A CYTOLOGICAL SURVEY OF WILD POPULATIONS OF TRIMEROTROPIS AND CIRCOTETTIX. (ORTHOPTERA, ACRIDIDAE). I. THE CHROMOSOMES OF TWELVE SPECIES

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INTRODUCTION

IN RECENT years a great deal of work has been carried out on the distribution of structurally different chromosomal types in wild populations of Drosophila (DOBZHANSKY 1947 a, b, c, 1948; DOBZHANSKY and EPLING 1944; WARTERS 1944; CARSON and STALKER 1947). Similar studies have also been carried out on some species of Chironomus (PHILIP 1942; HSU and LIU 1948). Comparisons have been made between different populations of the same species and between samples of the same population collected at different seasons of the year and in several successive years.

These studies have been almost entirely concerned with one particular type of chromosomal rearrangements, namely paracentric inversions. In the case of *Drosophila pseudoobscura*, the species which has been studied most extensively, it was found by DOBZHANSKY that individuals heterozygous for inversions were, as a rule, better adapted under natural conditions than either of the two homozygous types. Thus, if we call one gene-sequence A and the other A', individuals of the constitution AA' possessed a higher degree of fitness than either AA or $A'A'$ individuals, although the relative fitness of the various types showed regular seasonal fluctuations. Results such as these (which can be duplicated in laboratory experiments carried out under controlled environmental conditions in "population cages") explain the existence of the multiplicity of different gene-sequences known for the chromosomes of *D. pseudoobscura* and some other species of the genus Drosophila. Thus, in the example we have chosen, natural selection will never lead to the extinction of either sequence A or A', as it might if the viability of the heterozygotes were intermediate between the viabilities of the two homozygous types or lower than either of them.

Heterozygosity in respect of paracentric inversions is not, however, the only type of cytological heterogeneity present in natural populations of animals. In the grasshoppers such inversions seem to be completely absent in the wild populations of most species, doubtless because they would cause some degree of sterility in a group where chiasma formation occurs in the male.[1] Neverthe-

[1] The only authors who have found inversions in grasshoppers are DARLINGTON (1936), who found typical "inversion bridges" and acentric chromosome fragments in several individuals of *Chorthippus parallelus* and *Stauroderus bicolor*, and COLEMAN (1947) who states that they are common in grasshoppers, without giving any details.

less, in one group of grasshoppers a type of structural rearrangement is found in the populations of many species which is completely unknown in Drosophila. The group in question consists of the Trimerotropis-Circotettix-Aerochoreutes complex of genera which belong to the sub-family Oedipodinae (Banded-wing grasshoppers) and the structural rearrangements are transpositions ("shifts") of the centromere. Such populations were studied by the earlier workers on orthopteran cytology (CAROTHERS, KING, HELWIG) during the years 1914–1929, but these authors were concerned, in the main, with using this extremely favorable material to test and prove the independent segregation of the homologous chromosomes at meiosis. Only in the work of HELWIG (1929) do we find an approach towards a study of the population-dynamics of these cytologically polymorphic species of grasshoppers.

In the light of the extensive studies of DOBZHANSKY and the theoretical work of WRIGHT it now appears that it would be worth while to re-investigate the cytology of the natural populations of these Trimerotropine grasshoppers, with a view to determining the frequencies of the various chromosomal types, whether significant differences in respect to these frequencies exist between geographically remote or isolated populations, and whether these frequencies are determined by the same general principles as seem to govern the distribution of inversions in Drosophila populations. Such a task will necessarily involve several years' work and the present paper is merely a preliminary discussion of the problem, reporting briefly on the cytological conditions encountered in the eleven species of the group which we succeeded in collecting during a month's trip (June 1948) through New Mexico, Arizona, Nevada, Utah and Colorado, and one species which we studied several years ago.

TAXONOMY OF THE TRIMEROTROPINE GRASSHOPPERS

Of the three genera to be considered in this series of papers, Trimerotropis is by far the largest and, for reasons to be discussed below, was probably ancestral to Circotettix and possibly also to Aerochoreutes. With the exception of two species found in South America (one of which is endemic in Chile) it is confined to North America, ranging from Canada to the state of Oaxaca at the extreme southern end of the Mexican central plateau. It has been recently estimated (BALL, TINCKHAM, FLOCK and VORHIES 1942) that 43 species of Trimerotropis exist in N. America, but since the taxonomy of some sections of the genus is still in a confused state, this estimate is necessarily a rough one. Many of the species show extensive geographical variation so that in order to be certain of the existence of discontinuities between one form and another it is necessary to examine individuals from a large number of localities covering the whole range of the forms in question. To describe a new species, even on the basis of a large series of individuals *if these are all from a single locality*, is clearly unsafe in the case of many sections of Trimerotropis, since one may be dealing merely with a local variant of some previously recognized species. Many of the "species" of MCNEILL (1901) are synonyms created as a result of errors of this kind. In this respect the Trimero-

tropine grasshoppers are a complete contrast to Drosophila, where the external morphology of the species shows little geographical variation.

The majority of the forty-odd species of Trimerotropis are confined to the western half of the U. S. A. Only four occur east of the Mississippi; these are *T. maritima* Harris, which occurs on sandy ocean beaches from Maine to Florida, and which is represented by a distinct subspecies, *T. maritima interior*, along the shores of the Great Lakes; *T. acta* Hebard, from Southern Florida, *T. citrina* Scudder which ranges from Maryland to the Pecos river in Texas and New Mexico; and *T. saxatilis* McNeill which is found from N. Carolina to Arkansas and northeast Texas. A fifth eastern species is *T. schaefferi* Caudell, from the Gulf Coast of Texas. The remainder of the species are mainly confined to the Rocky Mountains, Intermontane Plateaus and Pacific Mountain System, although *pistrinaria* and *pallidipennis* extend into East Texas. The extent to which members of the genus occur in northern Mexico is only imperfectly known (*pallidipennis* ranges over most of the Mexican central plateau, and several species have been recorded from Baja California). Most of the Trimerotropi are essentially grasshoppers of arid regions and in the eastern U. S. A. they are only found on rocky hillsides (*T. saxatilis*), sandy coastal areas (*T. maritima*, *T. acta*, *T. schaefferi*) and other arid localities (*T. citrina*).

On cytological grounds we may divide the genus Trimerotropis into two sections. In the first of these are those species in which all the chromosomes (including the X) are acrocentric (rod-shaped). Since this is the condition which is almost universal in the Acrididae (except for a few aberrant genera) it is clear that these are the primitive species of the genus, in which the centromeres of all the chromosomes still retain an almost terminal position. We have previously (WHITE 1945) mentioned *T. maritima* and *T. citrina* as belonging to this group; to these COLEMAN (1948) has added *T. fontana* and *T. praeclara* and we are now able to add three more species (see below). We shall refer to this group of species as section A of the genus; it seems undesirable to create a named subgenus until it has been shown that all the species with acrocentric chromosomes form a taxonomically compact and homogeneous group.

Section B comprises those species of Trimerotropis in which some of the chromosomes have become metacentric (V-shaped). Since no reduction in chromosome number has taken place (except in *T. cyaneipennis*, which has 21 chromosomes in the male instead of 23) it is clear that these metacentric elements have arisen from acrocentric ones by some sort of shift of the centromere (that is, a homosomal rearrangement in the terminology of MULLER (1940)). The exact number of metacentric elements varies within group B from species to species, and in some species from individual to individual. In all species hitherto studied, however, the X chromosome is a metacentric; it must therefore have undergone a centromere shift early in the phylogenetic history of Section B.

Where the number of metacentric chromosomes varies from individual to individual it is clear that we have a rather complex situation in the natural populations of the species. A particular chromosome may be represented by

two acrocentric elements in one individual, by an acrocentric and a metacentric in another and by two metacentrics in a third. In most of the species of group B there are some chromosomes which are invariably metacentric and some which are sometimes metacentric and sometimes acrocentric; but group B also includes some species which show no cytological variation from individual to individual, certain chromosomes being invariably acrocentric, others invariably metacentric. We may call the latter cytologically monomorphic species, the former cytologically polymorphic.

The genus Circotettix is almost entirely confined to the mountainous regions of western N. America, only a single species (*verruculatus* Kirby) being found in the mountains of the eastern U. S. A. (Maine, Massachussetts, New Hampshire, Connecticut, New York, New Jersey and Pennsylvania to Michigan). The members of this genus are essentially characteristic of rocky, forested regions over 5000 feet. Morphologically, they may be distinguished from species of Trimerotropis by the fact that certain of the veins of the hind wing are thickened; as a consequence of this the insects make a loud clattering sound with their wings while in flight.

According to the revision of REHN (1921) there are eight species of Circotettix, namely *undulatus* (Thomas), *verruculatus* Kirby, *thalassinus* Saussure, *shastanus* Bruner, *splendidus* Rehn and Hebard, *rabula* Rehn and Hebard, *coconino* Rehn and *crotalum* Rehn. The genus is closely related to Trimerotropis, and may be regarded as a montane derivative of it. Its affinities are clearly with section B of Trimerotropis rather than with section A, *T. suffusa* (formerly included by some authors in Circotettix) forming a connecting link.

Cytologically, the four species of Circotettix that have been investigated all present the same type of chromosome set as the members of section B of Trimerotropis, that is, they all have the X chromosome and some of the autosomes metacentric. They differ, however, from all species of Trimerotropis except *T. cyaneipennis* in having only 21 chromosomes in the male instead of 23.

The genus Aerochoreutes (REHN 1921) includes only a single species, *A. carlinianus* (Thomas) from British Columbia, Washington, Idaho, Montana, Wyoming, Nevada, Utah and Colorado. We have no personal experience of this species, but according to a statement by HELWIG (1942) it possesses metacentric chromosomes of the same type as those found in Circotettix and section B of Trimerotropis. It may have evolved from the same stock, although REHN (1921) has stated that it shows some affinities to the Old World genus Bryodema, whose cytology has not been studied.

The centromere shifts which are so characteristic of section B of Trimerotropis and of the genera Circotettix and Aerochoreutes may be defined as evolutionary conversions of acrocentric (rod-shaped) chromosomes into metacentric (V- or J-shaped) elements. This process has taken place without any reduction of chromosome number, that is, it is not a centric fusion (WHITE 1945). In an individual heterozygous for a centromere-shift there will be a pair of homologous chromosomes, one of which is a rod, the other a J or a V. Such a pair will obviously form an asymmetrical bivalent at meiosis. On the other hand if the individual is homozygous for a centromere-shift (that is, if it has a

pair of homologous V's), these latter will form a symmetrical 'metacentric bivalent' at meiosis.

There can be no doubt that the conversion has been from acrocentric to metacentric chromosomes (and not *vice-versa*) since the acrocentric type is the one almost universally found in the Acrididae, and especially in the subfamily Oedipodinae and the primitive section A of Trimerotropis. Theoretically, a centromere shift could occur in several different ways. We earlier assumed that the centromere shifts in this group of grasshoppers had probably arisen by pericentric inversions. If so, bivalents heterozygous for such a transposition should show a characteristic inversion-loop at pachytene. According to COLEMAN (1948), however, no loops can be seen in such bivalents at pachytene, pairing being complete from one end of the bivalent to the other, with no loops, unpaired regions or other peculiarities. This observation would seem to indicate that the centromere shifts of the Trimerotropi simply involved the transference of the centromere (perhaps with a minute region of the chromosome on either side) from a quasi-terminal to an interstitial position. Whether such a rearrangement involves two or three breakage points is uncertain; if MULLER's (1940) theory, according to which a chromosome end ('telomere') can never become interstitial, is correct, than a centromere-shift must necessarily involve three breakage-points. Otherwise, it is possible that only two breakage-points are necessary for such a rearrangement.

MATERIALS AND METHODS

The testes of male individuals were fixed in the field, either in San Felice's fixative or in acetic alcohol (1:3). Material fixed in the former fluid was later sectioned at 24 micra and stained by Newton's method. The testes fixed in acetic alcohol, on the other hand, were stained in bulk by the Feulgen technique, the individual follicles being then dissected out on a slide in 50 percent acetic acid and the lower part of each follicle, containing only sperm, being removed and discarded. The upper parts of the follicles were then lightly squashed under a cover-glass which was subesquently soaked off in acetic alcohol, the preparation being finally mounted in diaphane.

These methods are very different from those employed by the earlier workers who used Iron Alum Haematoxylin and were consequently obliged to cut their sections at 7–12 micra. These investigators rarely, if ever, were able to study whole nuclei, their illustrations being composite drawings built up from observation of two or even three successive sections. It will be obvious that the more modern techniques, using dyes that do not stain the cytoplasm appreciably and which consequently premit much thicker preparations (sections or squashes) to be used, are not only far quicker but also far less likely to lead to errors of interpretation.

The text figures illustrating the present paper are camera-lucida drawings reproduced at a uniform magnification of $\times 1860$. We have taken the liberty of altering the relative positions of the chromosomes in drawing them, where overlapping of two or more chromosomes would lead to difficulties in interpretation if they were shown in their natural positions.

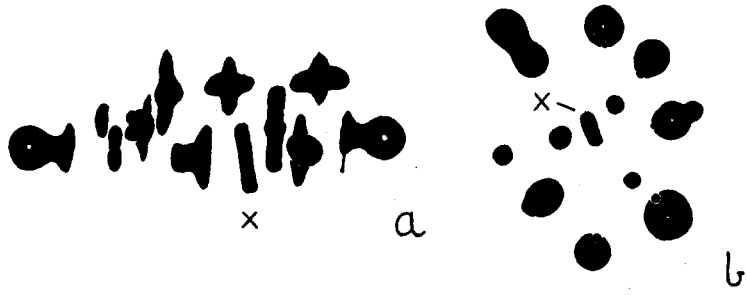
OBSERVATIONS

T. maritima Harris

We carried out a brief cytological examination of this species some years ago and found that it belongs to section A of the genus Trimerotropis, that is, all the 23 chromosomes in the male are acrocentric. We found no unequal bivalents or supernumerary chromosomes or any other cytological features of interest in five individuals studied.

T. citrina Scudder

A large population of this species was found along the sandy shores of the Pecos River, in the vicinity of Santa Rosa, N. M. (June 30). This is probably



TEXT-FIG. 1. *Trimerotropis citrina:* first metaphases. *a*, polar view; *b*, side view.

on the extreme western limit of the species, since HEBARD (1929) has shown that records from Colorado are erroneously based on material of *T. campestes*.

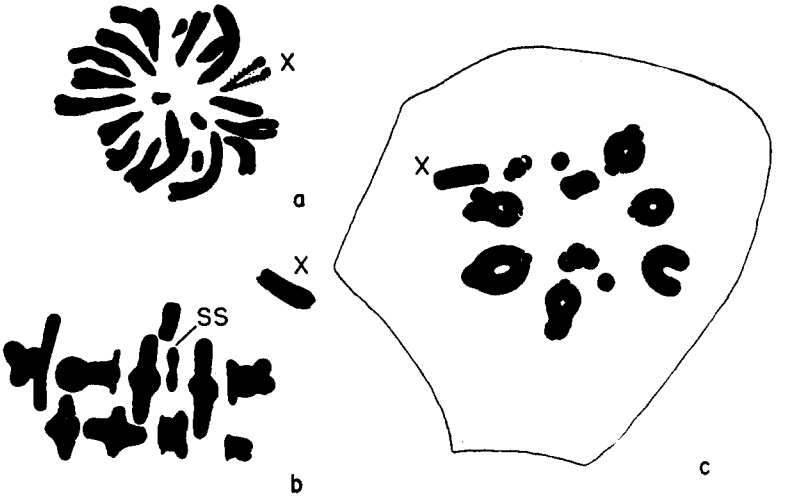
As is evident from the work of CAROTHERS (1931) this species belongs to section A of Trimerotropis—that is, it has all the chromosomes acrocentric. The three individuals studied by us did not show any cytological features of interest. The chiasma frequency is rather high for a Trimerotropis, as can be seen from figure 1. (the two largest bivalents frequently show three chiasmata each).

T. bilobata Rehn and Hebard

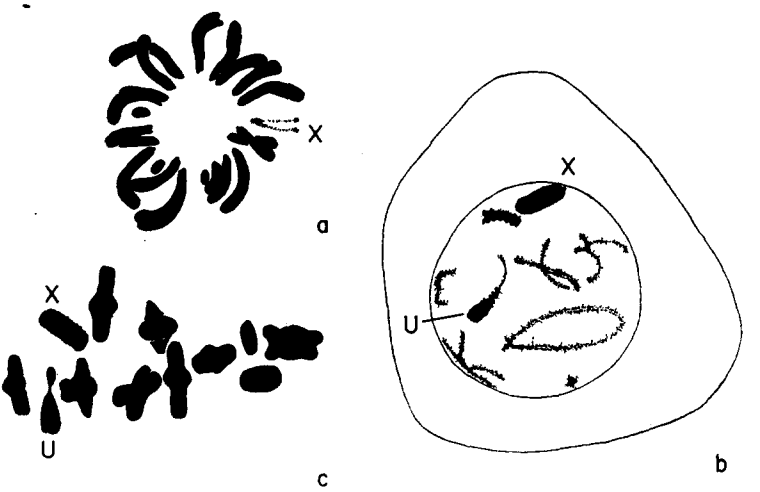
Three males and a single female of this species were collected in the sage-brush desert at a point about five miles northwest of Las Vegas, Nevada, on June 14, 1948.

As shown in figures 2 and 3, this species is a member of section A of the genus, all the chromosomes, including the X being acrocentric. Of the three males one possesses an unequal pair of chromosomes, while the other two are homozygous for the smaller member of this pair. In the homozygous individuals (fig. 2) the spermatogonial metaphases show three small chromosomes while in the heterozygous individual (fig. 3) there are only four small chromosomes, the homolog of one of them being one of the medium-sized chromosomes. In diplotene and diakinesis the unequal bivalent is very evident (fig. 3b) and one

can see that the 'extra' region which is present in the larger member of the pair is heterochromatic. At first metaphase the unequal bivalent shows up very clearly, the smaller chromosome being directed toward one pole, the larger one toward the opposite pole. Apparently a single chiasma is regularly formed in



TEXT-FIG. 2. *Trimerotropis bilobata:* cytologically homozygous individuals. *a*, spermatogonial metaphase; *b*, first metaphase in side view; *c*, in polar view. SS, the smallest bivalent (homozygous).



TEXT-FIG. 3. *Trimerotropis bilobata:* the individual with an unequal bivalent (U). *a*, spermatogonial metaphase (note that there are only 3 small chromosomes); *b*, diplotene (not all chromosomes shown); *c*, first metaphase in side view.

this bivalent (and never more than one). From a study of the small number of first anaphases and second divisions which occurred in the material it seems probable that the large and small members of this chromosome pair always separate at the first anaphase, and never at the second. We believe that the

'extra' region in the large member is proximal (that is, next to the centromere or including it) and that the chiasma is always at the distal end of the bivalent.

We hope to carry out more extensive work on the distribution of the long and the short types of this chromosome in natural populations of *T. bilobata*, a species which is widespread in the Great Basin.

T. latifasciata Scudder

Considerable doubt exists as to the specific distinctness of *T. latifasciata* Scudder (1880) and *T. laticincta* Saussure (1884). Provisionally, we shall consider them as synonymous, although TINCKHAM (1947) has followed MCNEILL (1901) in regarding them as distinct. The name *latifasciata* has been applied to specimens from the Great Basin area in which the band on the hind wing is narrower than in individuals from the Upper Sonoran zone of New Mexico and Arizona, heretofore called *lacticincta*. It is possible that the two forms are connected by a complete series of intermediates, constituting a cline, or they may prove to be "sibling species." HEBARD (1929) treats them, somewhat doubtfully, as distinct species. *T. melanoptera* NcNeill belongs to the same group of species and has an even broader band on the wing than *laticincta*.

TABLE 1

Trimerotropis latifasciata

Numbers of chromosomes in second meiotic divisions of individuals with one supernumerary chromosome.

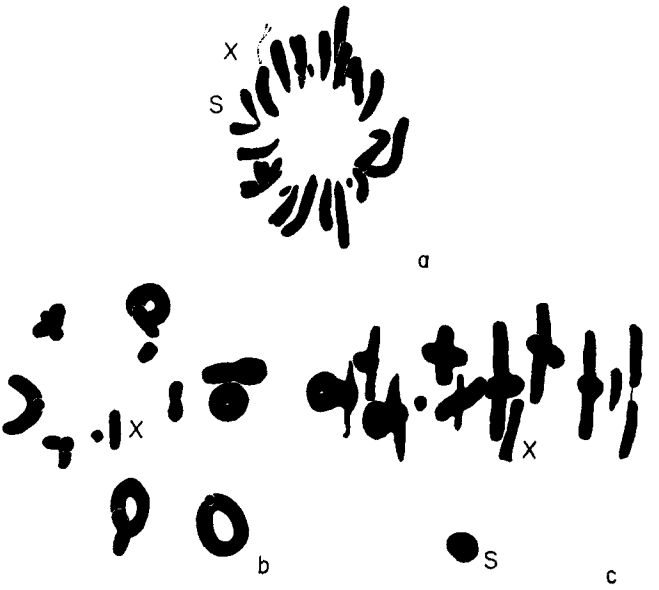
INDIVIDUAL NO.	11 CHROMOSOMES (THAT IS WITHOUT EITHER X OR SUPERNUMERARY)	12 CHROMOSOMES (THAT IS WITH EITHER X OR SUPERNUMERARY	13 CHROMOSOMES (THAT IS WITH BOTH X AND SUPERNUMERARY)
777 H	10	20	7
777 L	17	25	20
Total	27	45	27

T. snowi Rehn 1905 is a strict synonym of *latifasciata*.

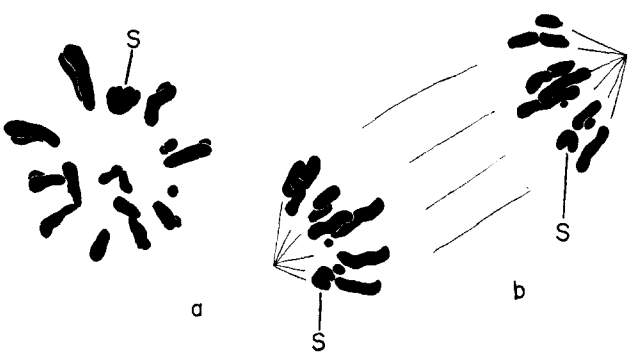
On July 1, 1948 we found a very dense population of *latifasciata* at Bottomless Lakes State Park, just E. of Roswell, N. M. The insects were extremely active and hard to catch, only 15 males being secured in about an hour's collecting. The rather local Truxaline *Pedioscirtetes maculipennis* was also common at this locality.

This proves to be one of those species of Trimerotropis in which all the chromosomes, including the X, are rod-shaped (acrocentric). It accordingly falls into section A of the genus. Of the 15 males two possessed a supernumerary chromosome, having 24 elements instead of 23 in the mitotic set. The extra element (fig. 4a) is a metacentric chromosome with arms of exactly (or almost exactly) equal length. In the two individuals with a supernumerary, this was present in every spermatogonial metaphase or anaphase examined, and in numerous cysts of spermatocytes in diplotene, diakinesis or first metaphase.

The supernumerary is thus not like those of Camnula (CARROLL 1920) which may be present in some cells and absent in others in the same individual; its mitotic behavior must be quite regular. At the first meiotic division it always seems to pass undivided to one pole with the other chromosomes, with-



TEXT-FIG. 4. *Trimerotropis latifasciata: a*, spermatogonial metaphase from an individual with a supernumerary chromosome (S); *b*, a first metaphase, in polar view, from an individual without any supernumerary; *c*, a first metaphase, in side view, from an individual with a supernumerary.



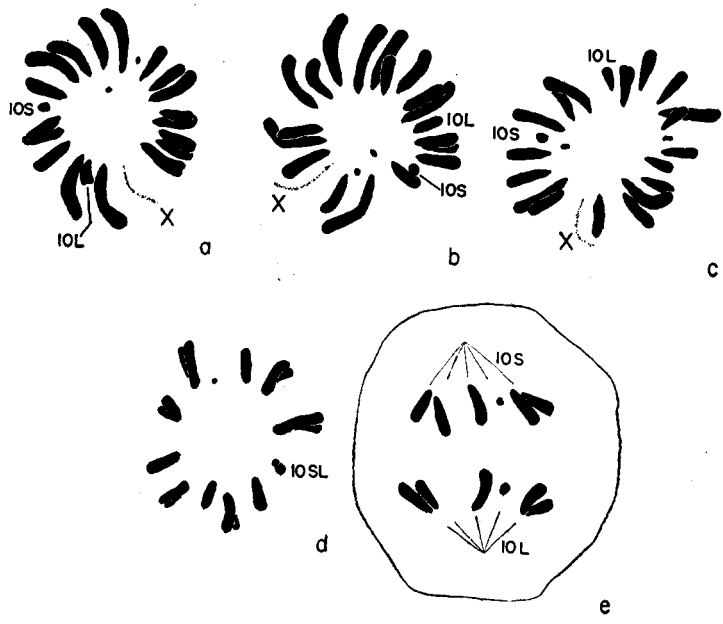
TEXT-FIG. 5. *Trimerotropis latifasciata: a*, second metaphase, showing the supernumerary (S); *b*, second anaphase, showing the division of the supernumerary.

out lagging on the spindle. None of the numerous anaphases and telophases of the first division which were studied suggested that the supernumerary was ever lost during the first division. A study of 99 second meiotic divisions in this material (table 1) is also quite compatible with the view that the supernumerary never divides and is never lost in the first division. Whenever it can be recognized as a metacentric element in second divisions (fig. 5a) one can always

see that it is split in preparation for the second anaphase, at which time it regularly divides.

T. sp. (= *T. titusi of* TINCKHAM, *not of* CAUDELL).

Two males and a female of a small Trimerotropis with distinctly-banded tegmina and yellow hind tibiae were collected June 24 at the entrance to Hualpai Mountain Park, near Kingman, Arizona. They agree in every respect with



TEXT-FIG. 6. *Trimerotropis sp.* (*titusi* of Tinckham): *a–c*, spermatogonial metaphases from individuals in which the 10th pair of chromosomes consists of two elements of unequal size (10 S and 10 L); *d*, a second metaphase in polar view, with one element made up of a 10 S chromatid and a 10 L one; *e*, a second anaphase in side view, with 10 S and 10 L separating from one another (not all chromosomes shown).

TINCKHAM'S (1947) description of a form which he collected at the same locality and also at a locality north of Prescott, Arizona. TINCKHAM identified his material as *T. titusi* Caudell, a species from the coastal regions of California, but a comparison of our material with paratypes of *titusi* at the Academy of Natural Sciences, Philadelphia, makes it clear that this determination was erroneous. At the present time we are quite unable to identify the Hualpai form; it may constitute a new species or be a rather distinct geographical race of some already known species.

As shown in figure 6, this species definitely belongs to section A of the genus Trimerotropis, since all the chromosomes are acrocentric. A study of the spermatogonial metaphases revealed that in both individuals there were only three (instead of the expected four) small chromosomes. Two of these, which are minute, obviously constitute a pair, but the third, which is considerably larger,

has no obvious mate. It is only when we come to study the meiotic divisions that the position becomes clear: both individuals have an unequal bivalent of the type met with in individual No. 724 of *T. bilobata*. Apparently, however, the chiasma which is formed in this bivalent occurs between the centromere and the 'supernumerary segment' of the larger homolog (which we call 10 L, in contradistinction to the shorter element 10 S). Thus the segregation of the 10 L and 10 S chromatids from one another does not take place until the second anaphase (fig. 6 e). The behavior of this pair of chromosomes is thus exactly like that of the similarly unequal pair described by CAROTHERS (1931) in 11 out of 71 individuals of *T. citrina* (see her figures 2, 3, and 10).

T. pallidipennis pallidipennis Burmeister

This species has a wider distribution than any other member of the genus Trimerotropis. It ranges over almost the whole of western N. America, from Texas to California and from British Columbia and Alberta to the state of Oaxaca, at the extreme southern end of the Mexican Central Plateau. In Central America it is completely absent, but it reappears in Ecuador and is widely distributed in South America as far south as Patagonia (REHN 1939). Essentially a species of arid regions, it appears to thrive in a great variety of habitats and is frequently one of the commonest grasshoppers met with in semi-desert regions. In the earlier literature this species is referred to as *T. vinculata* Scudder.

Our material of *pallidipennis* was obtained from the following localities:

(1) 25 miles N. of Van Horn, Culberson Co., Texas (3 males studied).
(2) San Augustine Pass, Organ Mts. Doña Ana Co., N. M. (15 males studied).
(3) Pecos River near Santa Rosa, N. M. (3 males studied).
(4) 12 miles E. of Shiprock, N. M. (1 male studied).
(5) 21 miles North of Abiquiu, N. M. (8 males studied).
(6) Chiricahua Mountain Pass ,Cochise Co., Arizona (2 males studied).
(7) 16 miles North of Bridgeport, Ariz. (6 males studied).
(8) 12 miles N. E. of Payson, Ariz. (10 males studied).
(9) Kingman, Ariz. (1 male studied).
(10) Mormon Mesa N. E. of Moapa, Nevada (1 male studied).
(11) 46 miles N. W. of Las Vegas, Nevada (5 males studied).

Cytologically, *pallidipennis* proves to be a member of section B of Trimerotropis, since it has the X chromosome and three pairs of autosomes always metacentric. This is the condition invariably found in all the males studied by us. On the other hand, COLEMAN (1948) reports that 2 out of 16 males studied by him (from Vancouver Island) had only two metacentric bivalents. If this report is reliable it would seem to indicate an interesting difference between the populations of the species at the extreme northern end of its range and those found further south.

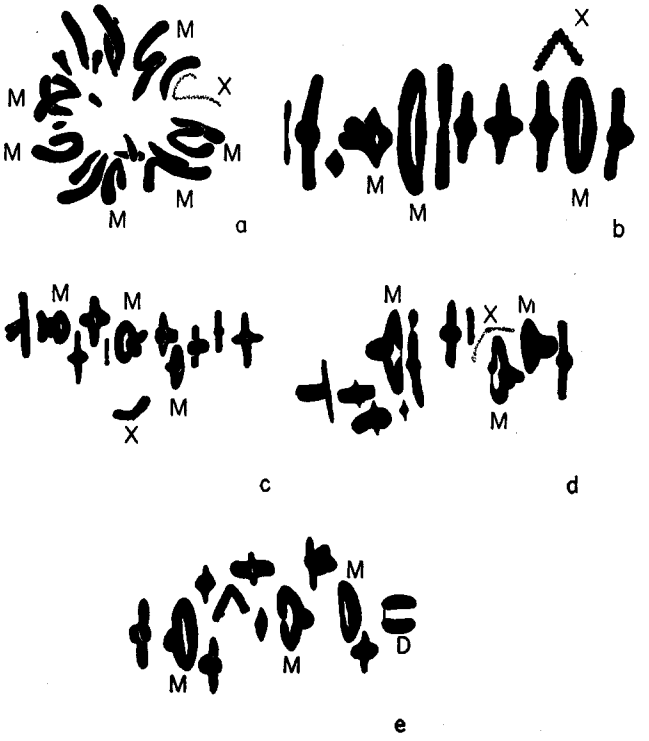
It will be seen from table 2 that in the overwhelming majority of the first spermatocytes all three metacentric bivalents form chiasmata in both arms.

TABLE 2

*Chiasmata in the three metacentric bivalents of T. pallidipennis**

INDIVIDUAL NO.	No. of Cells Having: 3 BIVALENTS WITH CHIASMATA IN BOTH ARMS	2 BIVALENTS WITH CHIASMATA IN BOTH ARMS	1 BIVALENT WITH CHIASMATA IN BOTH ARMS	0 BIVALENT WITH CHIASMATA IN BOTH ARMS
695 E	16	4	–	–
695 F	13	1	2	–
695 G	16	3	1	–
695 S	12	1	–	–
754 B	18	4	–	1
754 C	18	2	–	–
Total	93	15	3	1

* The actual number of chiasmata is not given in Tables 2–6; sometimes more than one is present in a chromosome arm, but this cannot always be determined with certainty at metaphase.



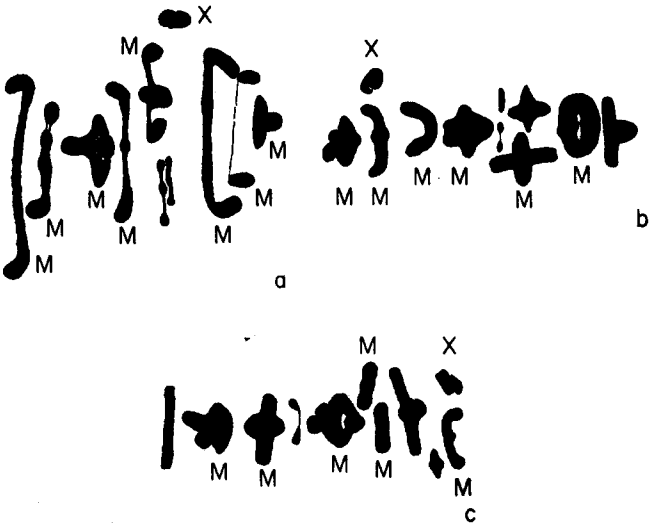
TEXT-FIG. 7. *Trimerotropis pallidipennis: a*, spermatogonial metaphase, with the six metacentric autosomes labelled M; *b–e*, first metaphases in side view, showing the three metacentric bivalents always present. *b* and *e* are from Feulgen squash preparations in which the chromosomes always appear larger than in sectioned material. In *e* one of the bivalents (D) shows a chiasma in the short arm and none in the long arm.

These bivalents form from one to three chiasmata, ring-bivalents with two chiasmata being the most common type. The acrocentric bivalents mostly have only one chiasma, occasionally two in the larger bivalents.

There is one autosomal bivalent in *pallidipennis* which quite frequently forms a single chiasma in the *short arm* (element D in fig. 7e). Occasionally it may form one chiasma in the short arm and one in the long arm, but this is exceptional. In a single first metaphase in one individual (No. 768E from 21 miles north of Abiquiu, N. M.) this element was represented by two univalents; obviously, either pairing or chiasma formation had failed to occur.

T. cyaneipennis Bruner

Two males of this species were studied cytologically. The first was collected



TEXT-FIG. 8. *Trimerotropis cyaneipennis: a*, first metaphase, side view, from individual No. 785; *b* and *c*, first metaphases from individual No. 730. M, metacentric bivalents; in *a* two of the eight metacentric bivalents have chiasmata in both arms, in *b* four of the six do so, in *c* five metacentric bivalents have chiasmata in both arms.

in a box canyon on Stonewall Mountain, approximately 18 miles southeast of Goldfield, Nevada (June 15), the second at Caliente, Nevada (June 20).

As determined by KING (1924) this species of Trimerotropis is apparently unique in having only ten pairs of autosomes, that is, the spermatogonia contain 21 instead of the usual 23 chromosomes. The first individual (No. 730) was homozygous for six pairs of metacentric chromosomes, the second one (No. 785) was homozygous for eight such pairs. In both the X was metacentric, as in other members of Section B. Neither individual possessed supernumerary chromosomes or was in any way cytologically heterozygous.

KING (1924) studied seven individuals of this species from the Grand Canyon. Most of these seem to have been heterozygous for one centromere-shift, but the potential heterozygosity was greater than this, since the number of meta-

TABLE 3

Chiasmata in the metacentric bivalents of T. cyaneipennis

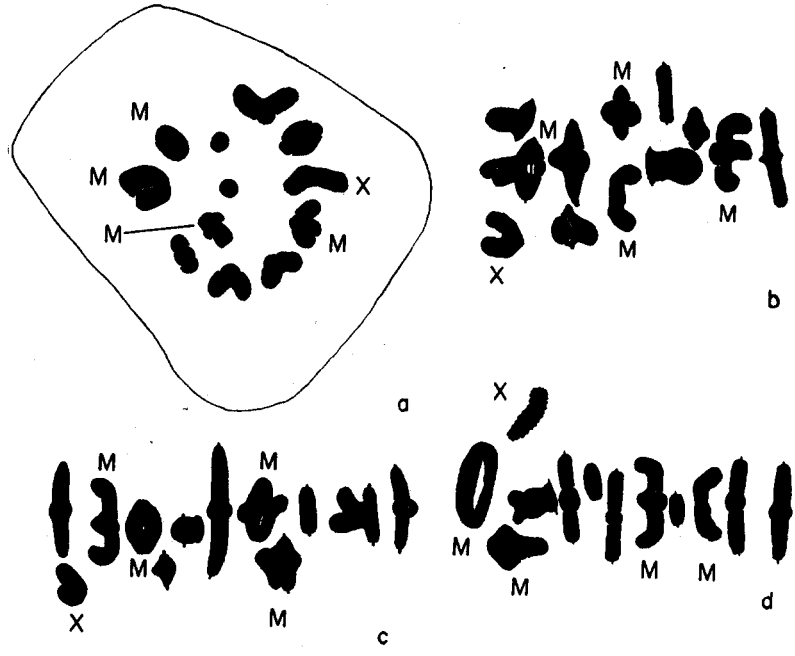
INDIVIDUAL NO.	No. of Cells Having: 5 bivalents with chiasmata in both arms	4 bivalents with chiasmata in both arms	3 bivalents with chiasmata in both arms	2 bivalents with chiasmata in both arms
730 (6 metacentric bivalents)	4	3	–	–
785 (8 metacentric bivalents)	1	3	3	8

centric chromosomes ranged from 13 (as in our No. 730) to 17 (as in our No. 785). One of KING's individuals possessed a supernumerary chromosome.

Some data on the distribution of the chiasmata in the metacentric bivalents of our two individuals are given in table 3. It will be noted that most of the metacentric bivalents form chiasmata in one arm only, which is not unexpected if these bivalents are liable to be heterozygous in some individuals.

T. suffusa Scudder

This is a highly variable species which may be separable into several geographical races. HEBARD (1929) concluded that *T. fallax* Saussure was at best



TEXT-FIG. 9. *Trimerotropis suffusa: a*, first metaphase in polar view; *b–d*, first metaphases in side view.

only a western subspecies of *suffusa*, but the exact status of the forms included in this group is still uncertain.

So far, we have only studied a single individual of *T. suffusa*, from a locality 21 miles north of Abiquiu, N. M. (June 29). This grasshopper was homozygous for four metacentric chromosomes, and in addition possessed a metacentric X, like all the species of section B. Although spermatogonial metaphases were not found in the slides, they must have contained nine metacentric elements and fourteen acrocentrics. This is very close to the average of 8.9 metacentrics determined by CAROTHERS (1917) for material of this species (her 'form B'). No supernumerary chromosomes were present in the Abiquiu individual, although they were found in some individuals of this species by CAROTHERS and COLEMAN. We give, in table 4 some data on the distribution of chiasmata in the four metacentric bivalents of the Abiquiu individual.

TABLE 4

Chiasmata in the four metacentric bivalents of T. suffusa (individual No. 769)

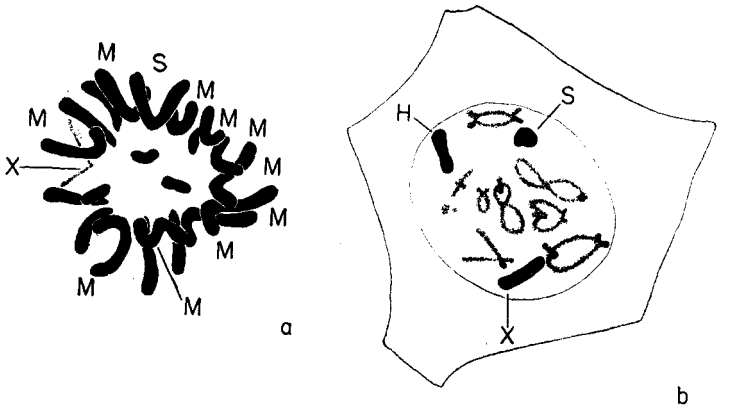
No. of Cells Having:			
4 bivalents with chiasmata in both arms	3 bivalents with chiasmata in both arms	2 bivalents with chiasmata in both arms	1 bivalents with chiasmata in both arms
—	4	33	13

C. undulatus Thomas

A single individual of this species was collected at Kingston Canyon, just below Toiyabe Range Peak, Nye Co., Nevada. Like other species of the genus, this one proves to have only ten pairs of autosomes.

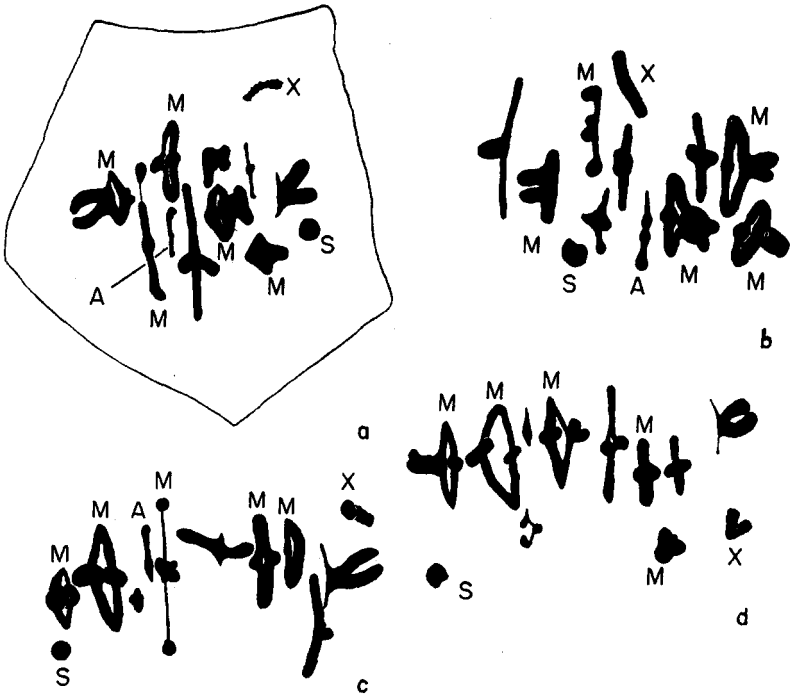
The individual studied possesses a supernumerary chromosome which like those of *T. latifasciata*, is a metacentric element with arms of equal (or almost equal) length, as can clearly be seen in spermatogonial metaphases; it is not difficult to distinguish the supernumerary from the metacentric autosomes, since the latter all have arms of distinctly unequal lengths (fig. 10 a). During the prophase of the first meiotic division the nuclei show three heteropycnotic bodies (fig. 10 b). One of these is regularly sausage-shaped and represents the X, the second is a heteropycnotic autosomal bivalent and the third is the supernumerary, very much condensed and appearing almost spherical or slightly bilobed or kidney-shaped.

The behavior of the supernumerary chromosome at the anaphase of the first meiotic division differs from that of the supernumerary in *T. latifasciata* and is somewhat variable. It nearly always lags behind the other chromosomes in the spindle (fig. 12 a and b). In the majority of cases it seems to pass undivided to one of the two daughter cells, appearing as a four-armed body, which may be included in the main interkinetic nucleus but which more frequently forms a small supplementary micronucleus adjacent to the main nucleus. In some instances, however, the supernumerary divides in the late anaphase of the first division, in which case its two halves always seem to pass to opposite poles, so



TEXT-FIG. 10. *Circotettix undulatus:* an individual with a supernumerary chromosome. *a*, spermatogonial metaphase, showing ten ordinary metacentric autosomes and the supernumerary (S); *b*, diplotene, showing the three heteropycnotic elements, the X, the supernumerary and a heteropycnotic autosomal bivalent.

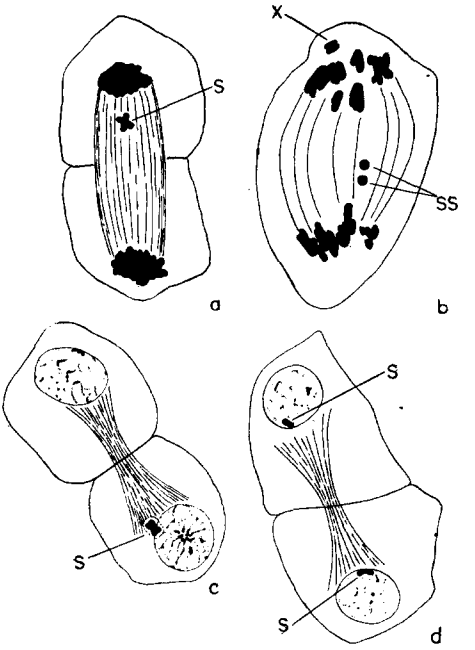
that each daughter cell receives a supernumerary element. The limited material available (a single cyst of first anaphases, telophases and interkinetic cells) did not provide any evidence of loss of supernumerary chromosomes during the first division, nor were any instances of the two daughter super-



TEXT-FIG. 11. *Circotettix undulatus:* first metaphases. S, the supernumerary chromosome, M., the metacentric bivalents. A, the small asymmetrical bivalent (not recognizable in *d*).

numeraries passing to the same pole seen. There were no cysts of second meiotic divisions in the material available, but it is reasonable to suppose that those supernumeraries which have divided in the first division do not do so in the second one, and that those which have not divided in the first division do so in the second. If so, an individual with a single supernumerary (such as the particular specimen studied) would produce equal numbers of sperms with and without the supernumerary.

The supernumerary shows marked positive heteropycnosis during inter-



TEXT-FIG. 12. *Circotettix undulatus:* first anaphases and telophases.

kinesis, that is, it remains condensed and dark-staining long after the other chromosomes, including even the X, have become de-condensed and weak-staining.

The present individual possessed five pairs of large metacentric chromosomes. At meiosis all of these may form chiasmata in both arms, but they do not always do so (table 5). In addition one of the two smallest bivalents is

TABLE 5

Circotettix undulatus—Individual No. 783 (with 5 metacentric bivalents)

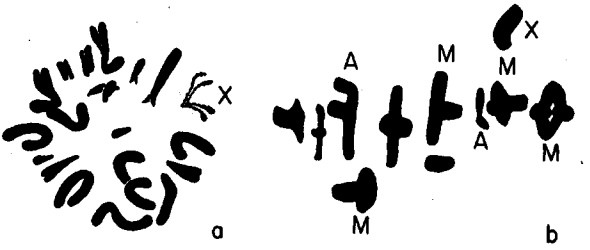
No. of Cells Having:		
5 bivalents with chiasmata in both arms	4 bivalents with chiasmata in both arms	3 bivalents with chiasmata in both arms
8	21	8

slightly asymmetrical (fig. 11 a, b, c). Apparently this little bivalent is made up of two chromosomes whose centromeres are not in the same locus, but a detailed study would be very difficult; in some cells the asymmetrical nature of the bivalent is not clear—this may depend on the position of the chiasma.

This species is identical with *C. lobatus* Saussure, under which name CAROTHERS (1917) described the cytology of eleven individuals from La Grande, Ore. In several of these individuals the smallest bivalent was heterozygous for a centromere-shift, as in our specimen, but in addition, several of CAROTHERS' individuals were heterozygous for such shifts in the larger chromosomes, although three out of the eleven were cytologically homozygous. Two of CAROTHERS' individuals possessed a supernumerary chromosome.

C. rabula altior Rehn

A single individual of this form was collected at a locality 21 miles north of Abiquiu, N. M. (June 29). Like other species of the genus it proves to have 21



TEXT-FIG. 13. *Circotettix rabula altior: a,* spermatogonial metaphase; *b,* first metaphase in side view. A, the asymmetrical bivalents.

chromosomes in the male (instead of 23, the usual number in the Acrididae). No supernumerary chromosome was present. As seen in the spermatogonial divisions (fig. 13 a) there were ten large metacentric chromosomes, one of which is the negatively heteropycnotic X chromosome which is clearly divided into its two chromatids at metaphase. There are three pairs of large or medium-sized acrocentric (rod-shaped) elements and two pairs of small chromosomes which usually appear as rods, but whose exact shape is not entirely clear in the spermatogonial metaphases.

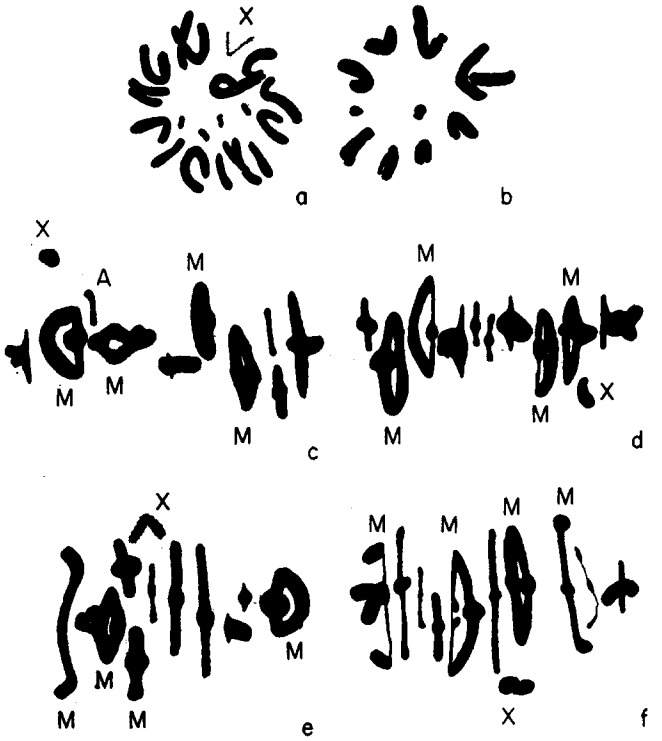
The first meiotic divisions in this individual show the X, four metacentric bivalents, four acrocentric bivalents and two asymmetrical bivalents of which one is quite large, the other much smaller (fig. 13 b). The metacentric bivalents almost always have chiasmata in both arms and sometimes one arm contains two chiasmata. The asymmetrical bivalents, on the other hand, have a much lower chiasma-frequency, since they apparently never form chiasmata in the region between the centromere of one homolog and that of the other. There is thus no reason to suppose that this individual produced any dicentric or acentric chromosome strands at meiosis, although the slides did not contain a sufficient number of first anaphases for a direct check on this point.

It is of course, not legitimate to speculate as to the genetic structure of a species from a cytological examination of a single individual, but certain con-

clusions seem to be justified. It is clear, for example, that *C. rabula altior* is a species in which heterozygosity for centric shifts occurs (the particular individual was heterozygous for two such). It also appears probable that the bivalents which show such heterozygosity have a type of chiasma-localization which prevents them from forming large numbers of inviable gametes (that is, ones with broken chromosomes or with acentric ones). Whether these bivalents show the same type of localization when homozygous is uncertain. We hope to obtain further data on this interesting species next year. The only previous record of cytological work on this species is by CAROTHERS (1917, p. 464) who studied a single individual from Ogden, Utah.

C. crotalum Rehn

This species of Circotettix, described by REHN (1921) has an extremely restricted distribution, being confined, so far as is known, to certain mountains



TEXT-FIG. 14. *Circotettix crotalum: a*, spermatogonial metaphase; *c*, second metaphase, *c–f*, first metaphases in side view. Abbreviations as in previous figures.

in southern Nevada, where it occurs from 8,000 to 10,200 feet in rocky limestone environments where pinyon, yellow pine and juniper are the dominant trees. The original series collected by REHN and HEBARD was obtained at two localities (Lees Canyon and Charleston Peak) in the Spring Mountains. Our material (49 males and a number of females) was collected June 22–23 at

Hidden Forest, a canyon below Sheep Peak, approximately 35 miles northeast of REHN and HEBARD'S localities and 30 miles north of Las Vegas. In this canyon, which is fairly thickly wooded, although surrounded on all sides by the yucca-dotted sagebrush desert, the species was extremely common, hardly any other Acrididae except a single individual of *Trimerotropis cyaneipennis* being seen. At this date the population of *C. crotalum* consisted of nymphs and newly-metamorphosed imagines in approximately equal numbers.

The Hidden Forest population of *C. crotalum* is very completely isolated, geographically. It is possible that the species occurs in other parts of the Sheep Range and in the Las Vegas and Desert Ranges which run parallel to it. But

TABLE 6

Chiasmata in the four metacentric bivalents of C. crotalum

INDIVIDUAL NO.	No of Cells Having: 4 BIVALENTS WITH CHIASMATA IN BOTH ARMS	3 BIVALENTS WITH CHIASMATA IN BOTH ARMS	2 BIVALENTS WITH CHIASMATA IN BOTH ARMS	1 BIVALENT WITH CHIASMATA IN BOTH ARMS
737 C	2	4	2	-
738 C	4	-	-	-
738 D	2	3	-	2
739 A	8	2	1	-
739 B	6	4	2	1
739 C	7	4	-	-
739 D	4	1	1	-
Total	33	18	6	3

all these ranges are separated by wide desert valleys which would seem to constitute formidable barriers to a species characteristic of pine forests. The species is thus one in which we might expect to be able to observe the effects of long isolation of the individual populations from one another, but the particular population studied was sufficiently large (several thousands of individuals at least) for the frequency of the various chromosomal types to be determined mainly by natural selection rather than by "drift."

C. crotalum, or at any rate this population of it, proves to be relatively uniform, cytologically. The X and four large pairs of autosomes are metacentric in all individuals studied. Five pairs of autosomes are always acrocentric, but one of the two smallest autosomes may be either acrocentric or metacentric, so that some individuals have one small asymmetrical bivalent. This, however, is extremely difficult to score consistently, so that it is unsuitable for statistical study. One of the four pairs of metacentric chromosomes has the two arms of almost exactly equal length, the other three have unequal arms ("J-shaped" chromosomes). At the first meiotic division it is usual for all the four metacentric bivalents to form chiasmata in both arms; but in some cells one, two or three of the metacentric bivalents have chiasmata in one arm only (see table

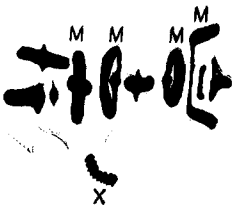
6). It is clear, however, that there is little chiasma-localization in the metacentric bivalents of this species.

The Hidden Forest population of *C. crotalum* does not appear to possess any supernumerary chromosomes—at least none were found in the 21 individuals studied cytologically. In this respect *crotalum* resembles *C. verruculatus* (HELWIG 1929) and differs from *C. undulatus* (=*lobatus*) in which both we and CAROTHERS (1917) have found supernumerary elements. In the case of *C. rabula* only two individuals have been studied cytologically (one by CAROTHERS, one by ourselves), so that it is uncertain whether supernumeraries exist or not.

C. crotalum is not completely homozygous, cytologically speaking, since one of the smallest chromosomes may be either acrocentric or metacentric; but it shows less heterozygosity than the other three members of the genus which have been studied, all of which may be heterozygous for centric shifts in several chromosomes. It is unfortunate that the centric shift in the small chromosome could not be studied in detail. We did find among the 21 individuals studied all three expected types—those homozygous for an acrocentric chromosome, those heterozygous, and those homozygous for a metacentric element —but these were so difficult to distinguish, on account of the small size of this bivalent, that we came to the conclusion that it would be dangerous to attempt to classify the individuals into the three types, since errors would undoubtedly be made.

C. coconino Rehn

A single male of this species, from Williams, Ariz., shows the general cytological characteristics of the genus, namely only ten pairs of autosomes and a



TEXT-FIG. 15. *Circotettix coconino:* first metaphase.

metacentric X. The four largest pairs of autosomes are metacentric, as in *C. crotalum*, no asymmetrical bivalents being present. There were no supernumerary chromosomes.

GENERAL DISCUSSION

Natural populations of grasshoppers belonging to the genera Trimerotropis and Circotettix seem to show four different types of cytological polymorphism:

(1) *Supernumerary chromosomes*, present in some individuals but not in others.

(2) *Supernumerary chromosome regions*, present in some individuals but not in others (leading to the presence of unequal bivalents when heterozygous).

(3) *Centromere-shifts* may be present in some individuals but not in others (leading to presence of asymmetrical bivalents when heterozygous).

(4) *Translocations* may be present in some individuals but not in others (leading to rings or chains of four chromosomes at meiosis when heterozygous).

For the most part, each species only shows one or two of these types of cytological variability. Thus translocations have only been found in *T. citrina* and *T. suffusa fallax* (HELWIG 1933), supernumerary chromosomes occur in *T. latifasciata*, *T. suffusa*, *T. cyaneipennis* and *C. undulatus* (but not so far as known, in the other species which have been studied); and centromere-shifts have not been recorded in any of the species belonging to section A of Trimerotropis.

Supernumerary chromosomes in grasshopper populations seem to be of two kinds: in the first place we have those studied by CARROLL (1920) in *Camnula pellucida*, which vary in number in different cells of the same individual, apparently because they undergo mitotic nondisjunction rather frequently. ROTHFELS (1948) has recently described an individual of *Neopodismopsis* in which several supernumerary elements were present, but here the number of supernumeraries varied from cyst to cyst (although constant within each cyst) In the second place we have supernumeraries of the type recorded by CAROTHERS for *T. suffusa* and studied by us in *T. latifasciata* and *C. undulatus*, which seem to be constant in number for all the cells of an individual (at least in the testis). This last type always seem to be metacentric elements (even in *T. latifasciata*, which has no other metacentrics), and their arms are always equal in length (or very nearly so). It is possible that they are isochromosomes, that is, that their two arms are homologous, but it is difficult to be certain of this. Always exhibiting positive heteropycnosis during the prophase of the first meiotic division, they show no heteropycnosis during the spermatogonial metaphases, when the X usually shows very pronounced negative heteropycnosis (in all those species of Trimerotropis and Circotettix which we have studied). Furthermore, the supernumeraries show no tendency to pair with the X at meiosis, so that there is no necessity to believe that they are in any way derived from it or homologous to any part of it.

Most of the discussions as to origin of supernumerary chromosomes which occur in the literature are somewhat unsatisfactory. Obviously, any supernumerary chromosome must have originated, either from some part of the chromosome complement of the species in which it occurs, or from another species, by hybridization (this may account for some supernumerary chromosomes in plants). The supernumeraries of *T. latifasciata* and *C. undulatus* are obviously not homologous to any part of the existing chromosome complement of those species, since they never pair at meiosis with any other chromosome. Does this mean that they were derived from some other species? We do not believe so, unless they have been handed down from ancestral species, without any hybridization having occurred. We believe that these elements were originally duplications of some part of the regular chromosome complement which have undergone an extensive series of rearrangements since their origin, thereby eliminating any structural homology to any member of the regular

complement. It is probable that these supernumeraries, when they first arose, showed mitotic instabilities of the type still shown by the supernumeraries of Camnula (CARROLL 1920) and Neopodismopsis (ROTHFELS in press). Such instabilities, due to an inefficient centromere-mechanism, may have led, on the one hand to frequent mitotic nondisjunction, and on the other to repeated deletions and duplications. The fact that the supernumeraries become contracted into an almost spherical shape during the prophase of meiosis suggests that they possess duplicated regions which exhibit some type of pairing. A study of individuals with two or more supernumeraries might help to elucidate this point. The fact that the supernumeraries of Trimerotropis spp. and Circotettix spp. are heterochromatic suggests that they are genetically semi-inert; but we feel sure that their widespread occurrence in some of these species (CAROTHERS 1917; WENRICH 1917) indicates that they are not entirely devoid of genetic properties. It is hardly profitable to speculate as to whether they were originally derived from the X chromosome or from autosomal heterochromatin. The fact that they do not show negative heteropycnosis during the spermatogonial divisions would seem, on the face of it, to indicate the latter: but it is by no means impossible that the X of these species (or their ancestors) contains (or contained) more than one type of heterochromatin, and that the supernumeraries were built up by repeated duplication of a small region in the X which did not show the typical "reversal of heteropycnosis" characteristic of the X as a whole (WHITE 1942).

Supernumerary chromosome regions, such as give rise to unequal bivalents in some individuals of *T. bilobata* and *T. sp.* have been previously recorded for many species of grasshoppers, for instance in *Brachystola magna, Arphia simplex* and *Dissosteira carolina* by CAROTHERS (1913).

Some confusion exists in the literature concerning the terminology to be applied in such cases. Thus some authors have referred to individuals with an unequal bivalent as heterozygous for a deficiency, others calling them heterozygotes for a duplication. These terms are derived from Drosophila genetics, and neither seems to be strictly applicable in such cases. An unequal bivalent consists of a short chromosome and a long one which contains a heterochromatic segment that is lacking in the short element. There is no reason to suppose that this heterochromatin represents a duplication of material present elsewhere in the chromosome complex, although it may do so. Thus the term duplication seems rather inappropriate. But to say that a chromosome lacking an inessential heterochromatic region is carrying a deficiency also seems confusing. These supernumerary chromosome regions in grasshoppers seem, in fact to be genetically similar to supernumerary chromosomes, but instead of constituting independent elements they are inserted into a member of the regular chromosome complement, usually one of the smaller ones.

Heterozygosity in respect of centromere shifts is obviously entirely different from heterozygosity for an extra chromosome region. At the time when we first reviewed the cytological situation in Trimerotropis and Circotettix (WHITE 1945) we considered the possibility that the 'asymmetrical bivalents' in some of the species might be due to pericentric inversions. Since that time, however, COLEMAN (1948) has shown that pachytene bivalents heterozygous

for these structural changes (that is, which will appear as asymmetrical bivalents at first metaphase) do not show any inversion-loops such as would be seen if pericentric inversions were present. On the contrary, pachytene pairing seems to be quite complete, the bivalents showing no unpaired regions. It is accordingly fairly clear that true centromere shifts, that is, transpositions of the centromere (possibly with a very short region on either side) are responsible for the asymmetrical bivalents.[2]

We have already considered (WHITE 1945) some of the consequences of heterozygosity in respect of a centromere shift. In such a bivalent a chiasma which occurs between the two centromeres will necessarily lead to the formation of a dicentric chromatid and an acentric one. Thus heterozygosity for centromere shifts would lead to the formation of a large percentage of inviable gametes unless the chiasmata were strictly localized at the other end of the chromosome, so that they were never formed between the two centromeres. A study of *C. rabula altior* and an inspection of the published figures of CAROTHERS and HELWIG suggests that such a localization does in fact occur in all those bivalents which are liable to be heterozygous in some individuals. We still do not have enough data, however, to determine whether in these cases chiasmata are *never* formed in the "prohibited" region, or whether they may occasionally occur there, leading to a few inviable gametes. Nor is it certain whether localization occurs in the female: it is conceivable that in oogenesis dicentric and acentric chromatids would be lost in the polar bodies.

Another unanswered question is whether localization of chiasmata or centromere shifts came first in evolution. In other words, did an already-existing localization permit centromere shifts to establish themselves in the wild populations of these grasshoppers, or did centromere shifts establish themselves first, leading to a high percentage of sterile gametes until natural selection gave rise to an increasing degree of chiasma-localization? All the species in which heterozygosity for centromere shifts occurs also show some bivalents which are homozygous for such shifts (and *T. pallidipennis* is homozygous for three shifts in the autosomes and shows no heterozygosity). But in the case of these bivalents which are homozygous for centromere shifts no chiasma localization is evident—or at any rate chiasmata are regularly formed in both arms of the bivalent. Thus in such cases the newly arisen metacentric type of chromosome would seem to have displaced the original acrocentric type in the natural populations of the species, in spite of the fact that the heterozygotes must have been relatively infertile (and of course in the initial stages of the process there would have been few if any individuals homozygous for the metacentric type of chromosome). A possible but entirely hypothetical explanation would be to suggest that in these cases chiasma localization was originally present, but that it disappeared after the original, acrocentric type of chromosome vanished from the populations. We still lack essential data bearing on this and related points: we do not even know, for example, whether the chiasma frequency of a particular chromosome is the same, irrespective of whether it is in an AA, AM or MM bivalent.

[2] CROUSE (1947) has reported the existence of a similar centromere shift which has occurred in the C chromosome of *Sciara ocellaris* in certain strains.

We have thought it worth while to give some data on the frequency of chiasma formation in the two arms of the metacentric bivalents (tables 2–6) since it seems likely that a bivalent which usually shows chiasma in both arms is *a priori* unlikely to show heterozygosity, while bivalents such as some of those of *T. cyaneipennis* and *T. suffusa* (tables 3 and 4), which normally show chiasmata only in one arm, may well be heterozygous in some individuals.In *C. crotalum* we conclude from table 6 that none of the four metacentric bivalents is likely to show heterozygosity in other populations of the species.

Genetically speaking, the effect of a centromere shift combined with chiasma localization may be rather similar to that of an inversion in Drosophila—that is, it may give rise to a group of linked genes which are inherited as a unit in heredity without being broken up by crossing over. And it may be that, just as in the case of *Drosophila pseudoobscura*, the heterozygous individuals have a higher viability than either of the homozygous types, thus leading to the perpetuation of both the acrocentric and metacentric types of chromosome. But much more work will need to be carried out before any such statement can be regarded as firmly founded in fact.

On the basis of the earlier work of CAROTHERS, WENRICH and KING and the more recent work of COLEMAN and ourselves we may now classify the species of Trimerotropis into the two sections A and B as follows:

Section A	*Section B*
(All chromosomes acrocentric)	(Some chromosomes, including always the X, metacentric)
T. maritima Harris (W)	
T. citrina Scudder (C, W)	*T. pallidipennis* Burm. (Co., W)
T. latifasciata Scudder (W)	*T. suffusa* Scudder (C, Wen., W)
T. bilobata Rehn and Hebard (W)	*T. cyaneipennis* Bruner (K, W)
T. sp. (=*titusi* of Tinckham) (W)	*T. caeruleipennis* Bruner (K)
T. fontana Thomas (Co.)	*T. thalassica* Bruner (K)
T. praeclara McNeill (Co.)	*T. gracilis sordida* Walker (Co.)

(C = CAROTHERS, Co. = COLEMAN, K = KING, Wen. = WENRICH, W = WHITE)

Of the species in section B, *pallidipennis* and *gracilis sordida* show relatively few metacentric chromosomes, the other four species much higher numbers. As far as our experience goes, *pallidipennis* seems to be a cytologically homozygous species in which three chromosome pairs are invariably metacentric, the remaining eight being always acrocentric. It is possible, however, that in some individuals of *pallidipennis* from Vancouver Island there are fewer metacentric chromosomes than in material from the Great Basin and the Southwest.

A full discussion of taxonomic relationships within the Trimerotropine grasshoppers would be premature at the present stage. Clearly, section A of Trimerotropis includes the more primitive species, in which none of the chromosomes have become metacentric. It is still uncertain, however, whether section B represents a strictly monophyletic group, descended from a single species in which centromere shifts established themselves in the X and in several autosomes. The alternative would be to suppose that the species of section B do not form

a monophyletic group, metacentric chromosomes having appeared in several ancestral species, not necessarily closely related to one another. It is virtually certain that Circotettix arose from section B of Trimerotropis.

SUMMARY

The genus Trimerotropis may be divided, on cytological grounds, into two sections. In the first of these all the chromosomes are acrocentric (rod-shaped), while in the second a varying number of elements (including always the X chromosome) have been converted into metacentric chromosomes by shifts of the centromere region from a subterminal to a submedian position. All species of the related genus Circotettix have chromosome complements of the second type, that is, with a certain number of metacentric chromosomes.

No chromosomal variation was encountered in small samples of *T. maritima* and *T. citrina*, which belong to the first section of Trimerotropis. In *T. latifasciata* a large metacentric supernumerary chromosome is present in about one seventh of the individuals of a population at Roswell, N. M. A similar supernumerary was also found in a single individual of *Circotettix undulatus*. In a population of *T. bilobata* from Las Vegas, Nevada, and in an unidentified species of Trimerotropis from near Kingman, Arizona unequal pairs of chromosomes (due to the presence of a supernumerary region in one homolog) were found in some individuals.

In *Circotettix crotalum*, *C. undulatus* and *C. rabula altior* heterozygosity in respect of the position of the centromere occurs in some bivalents of some individuals. It is pointed out that this condition must be accompanied by a special type of chiasma localization if it is not to lead to the formation of a large number of inviable or lethal gametes. In *Trimerotropis pallidipennis* 55 individuals from Texas, New Mexico, Arizona and Nevada showed no cytological variation or heterozygosity.

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