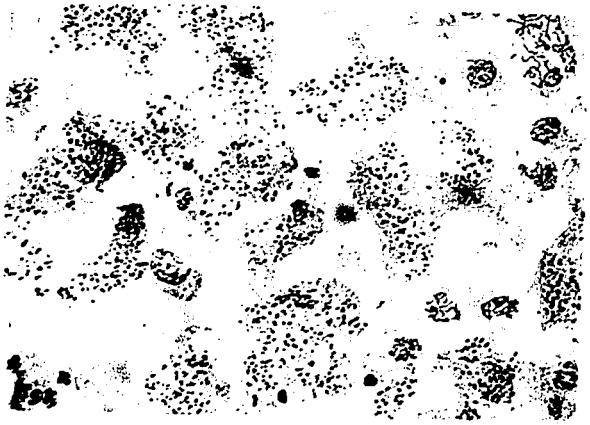


Fig. 77

Fig. 78

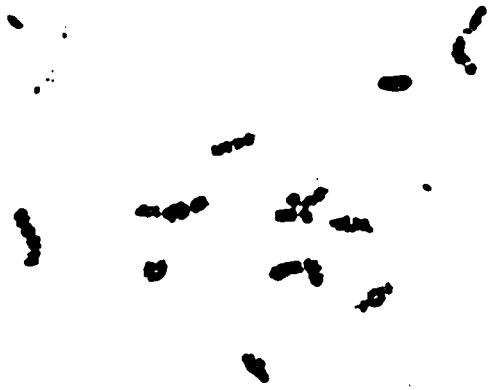


Fig. 79

Fig. 80

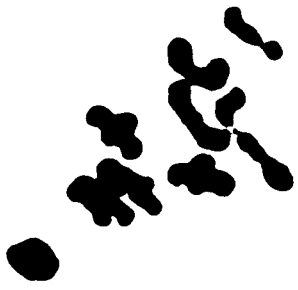


Fig. 81

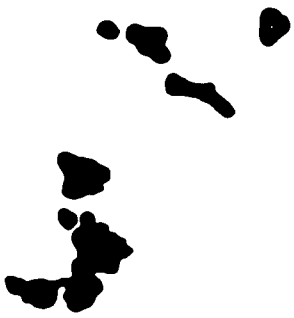


Fig. 76

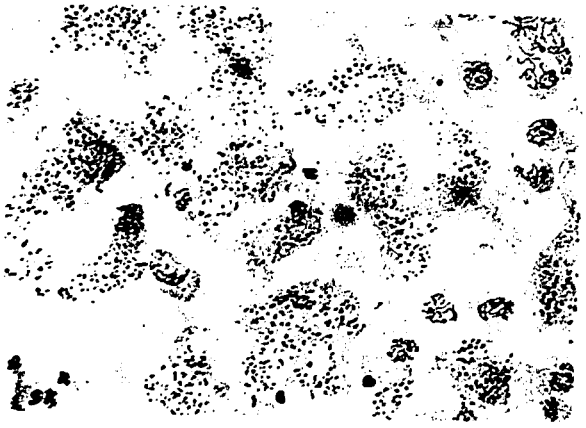


Fig. 77

Fig. 78

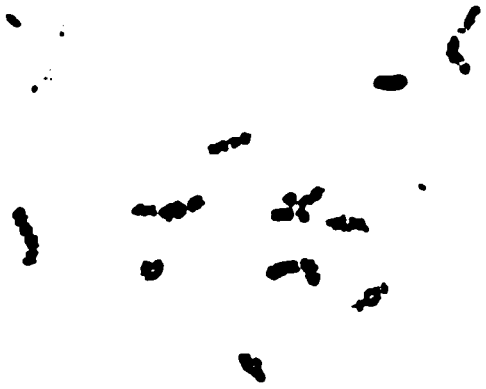


Fig. 79

Fig. 80

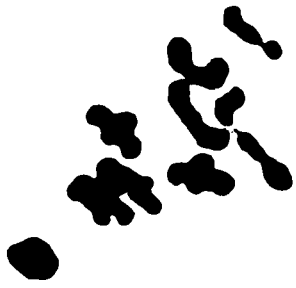


Fig. 81

Fig. 82 Anaphase I of G. sigillatus, an E-bridge occurs.

Fig. 83 Early spermatids of G. sigillatus.

Fig. 84 Spermatids of G. sigillatus, showing a small half-moon shaped apical body.

Fig. 85 Late spermatids of G. sigillatus, the apical body has disappeared.

Fig. 86 Karyotype of Scapsipedus marginatus.

Fig. 87 Metaphase I of S. marginatus, all of the chromosomes are homomorphic.

Fig. 82

Fig. 83

Fig. 84

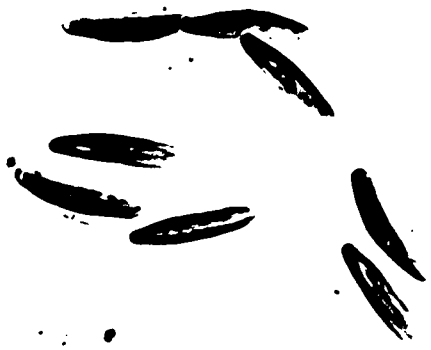


Fig. 85

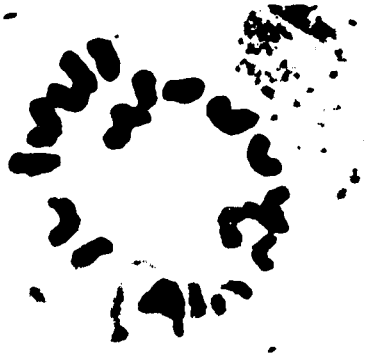


Fig. 86

Fig. 87

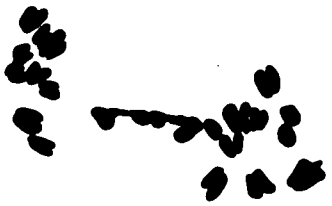


Fig. 82

Fig. 83

Fig. 84

Fig. 85

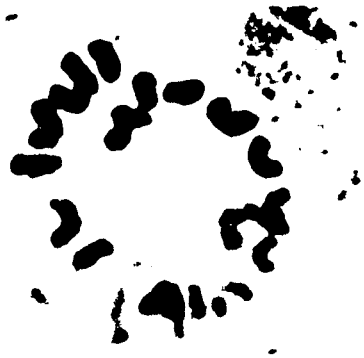


Fig. 86

Fig. 87

Fig. 88 Metaphase I of S. marginatus, showing an unequal bivalent.

Fig. 89 Metaphase I of S. marginatus, an achromatic gap occurs (900X).

Fig. 90 Karyotype of Melanogryllus desertus.

Fig. 91 Karyotype of Tartarogryllus burdigalensis.

Fig. 92 Diplotene stage of T. burdigalensis, the X chromosome appears as a dense mass.

Fig. 93 Metaphase I of T. burdigalensis, showing achromatic gaps (900X).

Fig. 88

Fig. 89

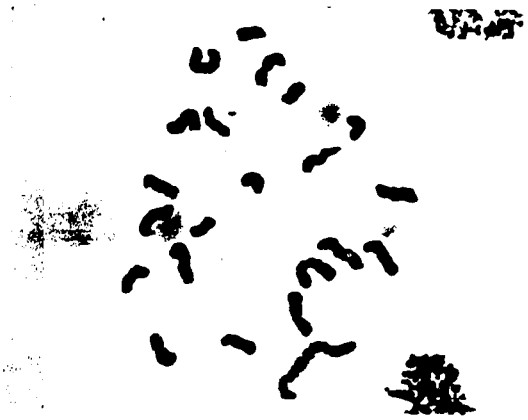


Fig. 90

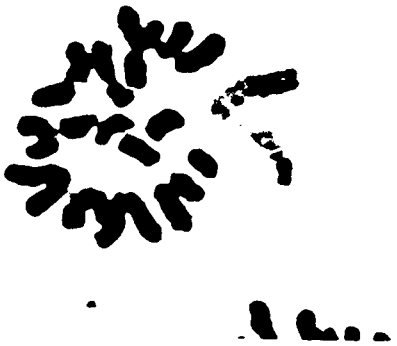


Fig. 91

Fig. 92

Fig. 93

Fig. 88

Fig. 89

Fig. 90

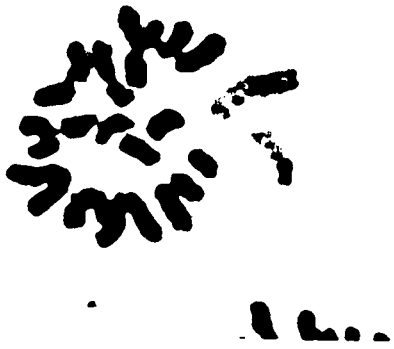


Fig. 91

Fig. 92

Fig. 93

Fig. 94 Diakinesis of T. burdigalensis, four ring-formed chromosomes can be observed.

Fig. 95 Karyotype of Neonemobius palustris.

Fig. 96 Metaphase I of N. palustris, the X chromosome appears as an irregular mass, having one end heterochromatin and the other end euchromatin.

Fig. 97 Anaphase I of N. palustris, double bridges occur.

Fig. 98 Telophase II of N. palustris, showing a chromosomal bridge.

Fig. 99 Metaphase I of N. palystris, a single unequal bivalent occurs.

Fig. 94

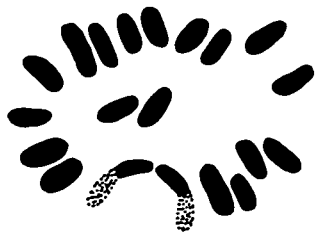


Fig. 95

Fig. 96

Fig. 97

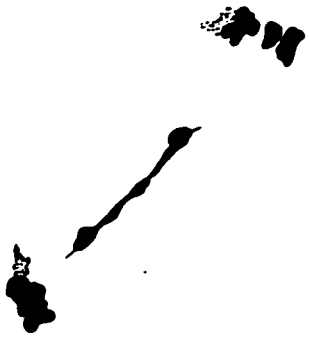


Fig. 98

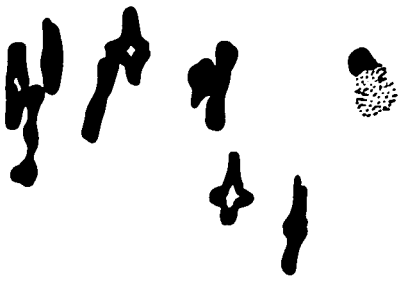


Fig. 99

Fig. 94

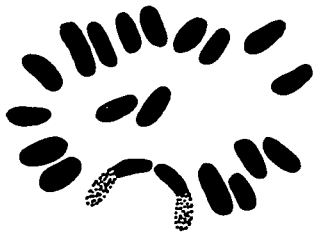


Fig. 95

Fig. 96

Fig. 97

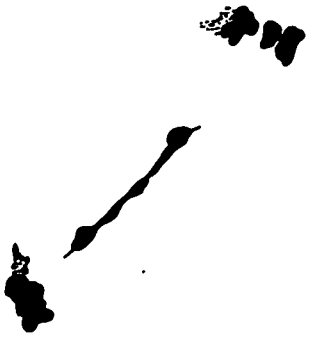


Fig. 98

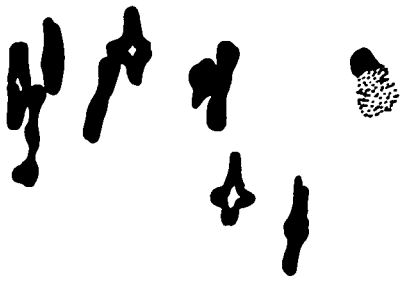


Fig. 99

Fig. 100 Metaphase I of N. palustris, showing achromatic gap.

Fig. 101 Karyotype of Neonemobius sp. near mormonius.

Fig. 102 Early meiotic prophase of N. sp. near mormonius, a giant nucleolus occurs.

Fig. 103 Metaphase I of N. sp. near mormonius, X chromosome is formed as an irregular mass, having one end euchromatin and the other end heterochromatin.

Fig. 104 Metaphase I of N. sp. near mormonius, achromatic gaps occur.

Fig. 105 Metaphase I of N. sp. near mormonius, showing a chromosomal break (arrow).

Fig. 100

Fig. 101

Fig. 102

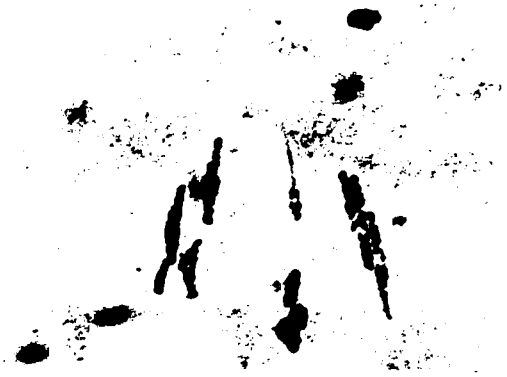


Fig. 103

Fig. 104

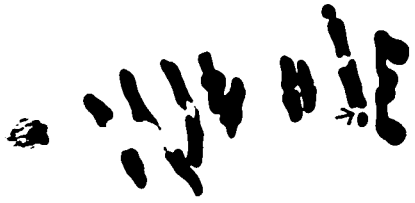


Fig. 105

Fig. 106 Anaphase I of N. sp. near mormonius, chromosomal bridges can be observed.

Fig. 107 Karyotype of Allonemobius fasciatus.

Fig. 108 Prophase I of A. fasciatus, the X chromosome is broken into pieces.

Fig. 109 Metaphase I of A. fasciatus, shows an extra small univalent.

Fig. 110 Metaphase I of A. fasciatus, showing a translocation bivalent (arrow).

Fig. 111 Anaphase I of A. fasciatus, a sticky bridge can be observed.

Fig. 106

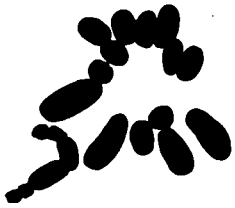


Fig. 107

Fig. 108

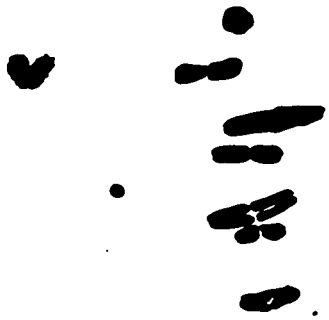


Fig. 109

Fig. 110

Fig. 111

Fig. 106

Fig. 107

Fig. 108

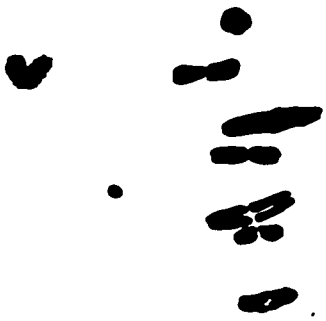


Fig. 109

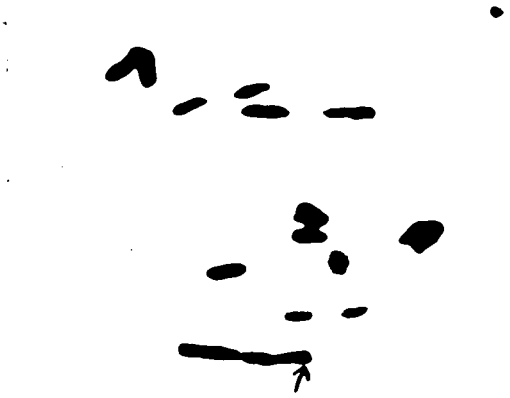


Fig. 110

Fig. 111

Fig. 112 Karyotype of Allonemobius allardi.

Fig. 113 Early meiotic prophase of A. allardi, the X chromosome appears as a big, slender ring-formed body.

Fig. 114 Anaphase II of A. allardi, the X chromosome moves to the pole slower than the autosomes and it forms a dicentric bridge.

Fig. 115 Metaphase I of A. allardi, one DNA body occurs.

Fig. 116 Metaphase I of A. allardi, showing two DNA bodies and a translocation bivalent.

Fig. 117 Metaphase I of A. allardi, achromatic gap can be observed.

Fig. 112

Fig. 113

Fig. 114

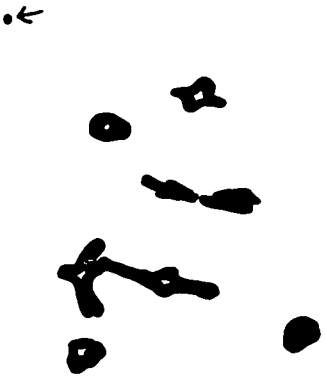


Fig. 115

Fig. 116

Fig. 117

Fig. 112

Fig. 113

Fig. 114

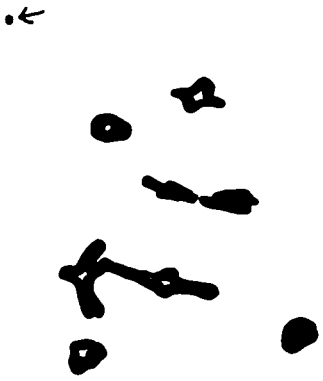


Fig. 115

Fig. 116

Fig. 117

Fig. 118 Karyotype of Allonemobius griseus griseus.

Fig. 119 Early meiotic prophase of A. g. griseus, the X chromosome appears as a J-shaped body.

Fig. 120 a. Metaphase I of A. g. griseus, the X chromosome appears as ring-formed body.
b. Metaphase I of A. g. griseus, the X chromosome appears as V-shaped body.

Fig. 121 Anaphase II of A. g. griseus, the X chromosome moves to the pole slower than the autosomes.

Fig. 123 Anaphase I of A. g. griseus, showing a sticky bridge.

Fig. 118

Fig. 119

a b

Fig. 120

Fig. 121

Fig. 123

Fig. 118

Fig. 119

a b

Fig. 120

Fig. 121

Fig. 123

Fig. 122 a,b. Metaphase I of A. g. griseus, showing a translocation bivalent.

Fig. 124 Karyotype of Eunemobius carolinus carolinus.

Fig. 125 Prophase I of E. c. carolinus, the X chromosome appears as a dense mass.

Fig. 126 Polyploid cell of E. c. carolinus (800X).

Fig. 127 Metaphase I of E. c. carolinus, showing an unequal bivalent.

a b

Fig. 122

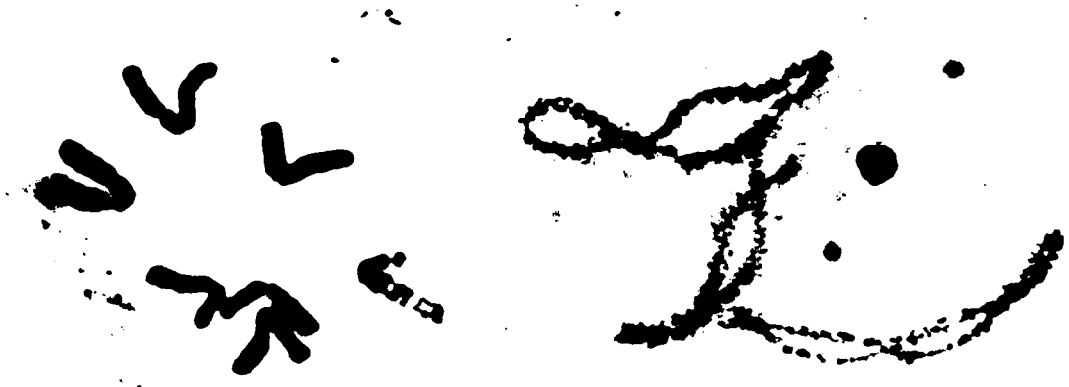
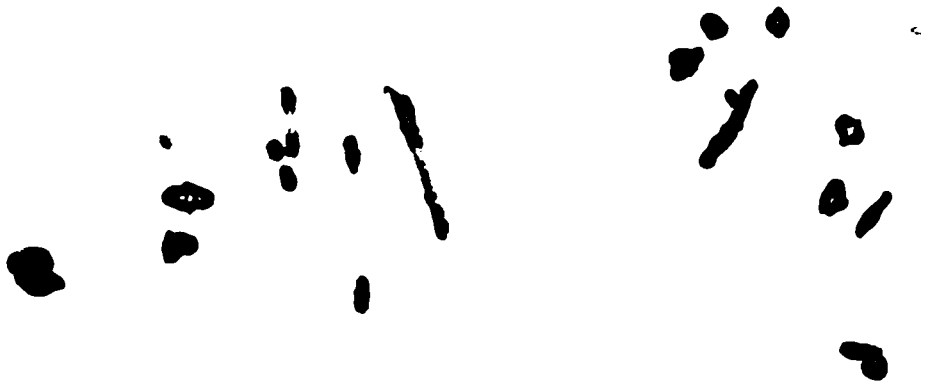


Fig. 124 Fig. 125

Fig. 126 Fig. 127



a b

Fig. 122

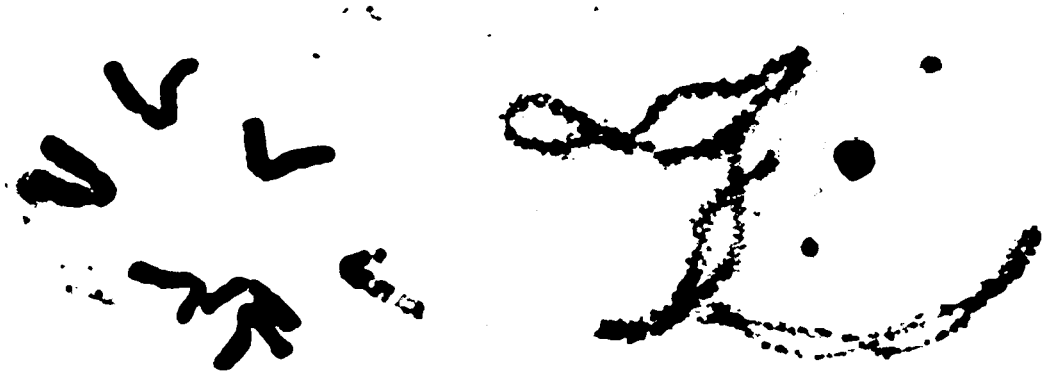


Fig. 124 Fig. 125

Fig. 126 Fig. 127

Fig. 128 Metaphase I of 'Nemobius' sp.? near bivittatus, showing n 11.

Fig. 129 Spermatogonial metaphase of A. g. griseus, showing the extra small piece (arrow) attached to the end of the minor arm of one of the members of the largest autosomes.

Fig. 130 The different structures of X chromosome during early prophase I: (a,b) Gryllinae; (c,d) Neonemobius; (e,f, g,h) Allonemobius (800X).

Fig. 131 The shape of the testes: (a) Gryllinae; (b,c) N. palustris; (d) N. sp. near mormonius; (e) A. fasciatus; (f) A. allardi; (g) A. g. griseus; (h) E. c. carolinus; (i) 'Nemobius' sp.? near bivittatus (4X).

Fig. 132 Metaphase I of Scapsipedus marginatus, showing breaks (arrows) produced by 0.5% caffeine.

Fig. 133 Metaphase I of Gryllus bermudensis, showing stickiness effect produced by 0.5% caffeine.

Fig. 128

Fig. 129

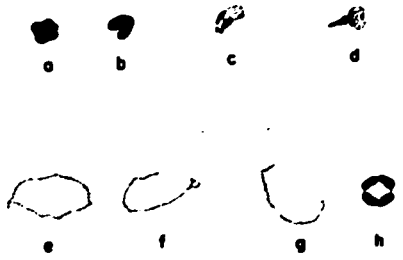


Fig. 130

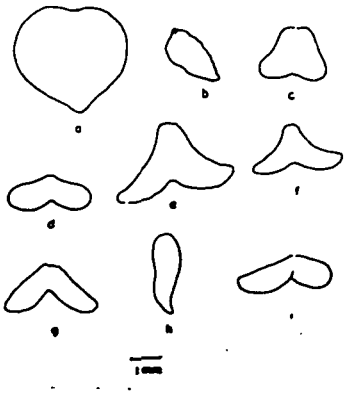


Fig. 131

Fig. 132

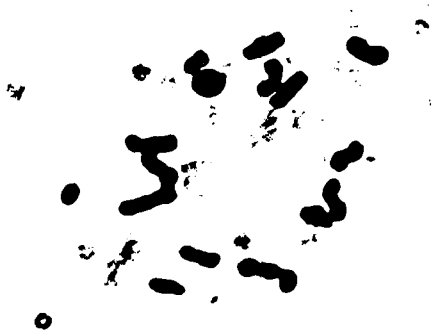


Fig. 133

Fig. 128

Fig. 129

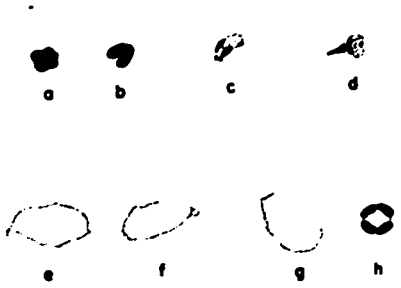


Fig. 130

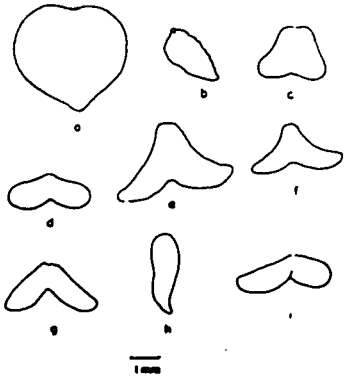


Fig. 131

Fig. 132

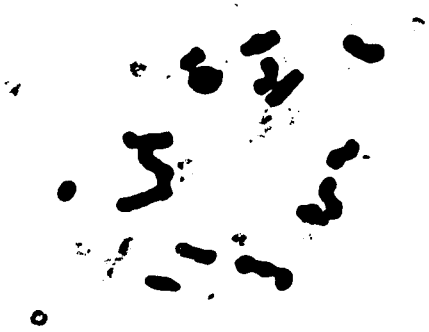


Fig. 133

Fig. 134 Metaphase I of Scapsipedus marginatus, all the chromosomes clumped into a dense mass (produced by 0.5% caffeine).

Fig. 135 Metaphase I of S. marginatus, showing achromatic gaps and breaks (arrow) produced by 0.5% caffeine.

Fig. 136 Anaphase I of Gryllus bermudensis, showing lagging chromosome produced by 0.5% caffeine.

Fig. 137 Anaphase I of G. bermudensis, showing sticky bridge produced by 0.5% caffeine.

Fig. 138 Prophase I of G. bermudensis, the chromosomes are connected with their chromatin threads (produced by 0.5% caffeine).

Fig. 139 Metaphase I of G. bermudensis, showing clumping effect produced by 0.5% caffeine.

Fig. 134

Fig. 135

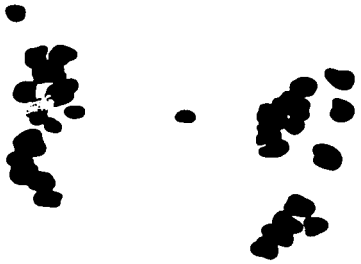


Fig. 136

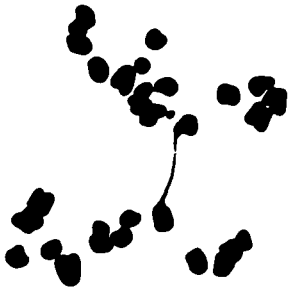


Fig. 137

Fig. 138

Fig. 139

Fig. 134

Fig. 135

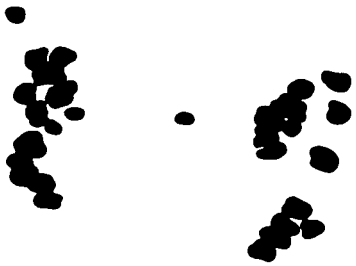


Fig. 136

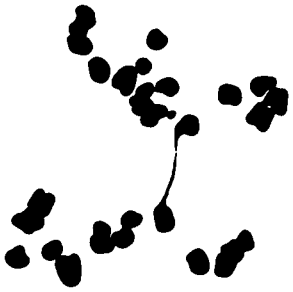


Fig. 137

Fig. 138

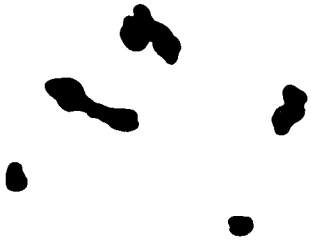


Fig. 139

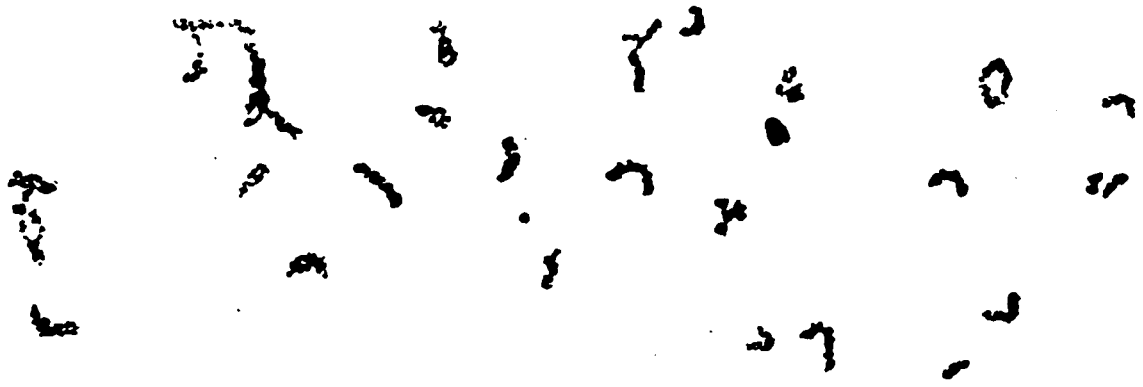
Fig. 140 a. Diplotene stage of Gryllus assimilis, showing stickiness chromosomes produced by 0.1% colchicine.
b. Diakinesis of G. assimilis, the degree of stickiness (produced by 0.1% colchicine) greatly reduce in this stage.

Fig. 141 Polyploid cell of G. assimilis produced by 0.1% colchicine.

Fig. 142 Anaphase I of Gryllus pennsylvanicus, showing breaks (arrow) produced by 0.05% colcemid.

Fig. 143 Prophase I of G. pennsylvanicus, showing stickiness of chromosomes produced by 0.05% colcemid.

Fig. 144 Anaphase I of G. pennsylvanicus, showing unequal segregation produced by 0.05% colcemid.



a b

Fig. 140

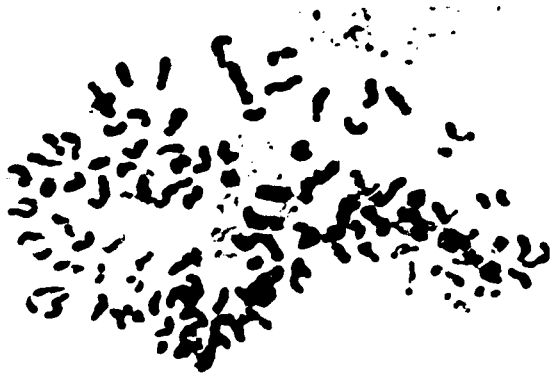


Fig. 141

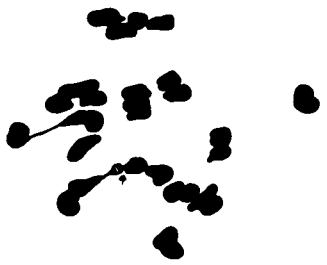


Fig. 142

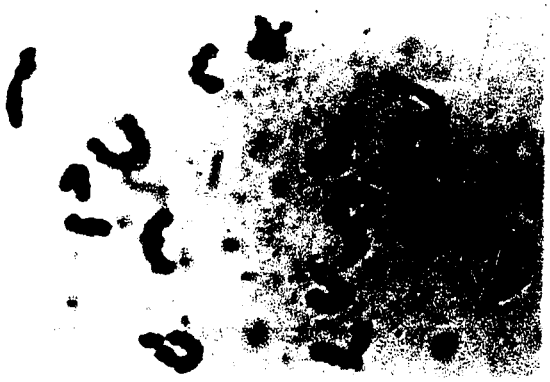
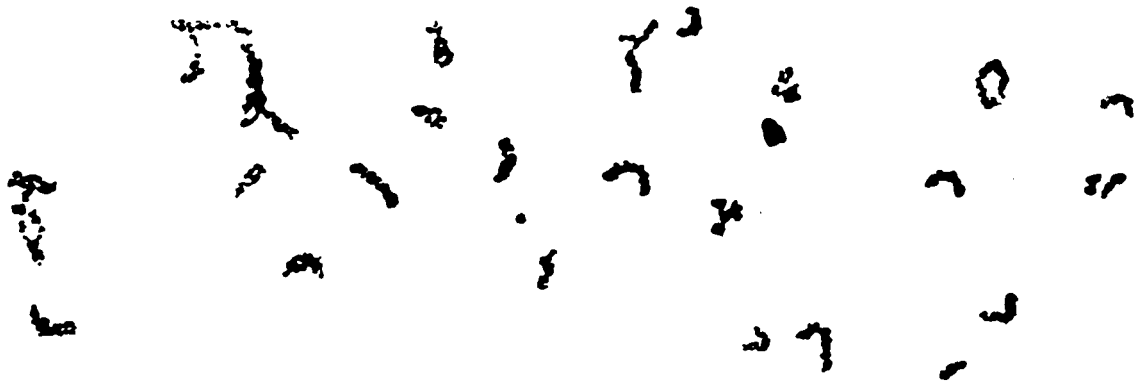


Fig. 143

Fig. 144



a b

Fig. 140

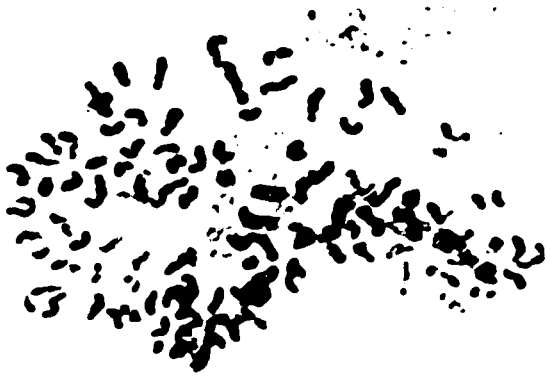


Fig. 141

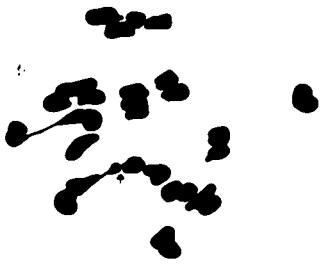


Fig. 142

Fig. 143

Fig. 144

Fig. 145 Telophase I of G. pennsylvanicus, showing a lagging chromosome produced by 0.05% colcemid.

Fig. 146 Anaphase I of G. pennsylvanicus, a sticky bridge (produced by 0.05% colcemid) can be observed.

Fig. 147 Prophase II of G. pennsylvanicus, showing c-mitotic effect produced by 0.05% colcemid.

Fig. 148 Metaphase I of G. bermudensis, showing chromosomal breaks produced by 0.5% cupferron.

Fig. 149 Prophase I of G. bermudensis, some chromosomes are connected by the sticky substance (produced by 0.5% cupferron).

Fig. 150 Metaphase I of G. bermudensis, two fragments occur as a result of 0.5% cupferron treatment.

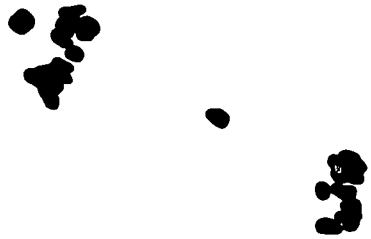


Fig. 145

Fig. 146

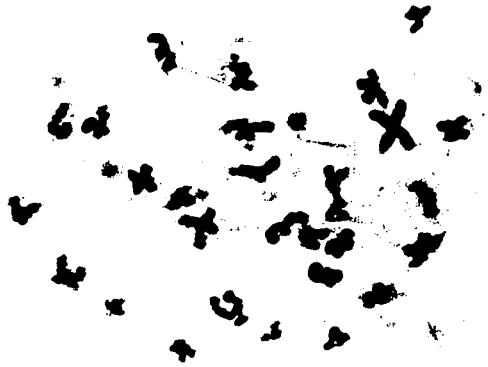


Fig. 147

Fig. 148

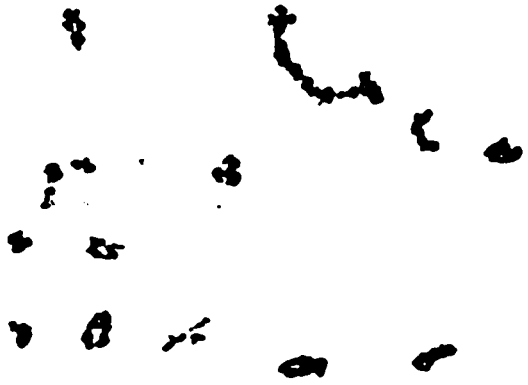


Fig. 149

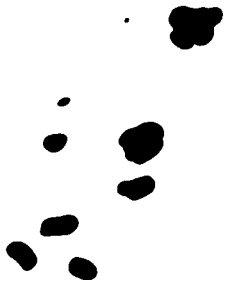


Fig. 150

Fig. 145

Fig. 146

Fig. 147

Fig. 148

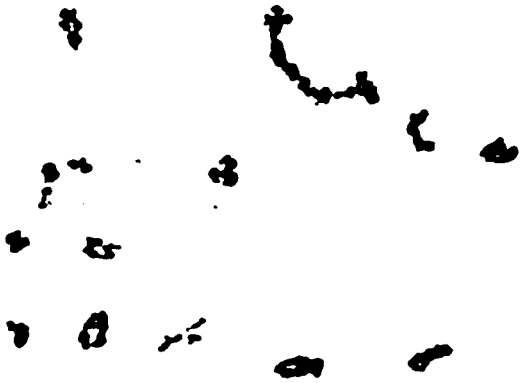


Fig. 149

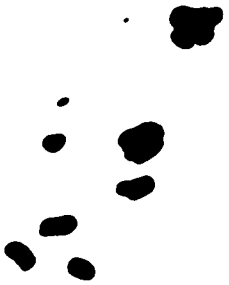


Fig. 150

Fig. 151 Metaphase I of G. bermudensis, showing four fragments produced by 0.5% cupferron.

Fig. 152 Metaphase I of G. assimilis, the autosomes are clumped into dense mass but the X chromosome stays apart, it is a result of ethyl acetate treatment.

Fig. 153 Prophase I of G. assimilis, the stickiness effect produced by glacial acetic acid.

Fig. 154 Metaphase I of G. bimaculatus, showing chromosomal breaks produced by 0.1% phenol.

Fig. 155 a. Prophase I of G. bimaculatus, showing stickiness chromosomes produced by 0.1% phenol.
b. Metaphase I of G. bimaculatus, showing stickiness chromosomes produced by 0.1% phenol.

Fig. 151

Fig. 152

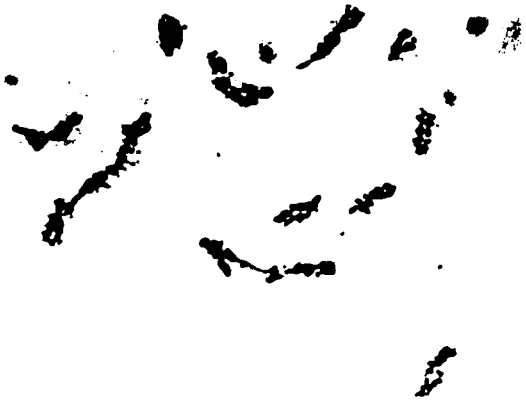
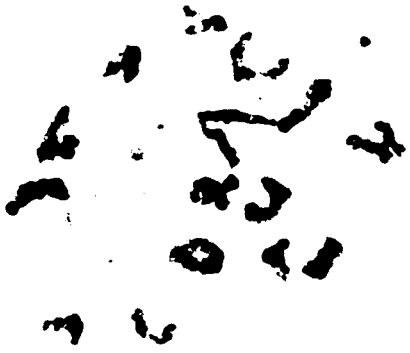


Fig. 153

Fig. 154



a

b

Fig. 155

Fig. 151

Fig. 152

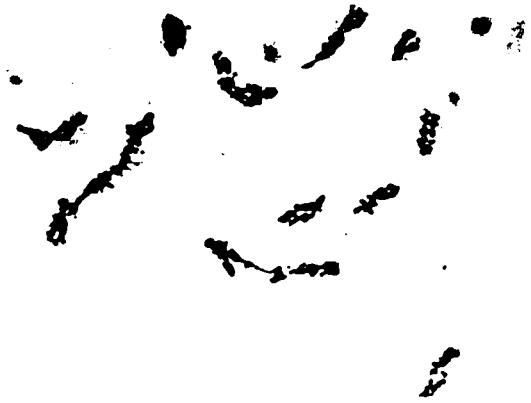
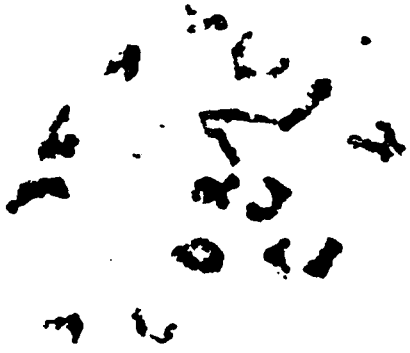


Fig. 153

Fig. 154



a

b

Fig. 155

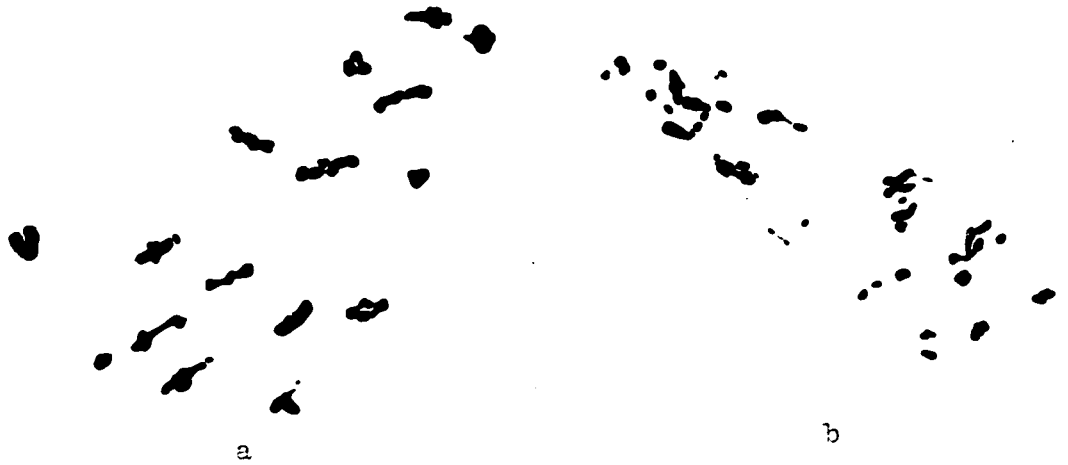
Fig. 156 a. Metaphase I of G. bimaculatus, the chromosomes scatter all over the cell because of the destruction of the spindle produced by 0.1% phenol.
b. Metaphase I of G. bimaculatus, showing the similar effect as in (a) produced by 0.1% phenol (800X).

Fig. 157 Metaphase I of G. bimaculatus, non-disjunction effect produced by 0.1% phenol.

Fig. 158 Anaphase I of G. bimaculatus, numerous fragments (as a result of 0.1% phenol treatment) can be observed.

Fig. 159 Anaphase I of G. bimaculatus, showing unequal segregation produced by 0.1% phenol.

Fig. 160 Anaphase I of G. bimaculatus, some chromosomes are lagged at equator area (produced by 0.1% phenol).



a b

Fig. 156

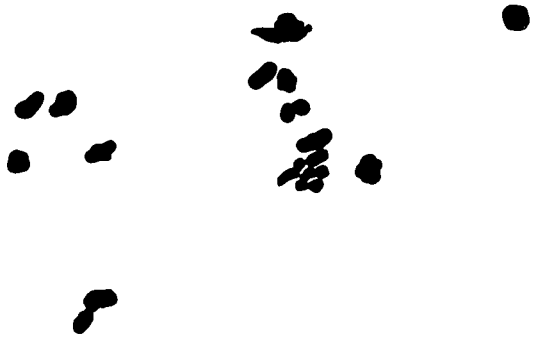


Fig. 157

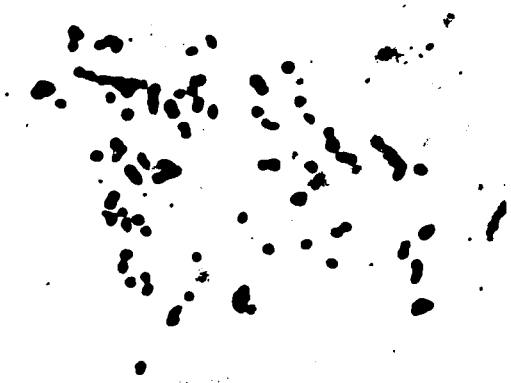
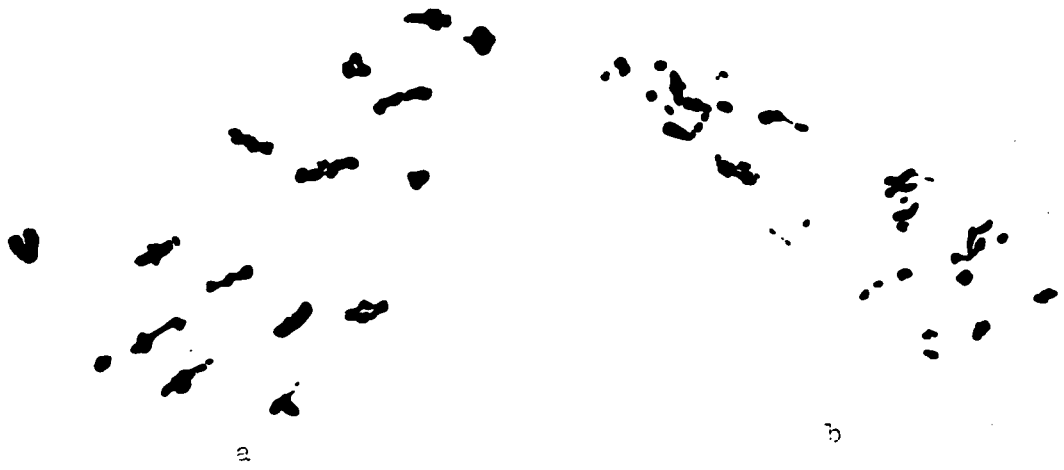


Fig. 158

Fig. 159

Fig. 160



a b

Fig. 156

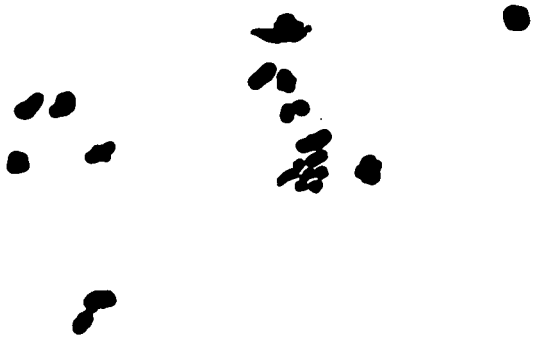


Fig. 157

Fig. 158

Fig. 159

Fig. 160

Fig. 161 Anaphase I of G. bimaculatus, dicentric bridges occur as a result of 0.1% phenol treatment.

Fig. 162 Anaphase I of G. bimaculatus, numerous sticky bridges (produced by 0.1% phenol) can be observed.

Fig. 163 Anaphase bridges of G. assimilis (irradiated with 1630r gamma ray and fixed at 24 hours after treatment).

Fig. 164 Anaphase bridges of Acheta domesticus (irradiated with 2174r gamma ray and fixed at 67 hours after treatment).

Fig. 165 Stickiness effect of gamma ray in G. assimilis (irradiated with 1848r and fixed at 67 hours after treatment).

Fig. 166 Stickiness effect of gamma ray in Allonemobius allardi (irradiated with 1087r and fixed at 67 hours after treatment).

Fig. 161

Fig. 162

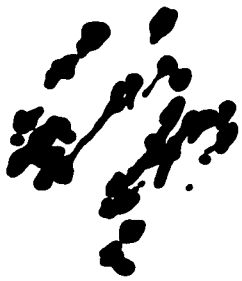


Fig. 163

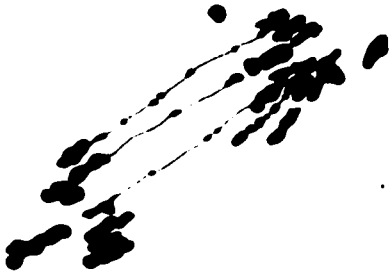


Fig. 164

Fig. 165

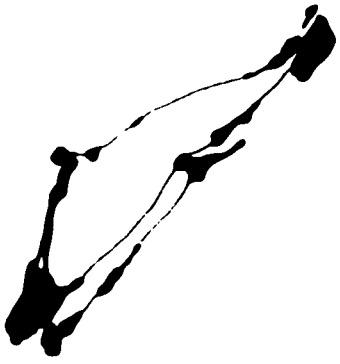


Fig. 166

Fig. 161

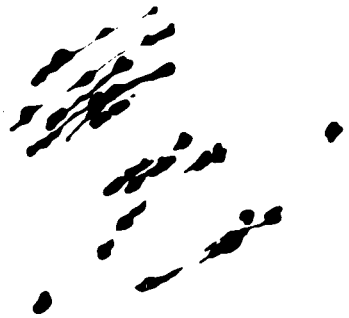


Fig. 162

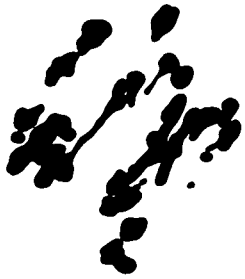


Fig. 163

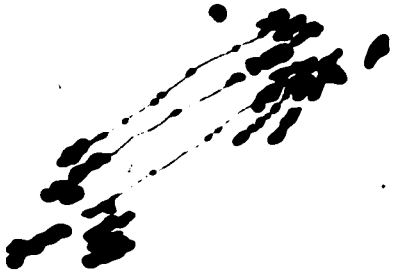


Fig. 164

Fig. 165

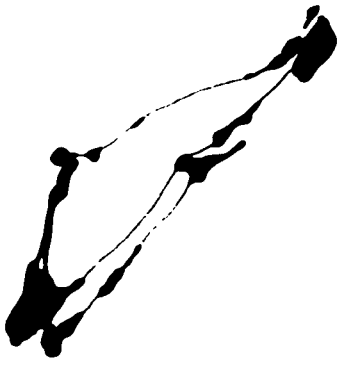


Fig. 166

Fig. 167 Metaphase I of G. assimilis, showing achromatic gaps as a result of gamma ray treatment (irradiated with 1467r and fixed at 48 hours after treatment).

Fig. 168 Metaphase I of G. pennsylvanicus, achromatic gaps and fragments occur (irradiated with 2174r gamma ray and fixed at 67 hours after treatment).

Fig. 169 Lagging effect of gamma ray in G. assimilis (irradiated with 1630r and fixed at 67 hours after treatment).

Fig. 170 Lagging effect of gamma ray in G. pennsylvanicus (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 171 Lagging effect of gamma ray in Acheta domesticus (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 172 Telophase I of G. assimilis, showing unequal segregation (irradiated with 1848r and fixed at 24 hours after treatment).

Fig. 167

Fig. 168

Fig. 169

Fig. 170

Fig. 171

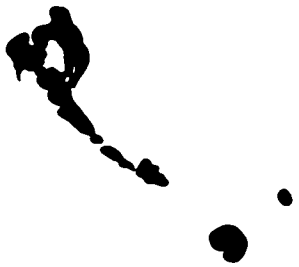


Fig. 172

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Fig. 171

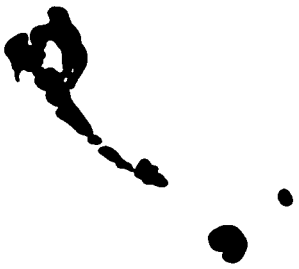

Fig. 172

Fig. 173 Telophase I of S. marginatus, unequal segregation and sticky bridge occur (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 174 Multipolar configuration of A. domesticus (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 175 Multipolar configuration of S. marginatus (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 176 Multipolar configuration of G. assimilis (irradiated with 2446r and fixed at 48 hours after treatment).

Fig. 177 The occurrence of giant spermatids as a result of gamma ray treatment in G. pennsylvanicus (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 178 Numerous fragments occurred in G. assimilis after irradiated with 1630r and fixed at 67 hours after treatment.

Fig. 173

Fig. 174

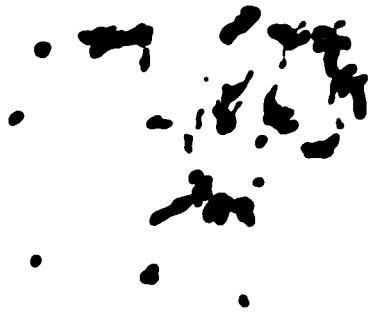

Fig. 175

Fig. 176

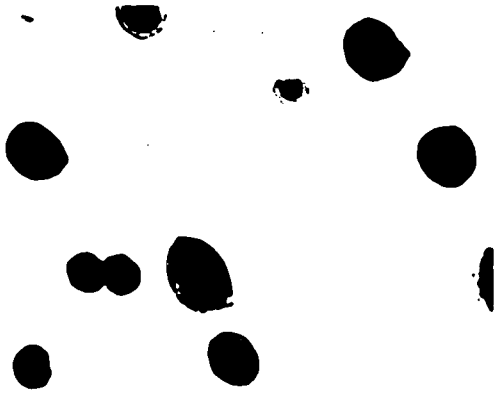

Fig. 177

Fig. 178

Fig. 173

Fig. 174

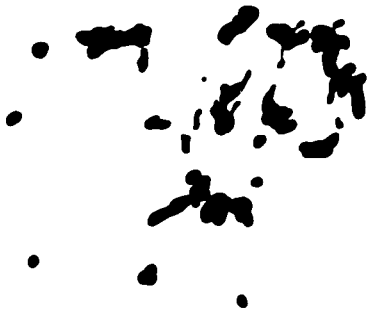

Fig. 175

Fig. 176

Fig. 177

Fig. 178

Fig. 179 Numerous fragments occurred in G. assimilis after irradiated with 2446r and fixed at 48 hours after treatment.

Fig. 180 Numerous fragments occurred in G. bimaculatus after irradiated with 2174r and fixed at 67 hours after treatment.

Fig. 181 Numerous fragments occurred in G. pennsylvanicus after irradiated with 2174r and fixed at 67 hours after treatment.

Fig. 182 Metaphase I of G. assimilis, showing one fragment (irradiated with 1630r and fixed at 24 hours after treatment).

Fig. 183 Metaphase I of A. domesticus, showing three fragments (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 184 Anaphase I of G. bimaculatus, showing numerous fragments (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 179

Fig. 180

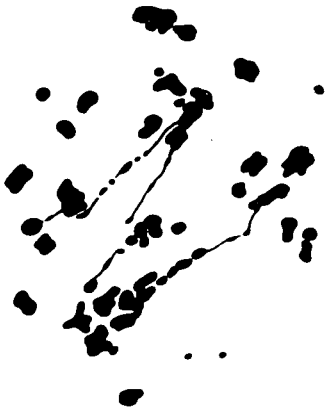

Fig. 181

Fig. 182

Fig. 183

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Fig. 180

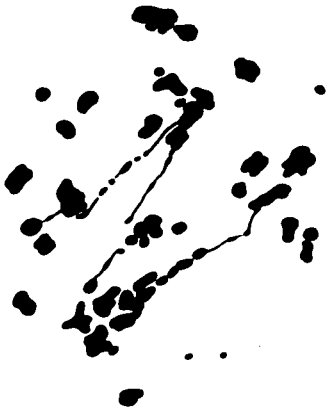


Fig. 181

Fig. 182

Fig. 183

Fig. 184

Fig. 185 Metaphase I of G. assimilis, showing a ring fragment (irradiated with 1848r and fixed at 24 hours after treatment).

Fig. 186 Anaphase I of G. assimilis, ring fragment and lagging chromosomes can be observed (irradiated with 1848r and fixed at 24 hours after treatment).

Fig. 187 Late anaphase I of G. assimilis, ring fragment and lagging chromosomes occur (irradiated with 1848r and fixed at 48 hours after treatment).

Fig. 188 Late metaphase I of A. allardi, only a few fragments occur (irradiated with 1087r and fixed at 67 hours after treatment).

Fig. 189 Telophase I of A. domesticus, showing interchange bridge and a few fragments (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 185

Fig. 186

Fig. 187

Fig. 188

Fig. 189

Fig. 185

Fig. 186

Fig. 187

Fig. 188

Fig. 189

Fig. 190 Metaphase I of G. assimilis, all the chromosomes are clumped into a dense mass (irradiated with 1848r and fixed at 24 hours after treatment).

Fig. 191 Metaphase I of S. marginatus, the chromosomes are clumped into a few groups (irradiated with 2174r and fixed at 67 hours after treatment).

Fig. 192 Breakage effect of ultraviolet in G. assimilis.

Fig. 193 Stickiness effect of ultraviolet in G. assimilis.

Fig. 190

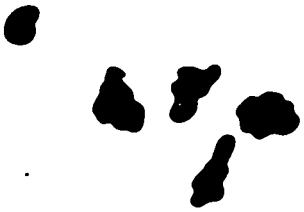


Fig. 191

Fig. 192

Fig. 193

Fig. 190

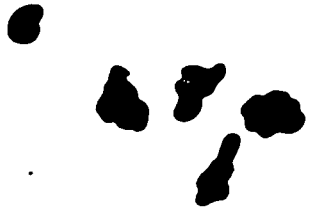


Fig. 191

Fig. 192

Fig. 193

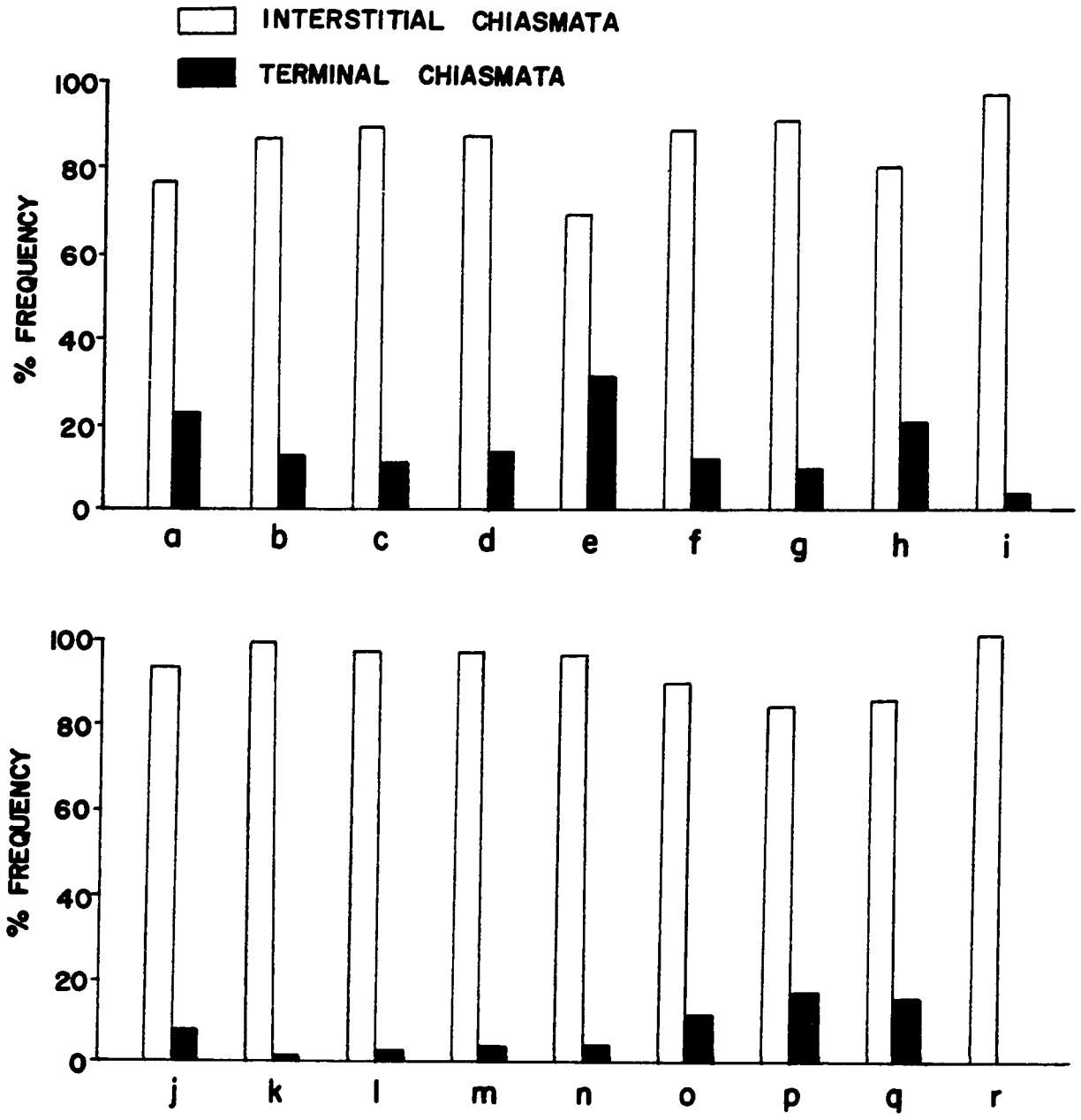


Fig. 194 Comparison of frequency of interstitial and terminal chiasmata in grylloid species:
(a) G. veletis; (b) G. pennsylvanicus; (c) G. assimilis (Antigua population); (d) G. assimilis (Jamaica population); (e) G. bimaculatus (Azores population); (f)G. bermudensis; (g)G. rubens; (h) G. campestris; (i) A. domesticus; (j) G. sigillatus; (k) S. marginatus; (l) T. burdigalensis; (m) N. palustris; (n) N. sp. near mormonius; (o) A. fasciatus; (p) A. allardi; (q) A. g. griseus; (r) E. c. carolinus.

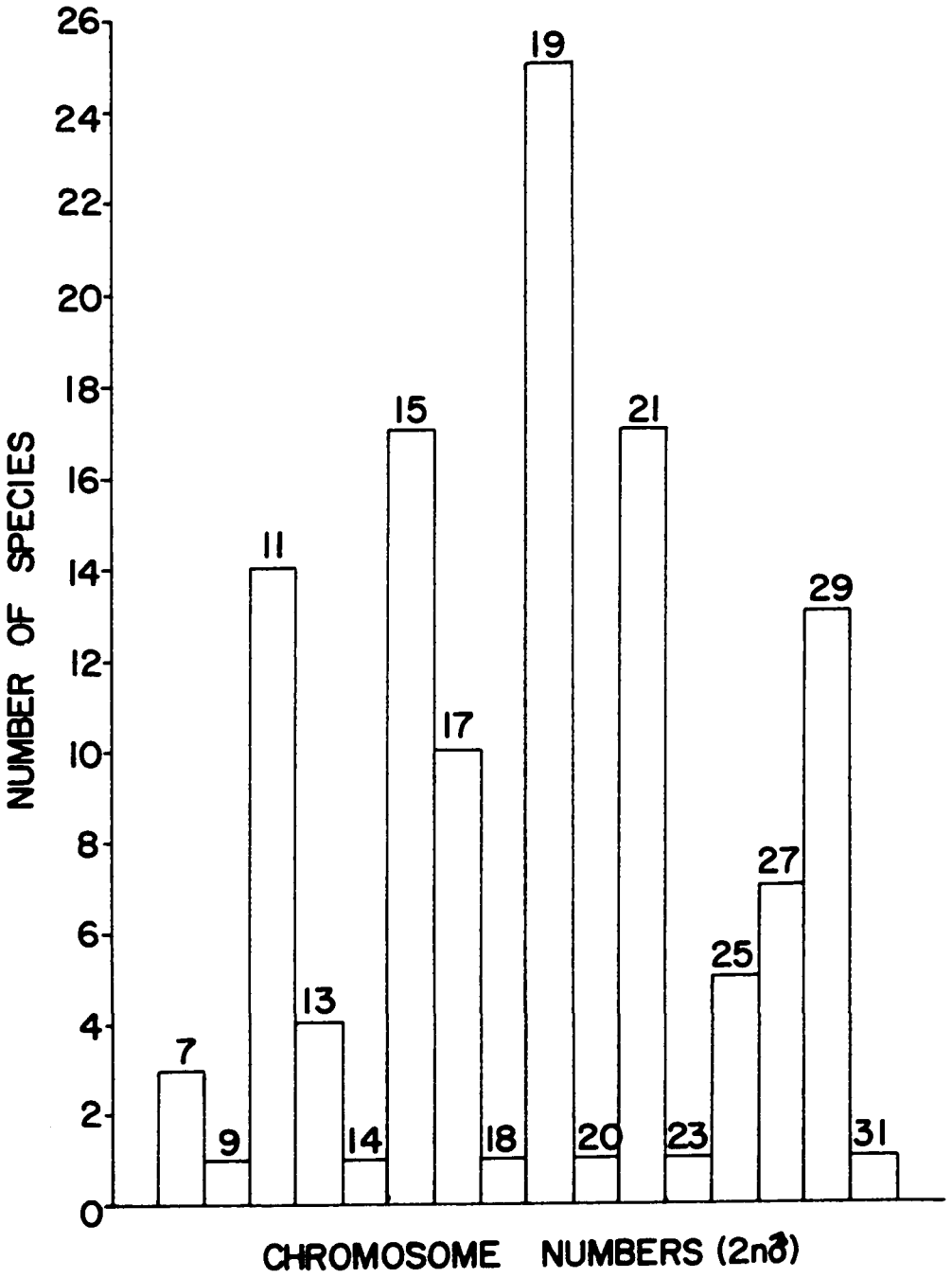
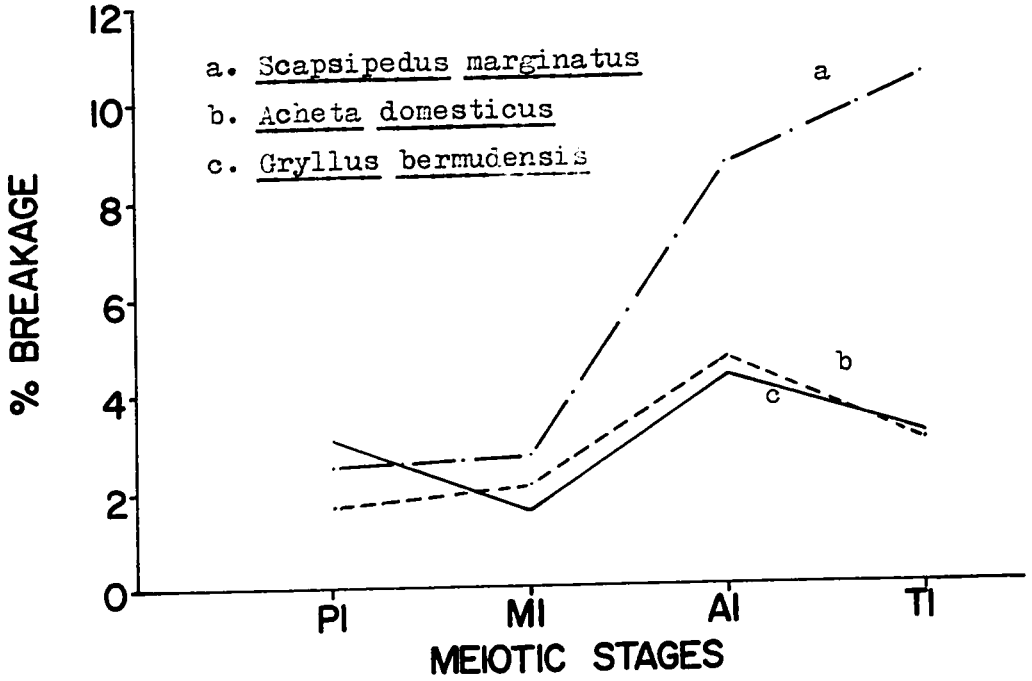
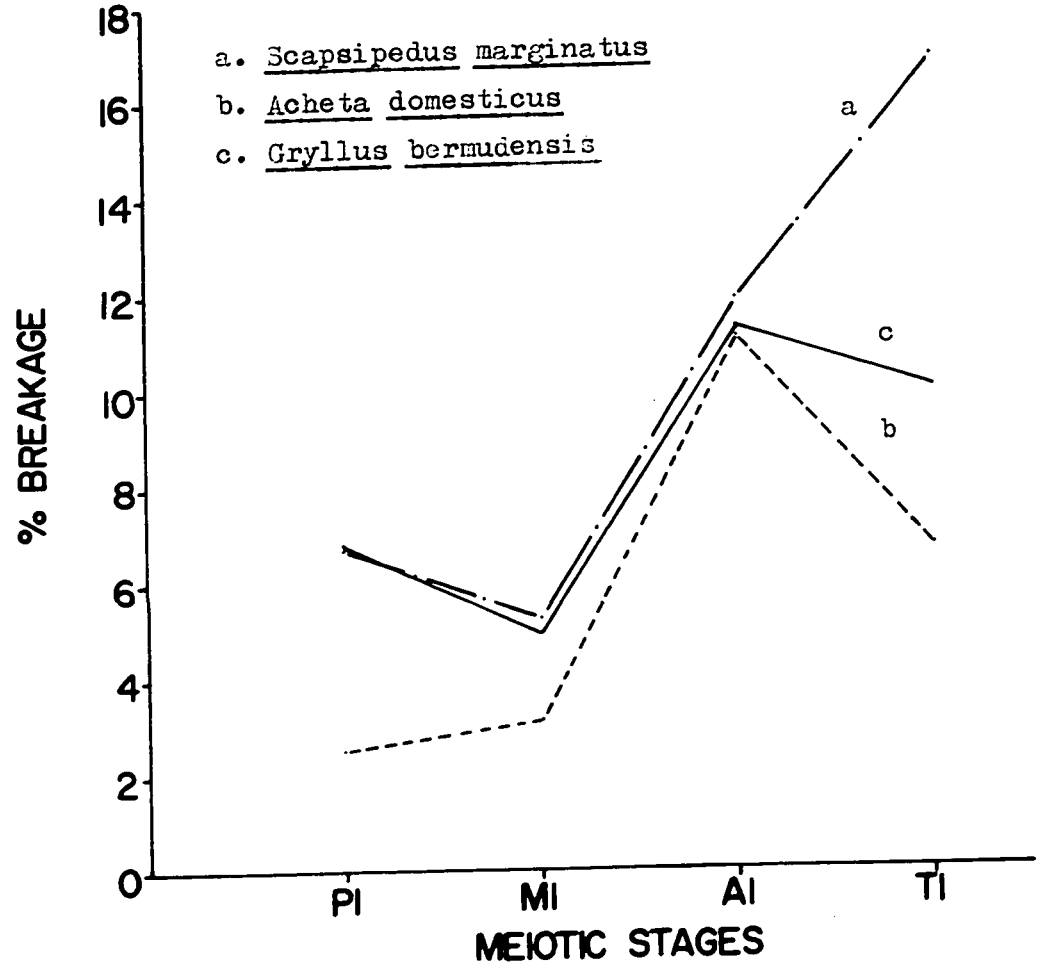


Fig. 195 Histogram showing the numbers of grylloid species having the same chromosome number.

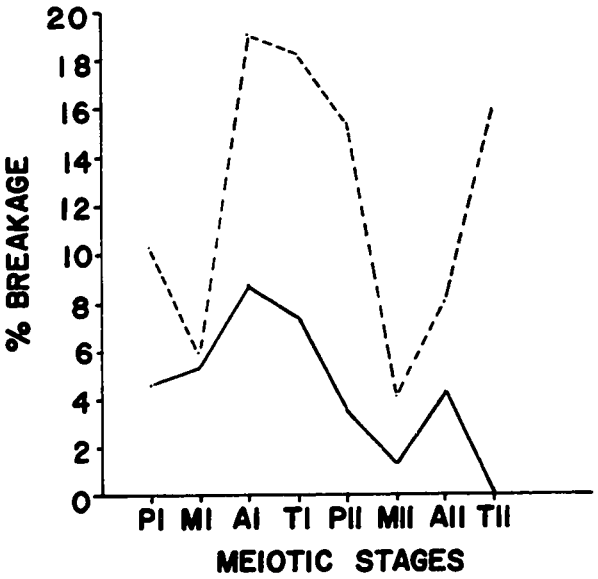


a. fixed at 5 hours after treatment.

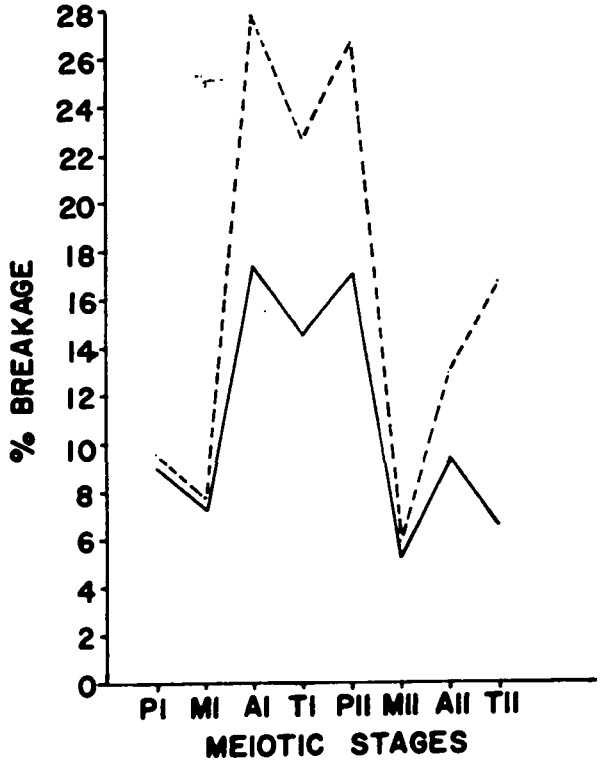


b. fixed at 24 hours after treatment.

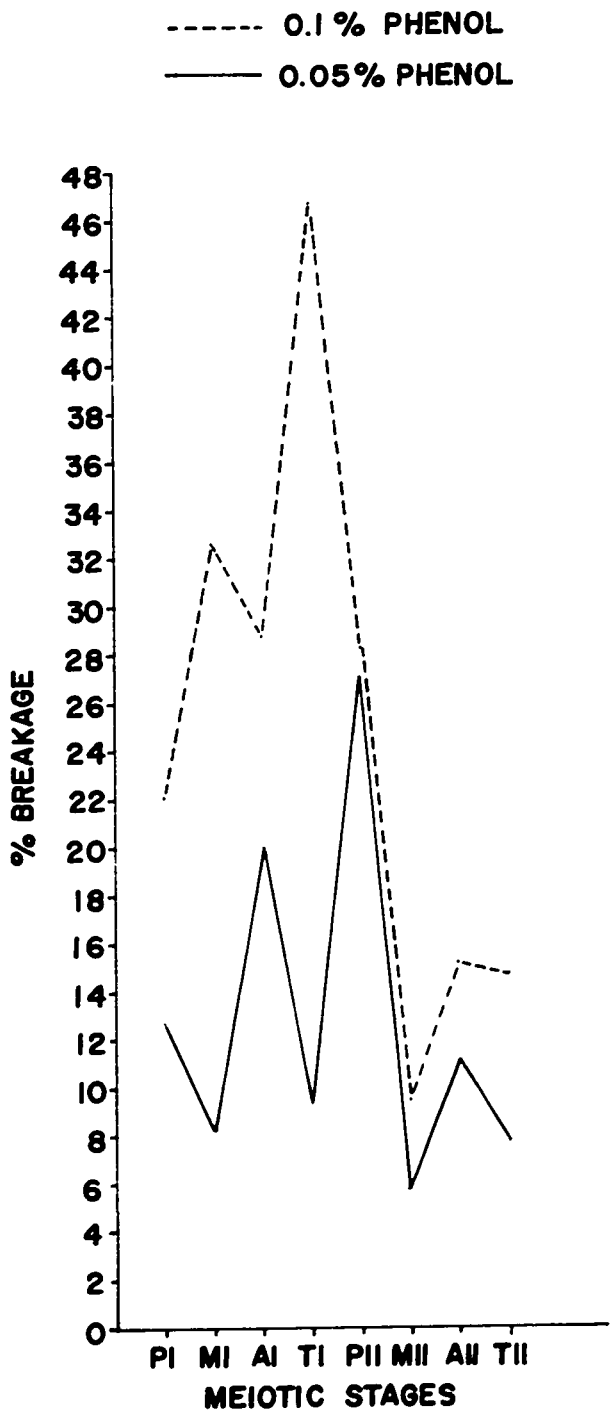
Fig. 196 Comparison of breakage frequency produced by 0.5% caffeine among Gryllus bermudensis, Acheta domesticus and Scapsipedus marginatus.



a. fixed at 12 hours after treatment



b. fixed at 24 hours after treatment



c. fixed at 72 hours after treatment

Fig. 197 Comparison of breakage frequency produced by 0.05% and 0.1% phenol in Gryllus bimaculatus.

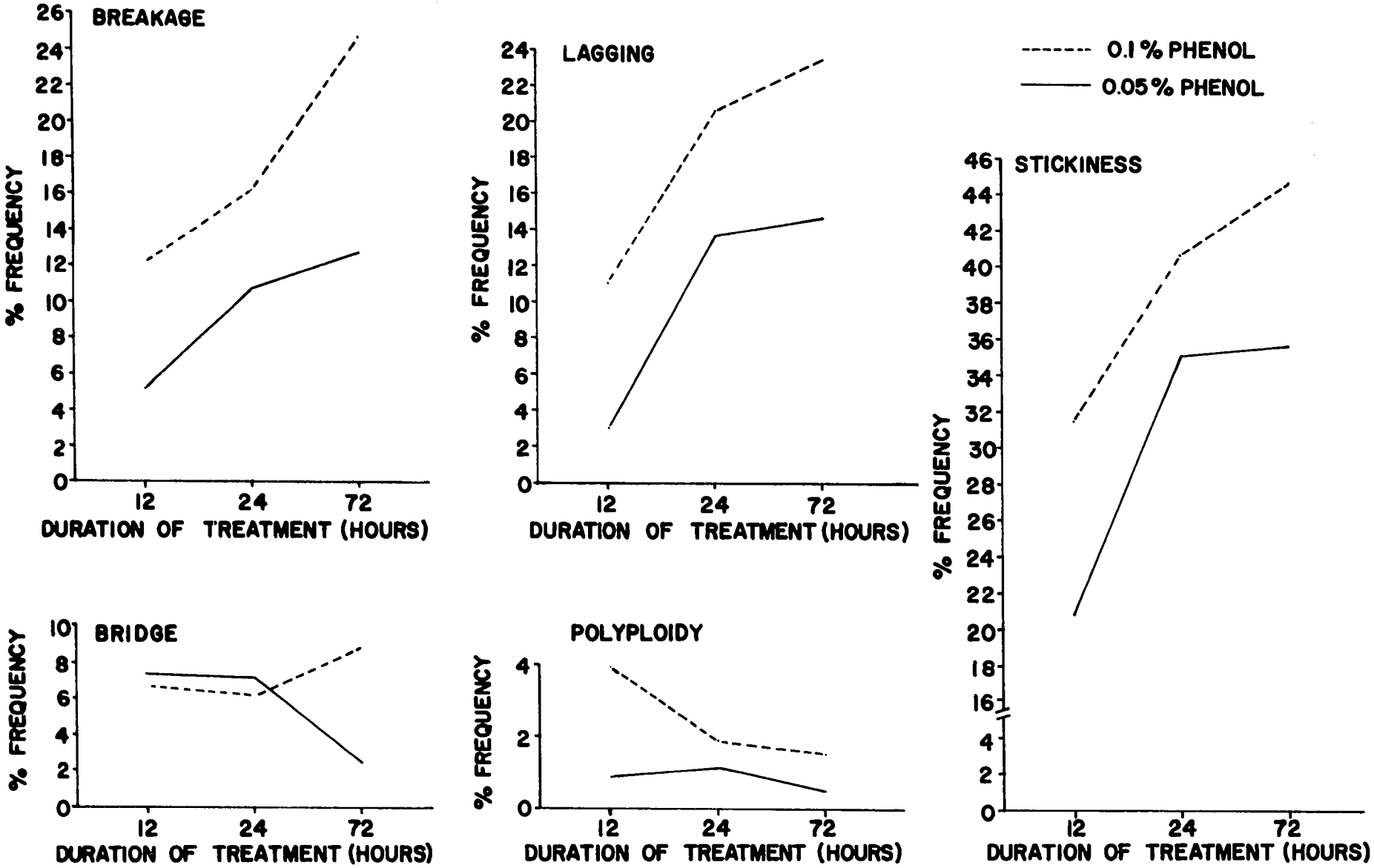


Fig. 108 Different frequency of chromosomal abnormalities produced between 0.05% and 0.1% phenol in Gryllus bimaculatus.

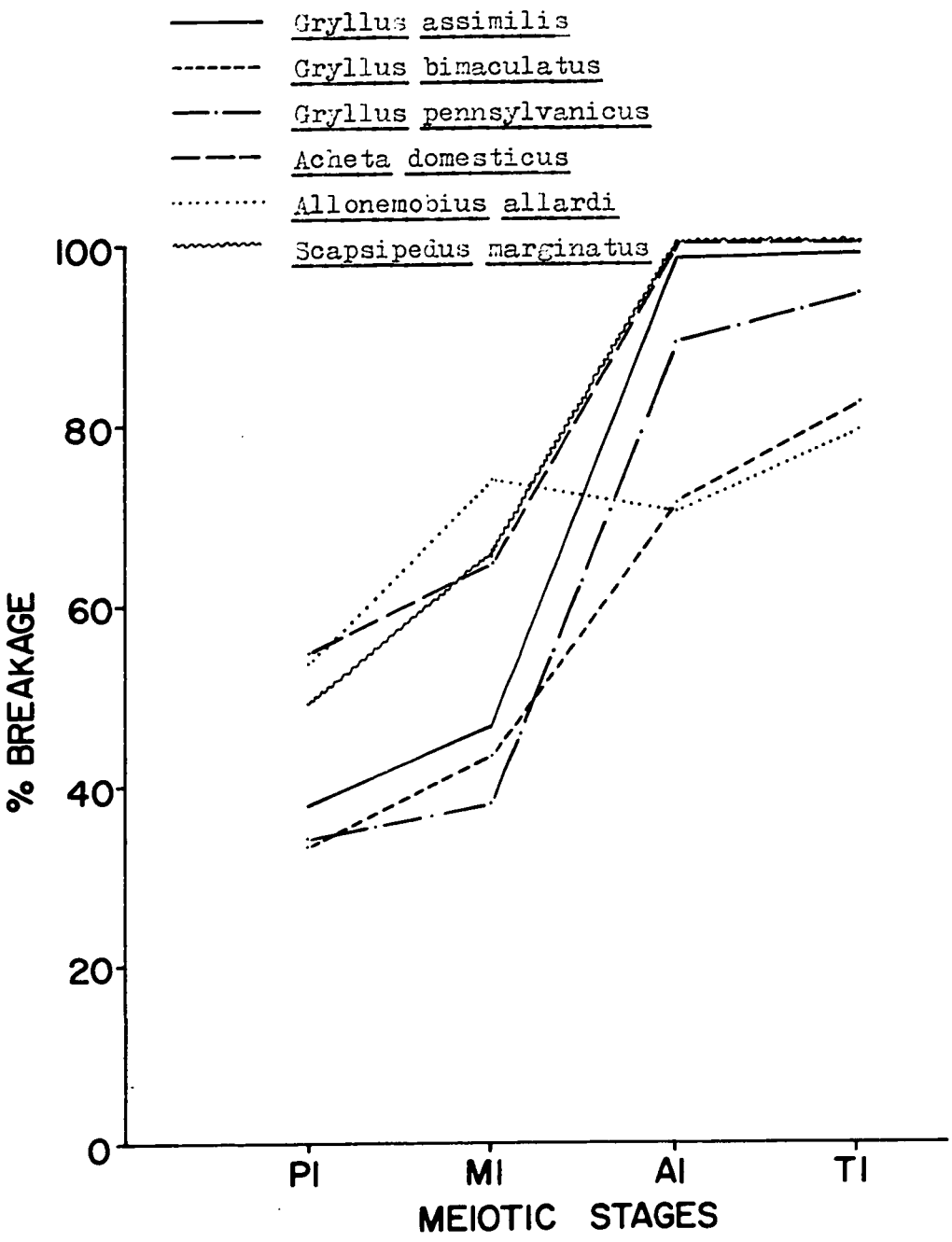


Fig. 199 Variation on the frequency of breakage produced by gamma rays in different grylloid species.

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