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The Cytology of Tasmanian Short-Horned Grasshoppers (Orthoptera: Acridoidea)

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WITH 1 PLATE AND 57 TEXT FIGURES

SUMMARY

The cytology of twenty-six of the twenty-nine species of short-horned grasshoppers (superfamily *Acridoidea*) recorded from Tasmania is described. Intraspecific cytological polymorphism is described in some species. Cytological evidence of phylogenetic relationships has been indicated where possible.

INTRODUCTION

Mainly because of their large size, and general suitability for cytological study the chromosomes of the short-horned grasshoppers (superfamily *Acridoidea*) have been the subject of wide research. In the largest and most widely studied family, the Acrididae, early workers (McClung, 1905; Davis, 1908) reported the male number as being uniformly twenty-three rod-shaped chromosomes, but Granata (1910) showed that *Pamphagus* possessed nineteen rod-shaped chromosomes. With few exceptions an XO sex chromosome system is found. Later work has shown that one group of subfamilies of the Acrididae is characterised by the male diploid number of nineteen rod-shaped chromosomes, whilst another and larger group is characterised by the male diploid number of twenty-three. These are usually called the ten and twelve chromosome groups, and correspond to the Chasmosacci and Cryptosacci groups of subfamilies (Roberts, 1941). Cytologically the Chasmosacci is a very uniform group as has been shown by Rao (1937) and Powers (1942). The twelve chromosome group, however, has some cytological variability. In more than forty genera the characteristic male diploid chromosome number of twenty-three is found (White, 1945); but "centric fusions" (White, 1945) have been responsible for lowering the chromosome number of some species, although the characteristic twenty-three arms are still found. The most notable of these is the *Stenobothrus, Chorthippus, Stauroderus, Gomphocerus, Chloealtis, Chrysochraon* group where the number has been reduced to seventeen by three centric fusions (McClung, 1914; Robertson, 1916; Carlson, 1936; Darlington and Dark, 1932; Klingstedt, 1939). Recognition of this type of change was first due to the work of Robertson (1916). Reduction in chromosome number due to centric fusions reaches its maximum in *Philocleon anomalus* where the haploid number is six the X being fused to an autosome so that an XY sex mechanism is attained (Helwig, 1941). In some few species genuine reduction in chromosome arm

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number, apparently by translocation with centromere loss, has occurred (Helwig, 1942, and others). In at least three genera of grasshoppers (*Trimerotropis, Circotettix, Aerochoreutes*) belonging to the subfamily Oedipodinae another type of change occurs whereby acrocentric chromosomes are converted to metacentrics without reduction in chromosome number (Carothers, 1917, 1921, 1931; King, 1923; Helwig, 1929; White, 1945, 1949; 1951; Coleman, 1948). Coleman (1948) has shown that such changes are not due to pericentric inversions as White (1945) suggests. The centromere shifts may be due to three break re-arrangements, the centromere with a small portion of chromatin on each side of it being re-inserted in an interstitial position.

Intraspecific variations reported in grasshoppers include supernumerary chromosomes, which appear to be of two types. Those reported by Carroll (1920) vary in number from cell to cell whilst others (Carothers, 1917; White, 1949) are constant from cell to cell—at least within the testis. Most of these appear to be heterochromatic elements but very little satisfactory evidence concerning their mode of origin exists. Unequal bivalents other than those occurring in the *Trimerotropis* group of the Oedipodinae have been reported by several workers (Carothers, 1913, 1931; White, 1949; and others). Since the inequality is due to an extra heterochromatic region, and not to be a duplication or deficiency of the chromatin normally present, it is better, as White (1949) suggests, to refer to the extra region as a supernumerary chromosome region. Except for those possessing supernumerary chromosomes, which do not appear to ever become established as permanent members of the set, no member of the Acrididae is known where the haploid chromosome number is more than twelve. It may be as White (1945) suggests that there is some real barrier which prevents the chromosome number rising above twelve.

In spite of the uniform cytology within the Acrididae chromosome studies have made important contributions to the taxonomy of the group. Routine chromosome counts show fairly conclusively the affinities with one or other of the subfamily groups, even where aberrant form masks the more usual taxonomic characters, as in *Psednura pedestris* studied in this survey. The genera of the Acridinae (*Stenobothrus* group) which have three pairs of metacentric chromosomes probably represent a natural group (White, 1945). White (1949) has divided the genus *Trimerotropis* into two groups on cytological grounds, and it may well be that these groups are taxonomically valid. The results of Powers (1942) indicate that, where no re-arrangements such as centric fusions or centromere shifts, occur, relationships at or above the species level are hard to determine as the homologies are rather obscured, apparently by extensive chromatin rearrangements not involving centromeres.

Other families of the short-horned grasshoppers have received less attention from cytologists than the Acrididae, but several workers, notably Robertson (1916, 1930) and Harman (1915, 1920), have shown that the Tetrigidae have a uniform set of seven acrocentric chromosomes.

Materials and Methods

Testes of grasshoppers were fixed, usually in the field, in acetic-alcohol (1:3) or in San Felice's modification of Navashin's fixative. Material fixed in acetic-alcohol was bulk stained by the Feulgen technique,

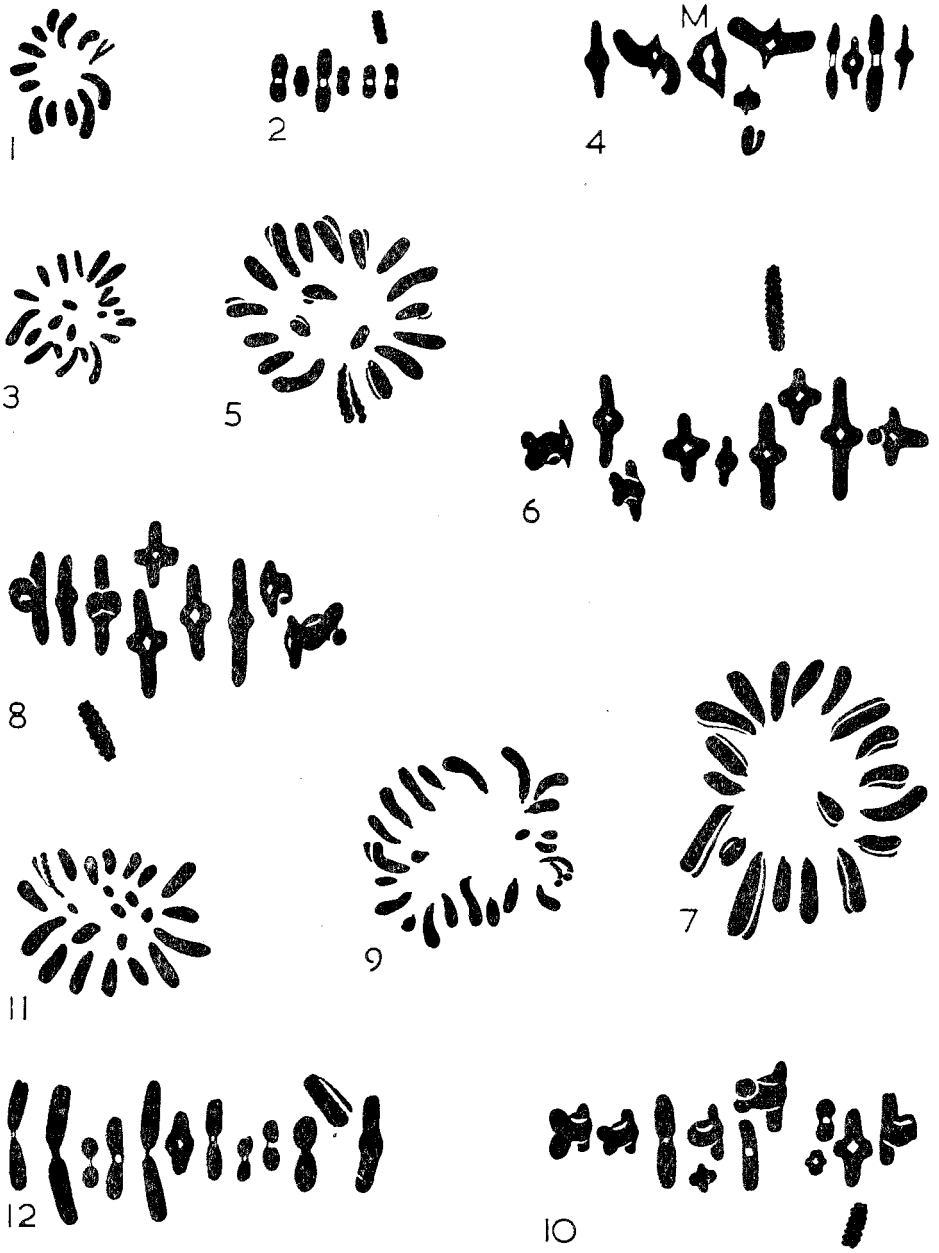
preparations being made according to the methods of Darlington and La Cour (1942). Before squashing on the slide the lower ends of the testis follicles, containing sperm only, were cut off. Acetic-alcohol was found to be the best fixative for all stages of mitosis and meiosis, and the Feuglen technique gave the quickest and most satisfactory staining. Material fixed in San Felice was microtomed at 20-24μ and stained in Newton's crystal violet.

Figures are reproduced at a magnification of X 1750.

TABLE I

CHROMOSOME NUMBERS OF TASMANIAN ACRIDOIDEA

Name of species and number of specimens studied	Collecting localities and altitudes	♂ chromosome number (2n)	Remarks
TETRIGIDAE			
Paratettix argillaceus (Erichs.) (4)	Nive R., Tarraleah Highway (800)	13 (fig. 1, 2)	Cytology typical of Tetrigidae
Tetrix sp. n.	Not collected.		
EUMASTACIDAE			
Moraba viatica (Erichs.) (5)	South Arm	19 (fig. 3, 4)	One pair of autosomes and X metacentric.
ACRIDIDAE (CHASMOSACCI)			
Monistria flavogranulata Sjöst (8)	Hobart, Ben Lomond (4200), Great Lake (3500), Bothwell (2500)	19 (fig. 5, 6)	
Psednura pedestris (Erichs.) (6)	Bridport, St. Helens	19 (fig. 7, 8)	Chromosome number & morphology typical of Chasmosacci group.
Psednura sp. n.	Not collected.		
ACRIDIDAE (CRYPTOSACCI)			
Kosciuscola sp. n. (5)	Great Lake (3500)	23 (fig. 9, 10)	
Phaulacridium vittatum (Sjöst.) (7)	Hobart, Ben Lomond (3400)	23 (fig. 11, 12)	
Phaulacridium nanum Sjöst. (6)	Avoca (600), Bothwell (1000), Bellerive, St. Helens	23 (fig. 13, 14)	
Urnisa rugosa Sauss. (3)	Bellerive	23 (fig. 15, 16)	
Ewarna includens (Walk.) (3)	Hobart (500)	23 (fig. 17-21)	One individual heterozygous for supernumerary chromosome region.
Brachyexarna lobipennis Sjöst. (5)	Hobart, Melton-Mowbray (800)	23 (fig. 22, 23)	
Macrotona australis (Walk.) (1)	Hobart (300)	23 (fig. 24, 25)	
Peakesia brunnea (White) (2)	Coles Bay	23 (fig. 26, 27)	
Cirphula pyrrhocnemis (Stöl.) (3)	St. Helens, Bellerive	23 (fig. 28, 29)	
Goniaea australasiae (Leach) (3)	Hobart (200)	23 (fig. 30, 31)	
Tasmaniacris tasmaniensis (Bol.) (30)	Many localities	23 (fig. 32-34)	One individual trisomic in one cyst.
Russalpia albertisi (Bol.) (2)	Mt. Wellington (4200)	23 (fig. 35, 36)	
Austracris guttulosa (Walk.)	Not collected.		
Gastrimargus musicus (Fabr.) (4)	Hobart, Bridgewater	23 (fig. 37, 38)	
Ocdaleus australis Sauss. (2)	Old Beach	23 (fig. 39, 40)	
Austroicetes frater (Brancs.) (2)	Lindisfarne (300)	23 (fig. 41, 42)	
Austroicetes pusilla (Walk.) (9)	Avoca (600), Lindisfarne	23 (fig. 43, 44)	One chromosome pair metacentric.
Austroicetes vulgaris (Sjöst.) (5)	Hobart, Mole Creek (800)	23 (fig. 45, 46)	Chiasmata frequently formed in short arms of chromosomes.
Chortoicetes terminifera (Walk.) (1)	Caragabal (N.S.W.)	23 (fig. 47, 48)	Recorded from Tasmania but cytology studied from N.S.W. specimen.
Cryptobothrus chrysophorus Rehn (6)	Hobart, Lindisfarne (300) Moorina (700)	23-27 (fig. 49-51)	Varying numbers of euchromatic supernumerary chromosomes.
Schizobothrus flavovittatus Sjöst. (2)	St. Helens	23 (fig. 52, 53)	
Genus & sp. n.1. (1)	Mt. Rufus (3500)	23 (fig. 54, 55)	
Genus & sp. n.2. (7)	Cradle Mt. (4000) Mt. Wellington (3700) Ben Lomond (4500)	23 (fig. 56, 57)	



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OBSERVATIONS

The names, with authorities, of all species of Acridoidea recorded from Tasmania are given in Table 1. Names are taken from the recent check list of Key (1952). Chromosome numbers, collecting localities and other information is given in this table. Most of the species show the chromosome number and morphology typical of the group to which they belong, and for these the information in the table, taken in conjunction with the figures is all that need be given. All Tasmanian species have XO sex mechanisms. The females have two X (sex) chromosomes and the males a single X chromosome. The unpaired X chromosome of the male is often recognisable at metaphase of spermatogonial mitosis by a characteristic undercondensation. During meiosis it is always recognisable as an unpaired chromosome which lies off the equatorial plate at first metaphase and segregates to one pole in advance of the autosomes. With only two exceptions the species studied have all their chromosomes acrocentric. Acrocentric chromosomes appear, superficially, to possess a completely terminal centromere but this is not the case as a small terminal portion of chromatin or short-arm exists beyond the centromere. The short-arm is often recognisable at mitosis as a terminal knob. In other species chiasmata in this region clearly demonstrate the existence of the short-arms, the bivalents having a characteristic appearance.

The following observations deal only with those species which call for further comment.

Family EUMASTACIDAE

Moraba viatica

Moraba viatica, the only Tasmanian Eumastacid, was collected during this survey for the first time since the original record of 1842. The male has nineteen chromosomes (figs. 3, 4). Eight pairs are rod-shaped (acrocentric) and one pair of autosomes and the X chromosome are V-shaped (metacentric).

The only published information concerning the cytology of the Eumastacidae is given by Rehn (1948), who lists chromosome numbers (determined by E. R. Helwig) of six American species distributed amongst five subfamilies. In these species the male diploid numbers vary from seventeen to twenty-three. In all cases the X chromosome is metacentric and all the autosomes acrocentric (personal communication from Dr. E. R. Helwig). In four species of Australian Eumastacidae studied by the

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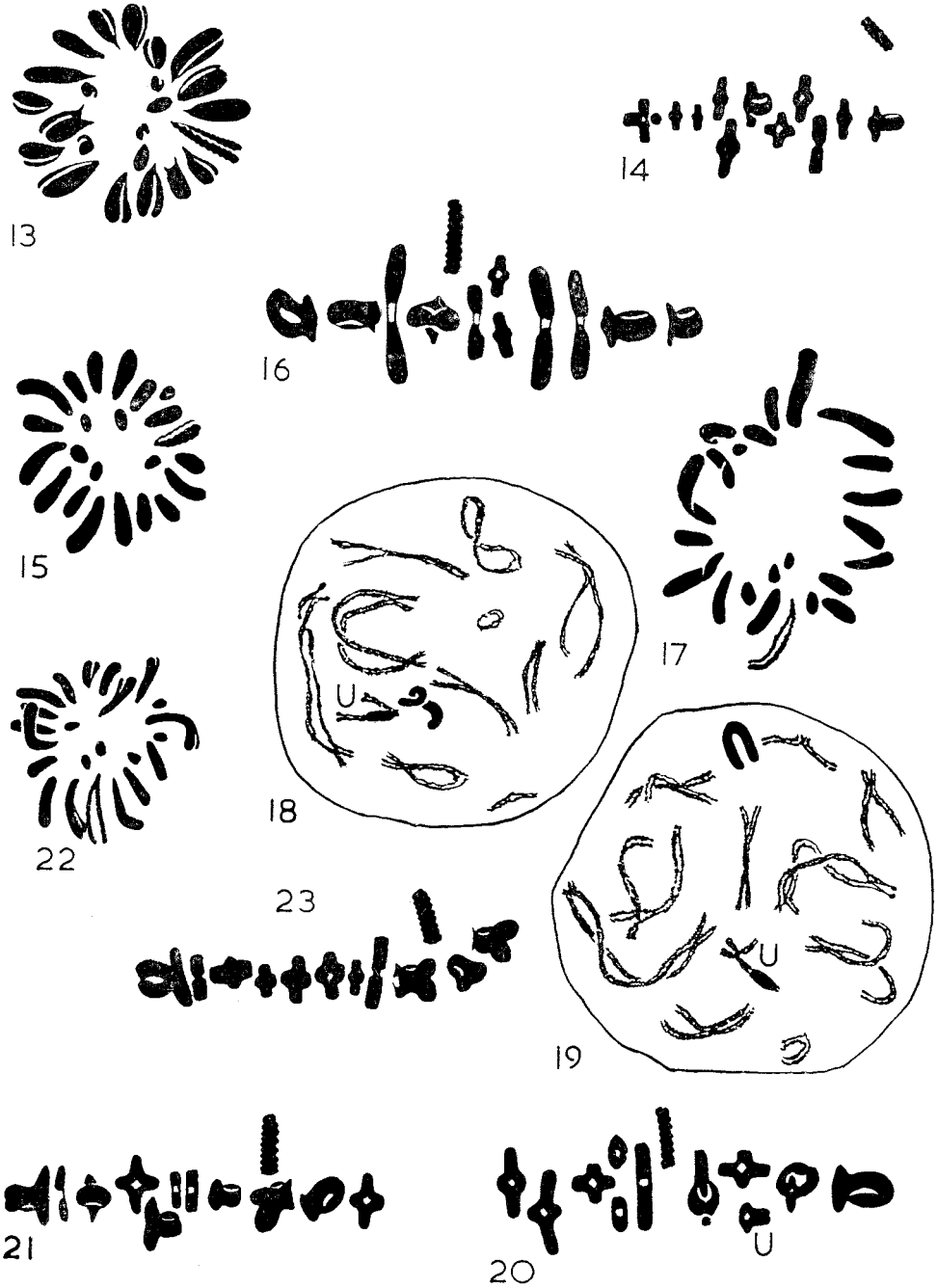
EXPLANATION OF FIGS. 1-12

Figure 1: *Paratettix argillaceus*, metaphase of spermatogonial mitosis.
Figure 2: *Paratettix argillaceus*, first metaphase.
Figure 3: *Moraba viatica*, spermatogonial metaphase. X chromosome and one autosomal pair metacentric.
Figure 4: *Moraba viatica*, first metaphase. M—metacentric bivalent.
Figure 5: *Monistria flavogranulata*, spermatogonial metaphase. X chromosome undercondensed.
Figure 6: *Monistria flavogranulata*, first metaphase.
Figure 7: *Psednura pedestris*, spermatogonial metaphase.
Figure 8: *Psednura pedestris*, first metaphase.
Figure 9: *Kosciuscola* sp. n., spermatogonial metaphase.
Figure 10: *Kosciuscola*, sp. n., first metaphase.
Figure 11: *Phaulacridium vittatum*, spermatogonial metaphase.
Figure 12: *Phaulacridium vittatum*, first metaphase.



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author the numbers range between fifteen and twenty-one, and in all four species at least one pair of autosomes are metacentric. The cytological differences may thus reflect the taxonomic differences between the Australian and American forms Rehn (1948) having placed the Australian Eumastacidae in a distinct new subfamily.

In *Moraba viatica* and other Australian species of Eumastacidae the chromosomes range in length from less than one micron to about five microns. This is approximately the same size as the chromosomes of the primitive family Tetrigidae. In the Acrididae studied the length varies from one micron to greater than eight microns. The size and general arrangement of the testis follicles in the Eumastacidae also resembles that of the Tetrigidae. The cytology of *Moraba* and other Australian Eumastacidae will be the subject of a later paper.

Family ACRIDIDAE

CHASMOSACCI GROUP OF SUBFAMILIES

The relationships of the Chasmosacci group with the larger Cryptosacci group are uncertain. Students of the Acrididae are not in agreement as to which group is the more primitive. Roberts (1941) considers, on the basis of their phallic structures, that the Chasmosacci are ancestral. Uvarov (1943) however, considers the Chasmosacci to have been derived from one subfamily of the Cryptosacci group. The very uniform cytology of the Chasmosacci suggests that they may be a group derived from Cryptosacci stock, two chromosomes being lost in the process. Such a change is known to have taken place independently in several of the Cryptosacci.

Monistria flavogranulata

This species has the diploid chromosome number characteristic of the Chasmosacci group. Eighteen rod-shaped autosomes and one rod-shaped X chromosome are found in the male (figs. 5, 6, 58, 59).

Psednura pedestris

Psednura has hitherto been assigned to the Cryptosacci group of subfamilies. Its chromosome complement of nineteen acrocentrics (figs. 7, 8, 60, 61) shows, however, that it belongs with the ten chromosome

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EXPLANATION OF FIGS. 13-23

Figure 13: *Phaulacridium nanum*, spermatogonial metaphase.
Figure 14: *Phaulacridium nanum*, first metaphase.
Figure 15: *Urnisa rugosa*, spermatogonial metaphase.
Figure 16: *Urnisa rugosa*, first metaphase.
Figures 17-21: *Exarna includens*.
Figure 17: Spermatogonial metaphase in individual with supernumerary chromosome region. Only five small chromosomes present.
Figure 18: Diplotene. The supernumerary region and the X chromosome are over-condensed. Chiasma in distal portion of unequal bivalent (U).
Figure 19: Diplotene. Chiasma in proximal portion of unequal bivalent.
Figure 20: First metaphase. Chiasma in proximal portion of unequal bivalent (U).
Figure 21: First metaphase from an individual without a supernumerary chromosome region.
Figure 22: *Brachyexarna lobipennis*, spermatogonial metaphase.
Figure 23: *Brachyexarna lobipennis*, first metaphase.


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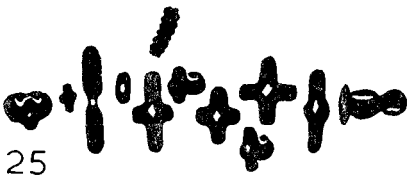
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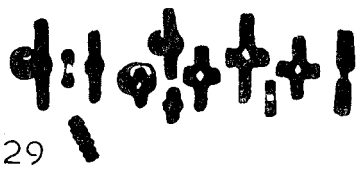
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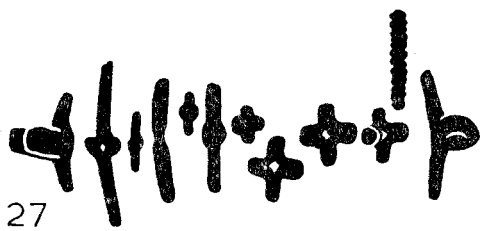
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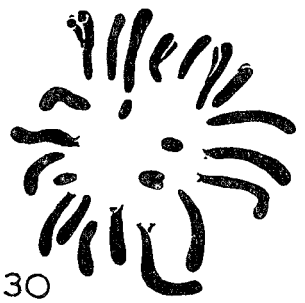
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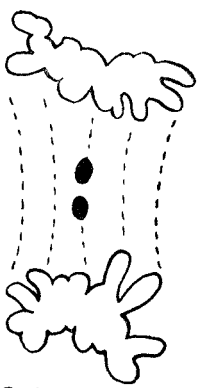
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group. Also the testis of this species is of the " radiating " type (Laird, 1943), which is found in the subfamilies usually placed in the Chasmosacci group. Dr. K. H. L. Key (personal communication) has noted other characters which agree with the above placing of *Psednura*.

CRYPTOSACCI GROUP OF SUBFAMILIES

Exarna includens

One specimen of the three studied shows an unequal chromosome pair. At spermatogonial metaphase in this individual only five small chromosomes are observed (fig. 17). In individuals without the unequal pair six small chromosomes occur at spermatogonial mitosis. In the individual with the unequal pair one of the smallest chromosomes has an intercalary supernumerary chromosome region inserted near its distal end. Like the supernumerary chromosome region observed by White (1949) in *Trimerotropis bilobata* this is heterochromatic being markedly overcondensed in the prophase stages of meiosis (figs. 18, 19). There is never more than one chiasma formed in the bivalent, but it may occur in either of two positions. If the chiasma occurs in the distal part beyond the supernumerary region (fig. 18) the unequal bivalent orientates on the metaphase plate so that the smaller chromosome is directed toward one pole and the larger chromosome toward the opposite pole (fig. 62). The large and small members of the pair then separate at first division (pre-reduction in the terminology of earlier workers). If, on the other hand the single chiasma occurs in the proximal portion of the chromosome (figs. 19, 20) the supernumerary region separates at the first meiotic division (post-reduction). A rough count indicates that the two types of bivalent occur with approximately equal frequency.

Failure of chiasma formation between the members of the unequal pair is observed in some cells (fig. 63) indicating that the supernumerary region may, perhaps, suppress crossing over in some cases.

Tasmaniacris tasmaniensis

Thirty individuals of this common species were studied. Apart from occasional tetraploid cells only one individual shows any cytological abnormality. In one cyst of cells in this specimen an extra euchromatic element is present which does not occur elsewhere in the testis. The extra element appears to be a duplication of one autosome caused by non-disjunction at a preceding spermatogonial division. It is thus homologous with

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EXPLANATION OF FIGS. 24-34

Figure 24: *Macrotona australis*, spermatogonial metaphase.
Figure 25: *Macrotona australis*, first metaphase.
Figure 26: *Peakesia brunnea*, spermatogonial metaphase.
Figure 27: *Peakesia brunnea*, first metaphase.
Figure 28: *Cirphula pyrrhocnemis*, spermatogonial metaphase.
Figure 29: *Cirphula pyrrhocnemis*, first metaphase.
Figure 30: *Goniaea australasiae*, spermatogonial metaphase.
Figure 31: *Goniaea australasiae*, first metaphase.
Figures 32-34: *Tasmaniacris tasmaniensis*.
Figure 32: Spermatogonial metaphase.
Figure 33: First metaphase.
Figure 34: Late first anaphase in trisomic cyst. The supernumerary element has divided into chromatids (shown in black) which are undergoing belated anaphase movement.

one autosomal pair but a trivalent is not formed at meiosis since the chiasma frequency of the bivalent is never greater than unity.

During meiosis the extra element orientates on the metaphase plate at the end of the first metaphase and divides into chromatids at late first anaphase (fig. 34). In none of the cells studied did the supernumerary chromosome pass to one pole without division or fail to complete division. In a trisomic grasshopper studied by Callan (1941) the supernumerary became included in one of the first division daughter cells without dividing in 50 per cent of the cells studied. In all other cases it reached the plate but failed to divide completely into chromatids and a diploid restitution nucleus was formed.

Austroicetes pusilla

Austroicetes pusilla differs from all other Tasmanian Acrididae in possessing one pair of metacentric chromosomes (M, fig. 44). When such metacentrics arise by centric fusion the haploid chromosome number is automatically reduced by one (White, 1945). Since the chromosome number of the species is that characteristic of the rest of the group it is possible that the change is of the type which occurs in the *Trimerotropis* group of Acrididae extensively studied by White (1949, 1951) and others. These changes are known as centric shifts, the precise mechanism for the change being unknown. In all species studied by White in which any centric shifts have occurred in the autosomes the X chromosome is metacentric. In *Austroicetes pusilla* this is not the case as the X is acrocentric, and the change can, perhaps, be more closely compared with that occurring in a South African grasshopper *Oedaleus nigrofasciatus* studied by Nolte (1939). In this species four pairs of autosomes are metacentric and the X chromosome is acrocentric. All the specimens of *Austroicetes pusilla* studied had the same pair of homologous chromosomes metacentric (figs. 43, 44, 72). Because of the small size of the sample studied (nine specimens), it is impossible to say whether the change is fully established in the species or not. Further analysis of populations may show that cytological polymorphism such as is found in the *Trimerotropis* group occurs in this grasshopper.

Austroicetes vulgaris

At first metaphase of meiosis (fig. 46) unusual bivalent configurations occur in this species. These are due to the localisation of chiasmata in the short arms of some of the chromosomes. Earlier workers (Darlington,

EXPLANATION OF FIGS. 35-46

Figure 35: *Russalpia albertisi*, spermatogonial metaphase.
Figure 36: *Russalpia albertisi*, first metaphase.
Figure 37: *Gastrimargus musicus*, spermatogonial metaphase.
Figure 38: *Gastrimargus musicus*, first metaphase.
Figure 39: *Oedaleus australis*, spermatogonial metaphase.
Figure 40: *Oedaleus australis*, first metaphase.
Figure 41: *Austroicetes frater*, spermatogonial metaphase.
Figure 42: *Austroicetes frater*, first metaphase.
Figure 43: *Austroicetes pusilla*, spermatogonial metaphase. One autosomal pair metacentric.
Figure 44: *Austroicetes pusilla*, first metaphase. M—metacentric bivalent.
Figure 45: *Austroicetes vulgaris*, spermatogonial metaphase.
Figure 46: *Austroicetes vulgaris*, first metaphase. The two bivalents at left each have a chiasma in their short arms.


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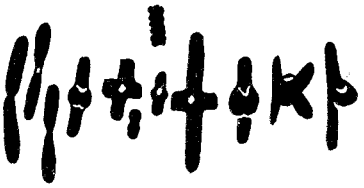
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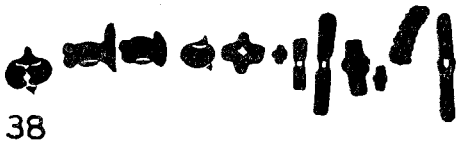
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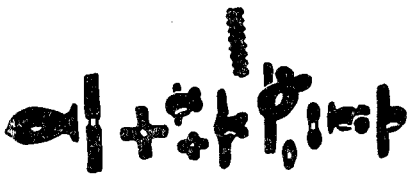
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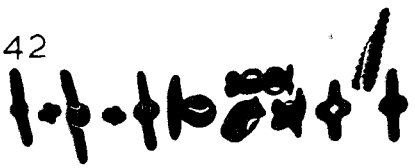
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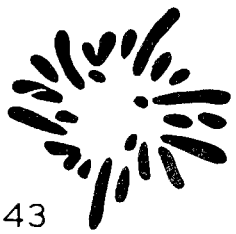
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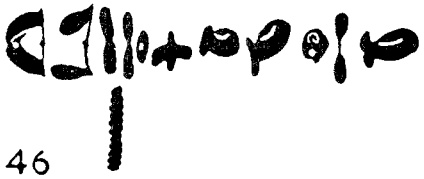
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1936, and others) have shown that the rod-shaped chromosomes of the Acrididae possess short arms in which crossing-over can occur. In nearly all the cells studied in *Austroicetes vulgaris* at least one bivalent shows a single chiasma in the short arm and none in the long arm. It is impossible to identify any one chromosome with certainty from cell to cell but it is probable that one of the larger chromosomes always undergoes chiasma formation in its short arm and only rarely in its long arm.

Cryptobothrus chrysophorus

Cryptobothrus chrysophorus is a typical member of the Cryptosacci group with twenty-three chromosomes. It, however, shows two abnormalities of some cytological interest. They are (1) most individuals possess supernumerary chromosomes; and (2) part of one individual studied is heterozygous for a reciprocal translocation.

Supernumerary chromosomes of grasshoppers previously studied seem to be of two general types. Carroll (1920) reports one, two or three extra elements present in different cells of the same animal. Single supernumeraries show precocious behaviour at prophase and nearly always segregate to one pole like the X. When two are present they pair to form a normal bivalent which does not show precocious behaviour at prophase and divides at anaphase like a normal euchromatic pair. Supernumeraries studied by White (1949, 1951) in wild populations of *Trimerotropis* and *Circotettix* behave somewhat differently. They are overcondensed at prophase and are constant from cell to cell. White has reported individuals with one, two or three extra elements. In White's material the supernumeraries nearly always pass to one first division pole undivided. When more than one is present bivalents or trivalents are sometimes formed but the elements often pass to one pole without prior pairing. A single supernumerary observed by the author in the grasshopper *Austracris proxima* shows the same behaviour as White has reported, the extra element passing to one pole without dividing at first division.

In *Cryptobothrus chrysophorus* the extra elements show no precocious behaviour at prophase. Their cycle of condensation and general behaviour is completely autosomal. This would indicate that they are euchromatic and not genetically inert as heterochromatic supernumeraries probably are (White, 1949, 1951). The origin of the extra elements in *Cryptobothrus* may possibly be due to reduplication of one of the smallest autosomes as a single supernumerary is the same size as members of the smallest chromosomal pair and behaves as autosomal univalents do at meiosis. The single extra element moves onto the plate at late metaphase (fig. 51) and usually

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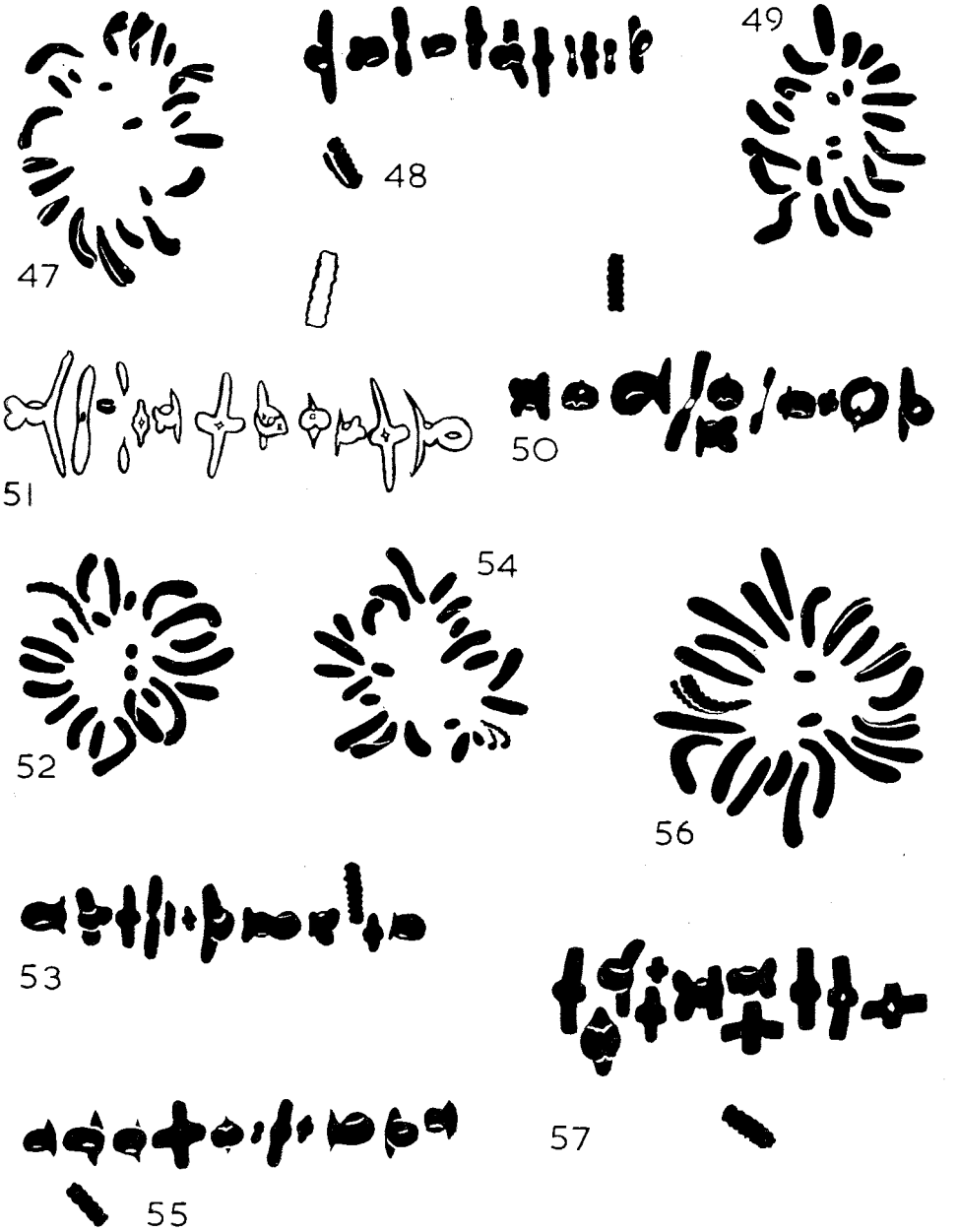
EXPLANATION OF FIGS. 47-57

Figure 47: *Chortoicetes terminifera*, spermatogonial metaphase.
Figure 48: *Chortoicetes terminifera*, first metaphase.
Figures 49-51: *Cryptobothrus chrysophorus*.
Figures 49, 50: Spermatogonial metaphase and first metaphase in an idividual with no supernumerary chromosomes.
Figure 51: Late first metaphase in cell with single supernumerary (shown in black).
Figure 52: *Schizobothrus flavovittatus*, spermatogonial metaphase.
Figure 53: *Schizobothrus flavovittatus*, first metaphase.
Figure 54: Genus and sp.n.1., spermatogonial metaphase.
Figure 55: Genus and sp. n.1., first metaphase.
Figure 56: Genus and sp. n.2., spermatogonial metaphase.
Figure 57: Genus and sp. n.2., first metaphase.



For references to figures see opposite page

divides into chromatids at late anaphase (fig. 70). One daughter chromatid is incorporated in each first division nucleus and these do not divide at second division. Sometimes the division of the univalent is incomplete at first division and it becomes incorporated in only one daughter nucleus. In these cases the supernumerary divides at second division. When two or four supernumeraries are present they regularly form one or two bivalents which are identical in size and behaviour with the smallest autosomal bivalent (figs. 67, 68). When three are present a bivalent and univalent are formed. Multivalent formation is not expected since the smallest bivalents never have more than one chiasma. The number of supernumerary chromosomes is not constant in all cells of the testis of one animal. This is due to the mitotic behaviour of the supernumeraries which is abnormal. At metaphase of spermatogonial mitosis they often lie off the equatorial plate, either above or to one side of it, and at anaphase are incorporated in one daughter nucleus without division (fig. 71).

In one cyst of cells in an individual of *Cryptobothrus* a quadrivalent is regularly formed (fig. 69). All other cells of this individual have eleven bivalents plus one or more supernumeraries, but in this cyst nine bivalents and a quadrivalent regularly occur in at least twenty cells. The quadrivalent is presumably due to a reciprocal translocation between two non-homologous autosomes during the spermatogonial divisions prior to meiosis. In some individuals supernumerary chromosome regions also occur (figs. 67, 68).

The cytology of *Cryptobothrus chrysophorus* will be treated in detail in a later paper.

Genus and sp. n.2.

This species is divided into several phenotypically distinct subspecies. It is worthy of note that no cytological differences between subspecies can be observed. The chromosomes of Genus and sp. n.2. do not closely resemble those of any other Tasmanian species except possibly *Tasmaniacris tasmaniensis*. In the majority of the twelve-chromosome group of Acrididae two or three pairs of autosomes are markedly smaller than the remainder, but in Genus and sp. n.2. only one pair differ significantly in size. (figs. 56, 57, 65, 66).

SUMMARY

The cytology of twenty-six species of Tasmanian short-horned grasshoppers is described. All have XO sex-determination mechanisms.

Moraba viatica (2n=19), and other Australian species of the family Eumastacidae are separated by clear chromosomal differences from the remaining Acridoidea. In size their chromosomes more closely resemble those of the family Tetrigidae than those of the Acrididae.

Psednura pedestris has the chromosome number and morphology and also the testis structure typical of the Chasmosacci group of subfamilies. On cytological evidence the Chasmosacci (ten chromosome) group appears to have been derived from the Cryptosacci (twelve chromosome) group.

Of three specimens of *Exarna includens* one shows heterozygosity for a precociously condensed supernumerary chromosome region.

One of the thirty individuals of *Tasmaniacris tasmaniensis* studied shows cytological abnormality. In this individual one cyst of cells has an extra chromosome which is probably a duplication of one member of a homologous pair of autosomes.

Two of the three species of *Austroicetes* studied show differences which mark them clearly from each other and from the rest of the Tasmanian representatives of their family. *Austroicetes pusilla* has one pair of metacentric chromosomes, whereas the remaining Acrididae have all their chromosomes acrocentric. In *Austroicetes vulgaris* localisation of chiasmata in the short arms of acrocentric chromosomes is frequent, whereas in all other species it is rare or non-existent.

In most individuals of *Cryptobothrus chrysophorus* supernumerary chromosomes are present. These vary in number from cell to cell within the testis of the same individual. The behaviour of the extra elements at meiosis is completely autosomal. One group of cells in one individual of *Cryptobothrus* shows regular quadrivalent formation whereas no quadrivalent is formed in any of the remaining cells. The quadrivalent is due to the individual being heterozygous for a reciprocal translocation in one cyst of cells.

Genus and sp. n.2. is shown to differ markedly in its chromosome morphology from all other species except *Tasmaniacris tasmaniensis*.

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REFERENCES

CALLAN, H. G., 1941.—A trisomic grasshopper. *J. Hered.*, 32, 296-298.

CARLSON, J. G., 1936.—The intergeneric homology of an atypical euchromosome in several closely related Acridinae (order Orthoptera). *J. Morph.*, 59, 123-161.

CAROTHERS, E. E., 1913.—The mendelian ratio in relation to certain Orthopteran chromosomes. *J. Morph.*, 24, 497-506.

———————, 1917.—The segregation and recombination of homologous chromosomes as found in two genera of Acrididae (Orthoptera). *J. Morph.*, 28, 445-520.

———————, 1921.—Genetical behaviour of heteromorphic homologous chromosomes of *Circotettix* (Orthoptera). *J. Morph.*, 35, 457-483.

———————, 1931.—The maturation divisions and segregation of heteromorphic homologous chromosomes in Acrididae (Orthoptera). *Biol. Bull.*, 61, 324-329.

CARROLL, M., 1920.—An extra dyad and an extra tetrad in the spermatogenesis of *Camnula pellucida* (Orthoptera), numerical variations in the chromosome complex within the individual. *J. Morph.*, 34, 375-455.

COLEMAN, L. C., 1948.—The cytology of some Western species of *Trimerotropis* (Acrididae). *Genetics*, 33, 519-528.

DARLINGTON, C. D., 1936.—Crossing-over and its mechanical relationships in *Chorthippus* and *Stauroderus*. *J. Genet.*, 33, 465-500.

DARLINGTON, C. D. & DARK, S. O. S., 1932.—The origin and behaviour of chiasmata. II. *Stenobothrus parallelus*. *Cytologia*, 3, 169-185.

DARLINGTON, C. D. & LACOUR, L. F., 1942.—*The Handling of Chromosomes*. London: Allen & Unwin.

DAVIS, H. S., 1908.—Spermatogenesis in Acrididae and Locustidae. *Bull. Mus. Comp. Zool. Harvard*, 53, 59-158.

GRANATA, L., 1910.—Le cinesi spermatogenetiche di *Pamphagus marmoratus* (Burm.). *Arch. Zellforsch.*, 5, 182-214.

HARMAN, M. T., 1915.—Spermatogenesis in *Paratettix*. *Biol. Bull.*, 29, 262-277.

———————, 1920.—Chromosome studies in Tettigidae. II Chromosomes of *Paratettix BB* and *CC* and their hydril *BC*. *Biol. Bull.*, 38, 213-231.

HELWIG, E. R., 1929.—Chromosomal variations correlated with geographical distribution in *Circotettix verruculatus* (Orthoptera). *J. Morph.*, 47, 1-36.

———————, 1941.—Multiple chromosomes in *Philocleon anomalus* (Orthoptera: Acrididae). *J. Morph.*, 69, 317-322.

———————, 1942.—Unusual integrations of the chromatin in *Machaerocera* and other genera of the Acrididae (Orthoptera). *J. Morph.*, 71, 1-33.

KEY, K. H. L., 1952.—A provisional check-list of the Acridoidea of Tasmania (Orthoptera). *Pap. R.S. Tas.*, 86, 127.
KING, R. L. 1923.—Heteromorphic homologous chromosomes in three species of *Pseudotrimerotropis* (Orthoptera: Acrididae). *J. Morph.*, 38, 19-36.
KLINGSTEDT, H., 1939.—Morphology and spermatogenesis of *Chorthippus bicolor* Charp. X *Ch. biguttulus* L. *J. Genet.*, 37, 389-420.
LAIRD, A. K., 1943.—A study of the types of male gonads found in the Acrididae (Orthoptera). *J. Morph.*, 72, 477-490.
MCCLUNG, C. E., 1905.—The chromosome complex of Orthopteran spermatocytes. *Biol. Bull.*, 9, 304--340.
———————, 1914.—A comparative study of the chromosomes in Orthopteran spermatogenesis. *J. Morph.*, 25, 651-749.
NOLTE, D. J., 1939.—A comparative study of seven species of Transvaal Acrididae, with special reference to the chromosome complex. *J. Ent. Soc. S. Af.*, 2, 196-260.
POWERS, P. B. A., 1942.—Metrical studies on spermatogonial chromosomes of Acrididae (Orthoptera). *J. Morph.*, 71, 523-576.
RAO., T. R., 1937.—A comparative study of the chromosomes of Indian Pyrgomorphinae (Acrididae). *J. Morph.*, 61, 223-255.
REHN, J. A. G., 1948.—The Acridoid family Eumastacidae (Orthoptera): a review of our knowledge of its components, features and systematics, with a suggested new classification of its major groups. *Pro. Acad. Nat. Sci. Philad.*, 100, 77-139.
ROBERTS, R. R., 1941.—A comparative study of the subfamilies of the Acrididae (Orthoptera) primarily on the basis of their phallic structures. *Proc. Acad. Nat. Sci. Philad.*, 92, 201-246.
ROBERTSON, W. R. B., 1916.—Chromosome studies. I. Taxonomic relationships shown in the chromosomes of Tettigidae and Acrididae. V-shaped chromosomes and their significance in Acrididae, Locustidae and Gryllidae chromosomes and variation. *J. Morph.*, 27. 179-331.
———————, 1930.—Chromosome studies. V. Diploidy and persistent chromosome relations in partheno-produced Tettigidae (*Apctettix eurycephalus* and *Paratettix texanus*). *J. Morph.*, 50, 209-257.
UVAROV, B. P., 1943.—The tribe Thrinchini of the subfamily Pamphaginae and the inter-relationships of the Acridid subfamilies. *Tran. R. Ent. Soc. Lond.*, 93, 1-72.
WHITE, M. J. D., 1945.—*Animal Cytology and Evolution.* Cambridge: University Press.
———————, 1949.—A cytological survey of wild populations of *Trimerotropis* and *Circotettix* (Orthoptera, Acrididae). I. The chromosomes of twelve species. *Genetics*, 34. 537-563.
———————, 1951.—A cytological survey of *Trimerotropis and Circotettix* (Orthoptera, Acrididae). II. Racial differentiation in T. *sparsa*. *Genetics*, 36, 31-53.

EXPLANATION OF PLATE

(Figs. 58-72)

Microphotos of Feulgen squashes reproduced at a uniform magnification of X1600.

Figure 58: *Monistria flavogranulata*, spermatogonial metaphase.
Figure 59: *Monistria flavogranulata*, first metaphase.
Figure 60: *Psednura pedestris*, spermatogonial metaphase.
Figure 61: *Psednura pedestris*, first metaphase.
Figure 62: *Exarna includens*, first metaphase. The unequal bivalent (near centre) has a terminal chiasma.
Figure 63: *Exarna includens*, first metaphase. The unequal sized chromosomes are unpaired.
Figure 64: *Goniaea australasiae*, diplotene. Two bivalents are precocious and one is slightly precocious.
Figure 65: Genus and sp. n.2., late prophase of spermatogonial mitosis. One of the smallest pair of autosomes lies beneath a large chromosome and is almost obscured. The size distribution of the chromosomes shows only one pair to be markedly smaller than the remainder.
Figure 66: Genus and sp. n.2., first metaphase.
Figure 67: *Cryptobothrus chrysophorus*, first metaphase. Two supernumerary chromosomes are present forming an extra small bivalent.
Figure 68: *Cryptobothrus chrysophorus*, first metaphase. Four supernumerary chromosomes forming two extra small bivalents. One bivalent (third from right) has a supernumerary chromosome region. Figs. 67 and 68 are from the same individual.
Figure 69: *Cryptobothrus chrysophorus*, diakinesis. A cell from the cyst in which reciprocal translocation has occurred. Nine bivalents, one quadrivalent, the unpaired X chromosome and a single supernumerary are present.
Figure 70: *Cryptobothrus chrysophorus*, first anaphase. The single supernumerary divided into chromatids which are still near the equatorial plate (at right).
Figure 71: *Cryptobothrus chrysophorus*, spermatogonial mitosis. The right hand cell has seven small chromosomes. Three are supernumeraries and one of these is left off the spindle (upper left). In the cell seen in side view one supernumerary lies off the plate. Figs. 69 and 70 are from the same individual.
Figure 72: *Austroicetes pusilla*, first metaphase. Left hand bivalent beginning to separate. Metacentric bivalent second from left.


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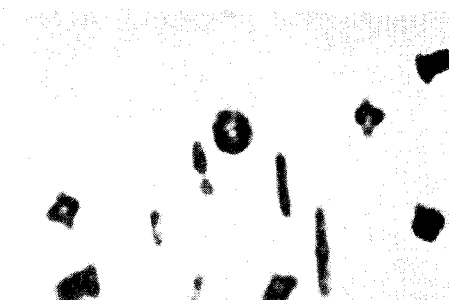
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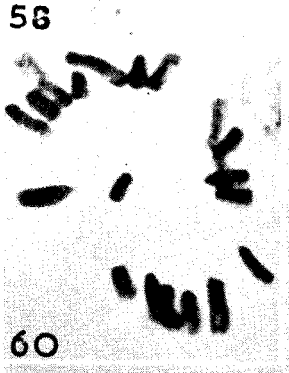
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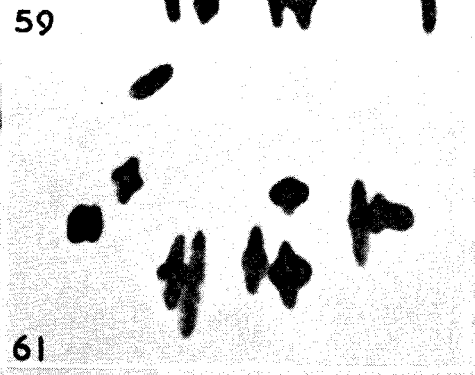
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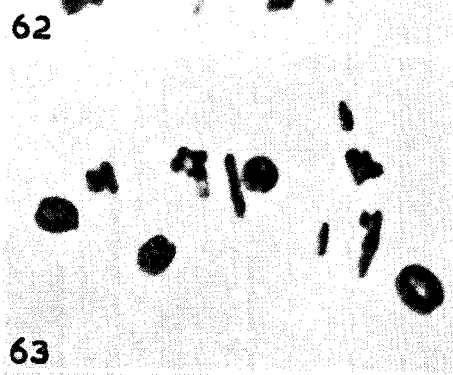
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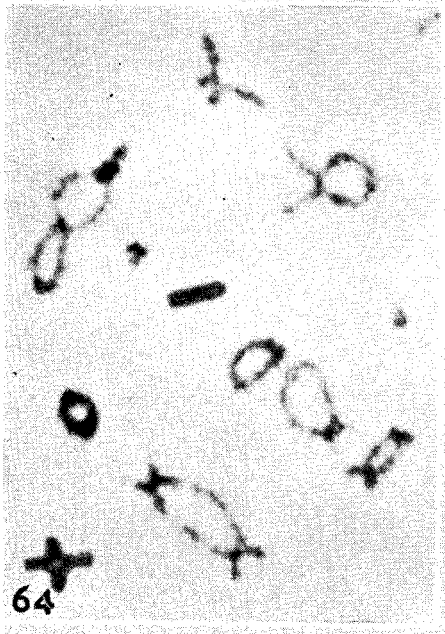
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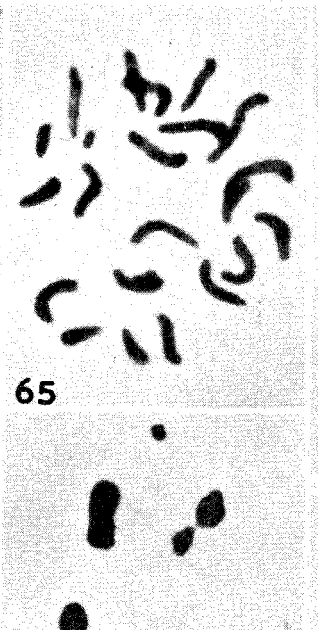
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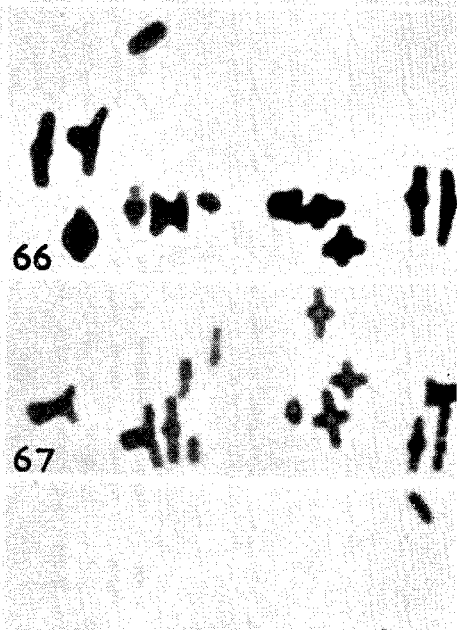
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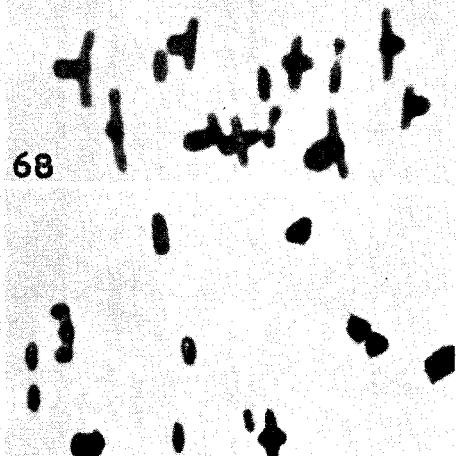
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