

Meiotic orientation and segregation of asynaptic sex chromosomes in Alticidae (Coleoptera)

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VIRKKI, N., 1973. Meiotic Orientation and Segregation of Asynaptic Sex Chromosomes in Alticidae (Coleoptera). *An. Esc. nac. Cienc. biol., Méx.*, **20**: 35-51.

Fecha de publicación: Junio de 1973.

SUMMARY: In the tribe Alticini, and in the subtribe Oedionychina, of the fleabeetles, the sex chromosomes do not pair in the male meiosis, but in spite of this, segregate correctly in A I. In Alticini, X and Y amphiorientate and are brought to equator as two independent univalents. They stay there until latest A I, when they segregate from one another. In Oedionychina, X and Y (or multiple Y's) form a "distance bivalent" (or multivalent) maintained by a gel body. Segregation is simultaneous with the autosomes.

The case of Alticini is similar with that of Tipulidae (Diptera), and can be explained in the same way. The cases of Oedionychina imply different values for the centromeres in the orientation, and limited capacity to accommodate centromeres for the half-spindles.

The movements of chromosomes during cell division can be classified in three major categories. Firstly, the premetaphasic movements, many times violent and asynchronized, and due to the tentative connections the centromeres individually make with the poles. These movements finally lead to the orientation of the chromosomes in the equator of the achromatic spindle. Secondly, the tranquil and relatively immobile metaphase. Thirdly, the usually well synchronized anaphase movement, which separates and segregates the chromatids (in mitosis) or chromosomes (in meiosis) from one another.

For a chromosomal body (chromosome, bivalent, or multivalent), to be able to orientate and congregate in the equator of a bipolar system as is the spindle, two prerequisites are necessary: 1. It must have two or more functionally independent centromeres. 2. The centromeres must be connected by some means with one another (Fig. 1). Without these prerequisites, every single centromere would lead its corresponding chromatid directly to one of the poles. These being the general rules, there are, however, cases where the prerequisite number 2 seems

to be lacking, without affecting the regularity and normality of segregation. Let us see some cases of the male meiosis of the beetle family Alticidae.

1. Tribe Alticini

The common karyotype formula is $11^{II} + X + Y$ (Figs. 2 and 3; see also Virkki 1970). The two sister centromeres of each sex univalent connect with the opposite poles (amphiorientation), and both univalents equatorize independently from one pole to another. Amphiorientation normally predicts an equatorial division, but not in this case. In anaphase I, X and Y stay at the equator until the end of the phase, when the segregation finally takes place. Consequently, the result is the same as if the two would have been conjugated.

A similar and well analyzed case is known from the tipulide *Nephrotoma ferruginea*, and the interpretation given by Dietz (1969) can be applied also here. According to his hypothesis, in every half-spindle, microtubuli of traction fibres of the two amphioriented univalent, prevented from an early division by some means, perhaps by unusually strong "collochores", enter in a thermodynamic relation in the following manner (see Fig. 4).

The onset of the anaphasic traction is not completely synchronized in all chromosomal spindle fibres. It is most probable that one of the four fibres of the sex univalent starts is slightly earlier than the rest of them. From the paracrystal of the microtubuli, molecules are freed to the nearby surroundings. "Healing" adjustments in the microtubuli cause tension which can be neutralized only halting the centromere towards the pole, because the opposite end of the fibre is firmly anchored in the polar gel body and does not move. With their free energy, the released molecules reduce the free energy of the system, where both sex univalents lie close together in the narrowing anaphase cell. Thus hydration is induced in the neighboring fibre. The antagonist of this fibre is now free to lead its chromosome (both chromatids) to the pole. When it starts shortening, it too releases free molecules that by means of increased free energy induce hydration of the neighboring fibre, the antagonist of which becomes now free to lead its chromosome to the opposite pole.

2. Tribe Oedionychini, subtribe Oedionichina

The common karyotype formula is $10^{II} + X + Y$ (Fig. 5; see also Virkki 1970). The two sister centromeres of a sex univalent connect with the same pole (synorientation), opposite to the pole with which the two sister centromeres of the other sex univalent are connected. In spite of this, the chromosomes do not migrate to the poles, but stay close to the equator, forming a "distance bivalent" which endures until anaphase I. The position of the distance bivalent in the cell is always lateral, separated from the autocomal spindle by a space where mitochondria often float. In other words, the spindle of metaphase I is bipartite (the poles are common for both autosomal and sex portion). The anaphasic disjunction of the sex chromosomes is more or less simultaneous with that of the autosomes.

It is possible to arrange in living preparations a collision of such spermatocytes with fixed, sharp points. The distance bivalent is often chopped out of the cell and of the main spindle in such collisions. Its shape and the distance bet-

ween X and Y is little affected thereby (Virkki 1972). Micromanipulation has also produced indications of high viscosity of the material between X and Y in the distance bivalent. It is obvious that a premature disjunction of this distance bivalent is impeded by a viscous, presumably gelatinous, body which forms in late premetaphase I. More generally, it seems possible that such a body may play an important role in maintaining together all metaphasic chromatids, bivalents and multivalents, rendering less important than it has been thought, such devices as collochoses, terminalized chiasmata, etc.

Let us still see some related cases, where the asynaptic sex chromosomes are multiple. *Omophoita clerica* Erichson has three very markant sex chromosomes: X looks like J, Y_1 and Y_2 like I and V, respectively (Figs. 6 and 7; see also Virkki 1967).¹ In premetaphase I, the orientation of the three is variable, but

at the full metaphase, the orientation $\frac{X}{Y_1 + Y_2}$ is established. The segregation al-

ways follows the pattern of orientation: X is separated from the Y's.

Asphaera daniela Bech. Has seven asynaptic sex chromosomes: X is large and looks like V, the six Y chromosomes are small and look like v (Figs. 7; see also Virkki 1968). The final orientation at metaphase I is always

$\frac{X}{Y_1 + Y_2 + Y_3 + Y_4 + Y_5 + Y_6}$, and the segregation occurs according

to this.

These cases introduce quantitative aspects of orientation related with the hypothesis of Dietz. Apparently, each sexual half-spindle of *Omophoita clerica* has a given quantity of precursor of the traction fibres, sufficient to arrange the orientation of X, or of $Y_1 + Y_2$, but insufficient for orientation of the combinations $X + Y_1$ and $X + Y_2$. This can be expressed by an equation $x = y_1 + y_2$, where x is the amount of precursor necessary for orientation of the X chromosome, and y_1 and y_2 the corresponding amounts for Y_1 and Y_2 , respectively. This implies different values for centromeres: whereas that of X needs all the precursor available, those of the Y's can be arranged with less, perhaps with 50% of the total amount each.

Similarly, a sexual half-spindle of *Asphaera daniela* is capable of accomodating either one X or 6 Y's, but no other combinations ($x = y_1 + y_2 + y_3 + y_4 + y_5 + y_6$). In the simple cases of Oedionychina, x equals to y, because every sexual half-spindle can accomodate only one sex chromosome, either X or Y.

Thus centromeres can have a different value in the orientation, and the half-spindles, a limited capacity to accomodate centromeres.

¹The female of this and the following species is cytologically unknown. The identification of the sex chromosomes is only tentative.

RESUMEN

En la tribu Alticini, y en la subtribu Oedionychina, de los Alticidae (Coleoptera), los cromosomas sexuales no se conyugan en la meiosis del macho. No obstante, se segregan correctamente en al A I. En Alticini, X y Y se anfiorientan y llegan al ecuador como dos univalentes independientes. Se quedan allí hasta el final de la A I, cuando se segregan de uno a otro. En Oedionychina, los X y Y (o Y's múltiples) forman un "bivalente (o multivalente) de distancia", que está mantenido por un cuerpo gelatinizado. La segregación es simultánea con los autosomas.

El caso de Alticini es similar con el de Tipulidae (Diptera), y puede interpretarse en la misma manera. El caso de Oedionychina implica valores diferentes a los centrómeros en el proceso de orientación, y capacidad limitada de acomodar centrómeros a los semihusos acromáticos.

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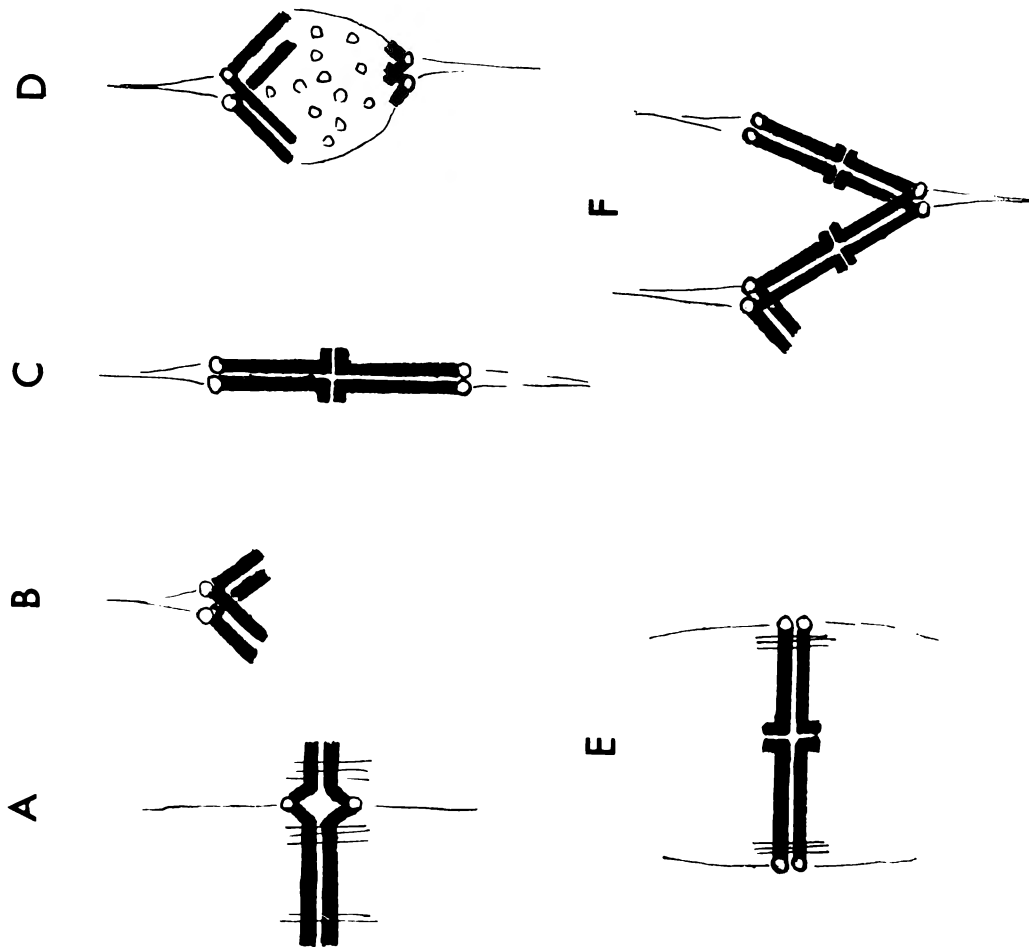


FIG. 1. Examples of linkage and orientation of centromeres. The crosswise lines in A and E suggest colchochore, sites that resist rapid separation of chromatids. —A. Amphiorientation, the regular situation in meiotic chromosomes and many meiotic univalents. B. Synorientation in a univalent. This tends to lead the chromosome to a pole immediately. This is regular kinetics of X chromosome in XO systems. C. Double synorientation. A regular bivalent; association maintained by a chiasma. D. Double synorientation; association maintained by nucleolus. Xy_p sex bivalent of beetles. E. Double amphiorientation. This occurs in M I in the case of postreduction. Association maintained by chiasma and colchochore. F. Triple synorientation in a trivalent. Association maintained by chiasmata.

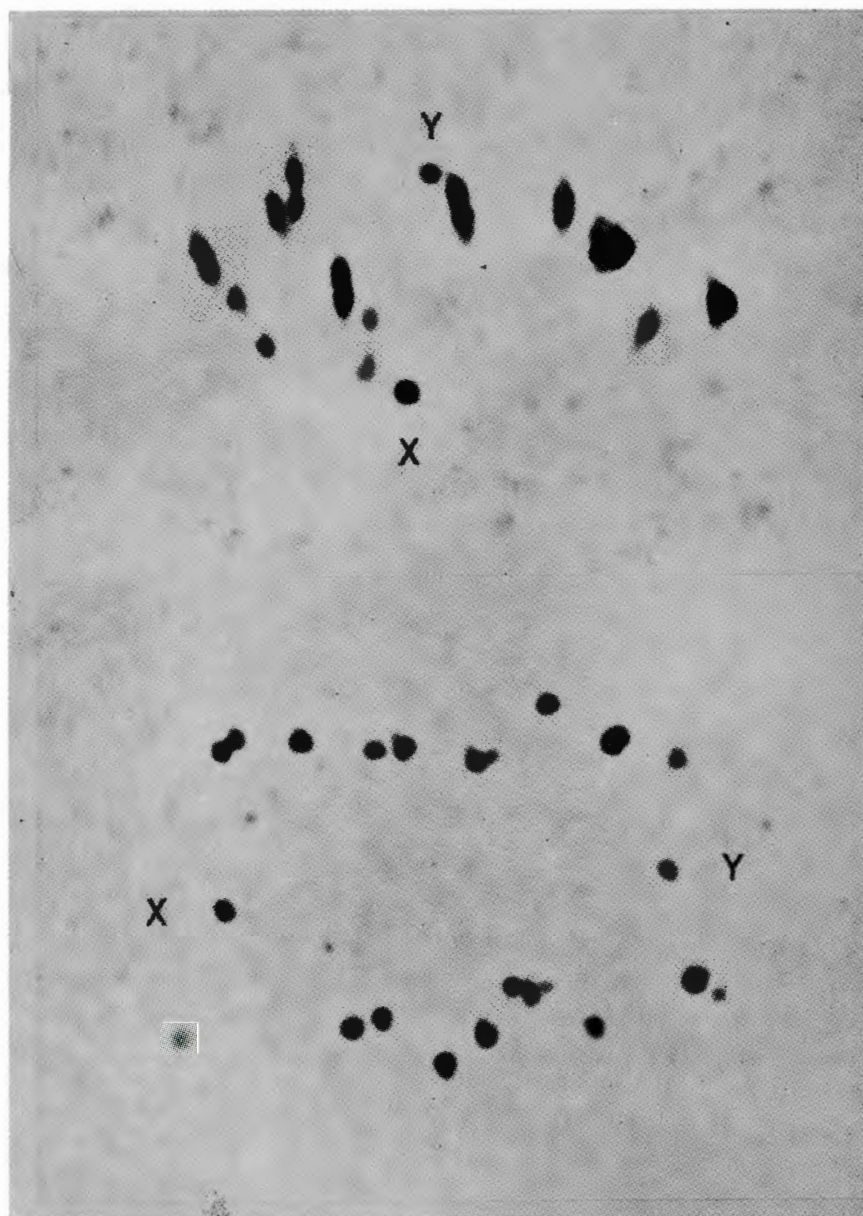


FIG. 2. Top: *Haltica jamaicensis* F. M I. Amphioriented sex chromosomes (X, Y) in the metaphase plate. 3100X. Bottom: *Haltica ludoviciana* Fall. Early A I. Sex chromosomes stay at the equator. 2200X.



FIG. 3. *Haltica ludoviciana* Fall. 2200X. Top: Late A I. Narrowing of spindle, approximation of X to Y. Bottom: T I. X and Y segregated from one another. Note the lengthy, almost dumbbell look of the sex chromosomes as compared with Fig. 1: the chromatids have turned 180° and hang together only by their ends (end collochores).

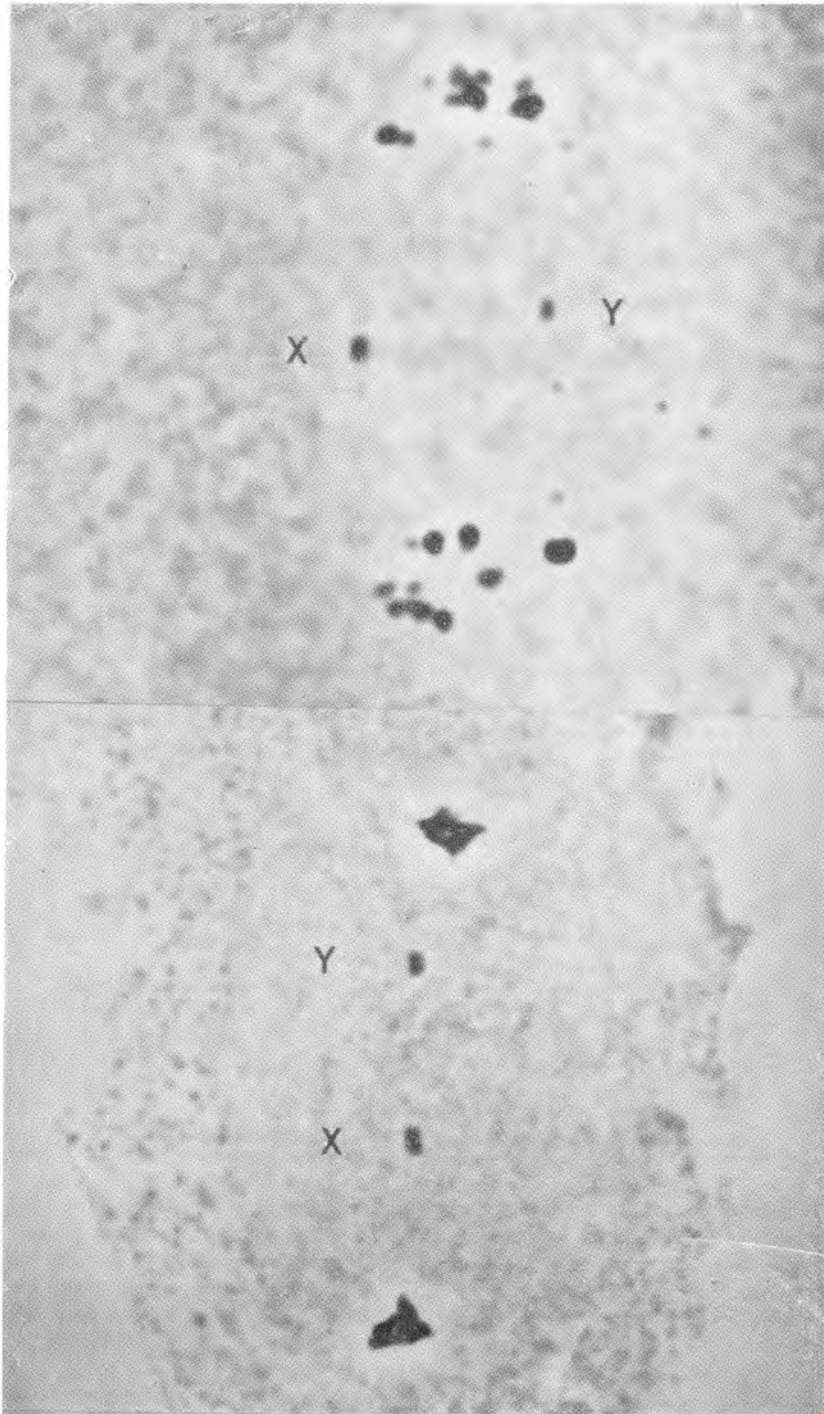


FIG. 4. Explanation of the segregation of *Altica sex* chromosomes, abbreviated after Dietz. Doble arrow ($\leftarrow \rightarrow$) marks a traction fibre that is expelling constituting molecules and repairing the losses by shortening; the neighboring fibre is subject to hydration by increased free energy. The peripheral ends of the fibres are anchored in polar gel bodies. —A. Expelling of molecules and tension caused by healing start in the fibre marked with arrows. B. The same starts in the fibre lower left. In both half-spindles, the neighboring fibres are hydrated and destructed by increased free energy. C. Freed of antagonist traction, the functioning fibres expel continuously molecules, shorten, and lead the sex chromosomes to opposite poles.

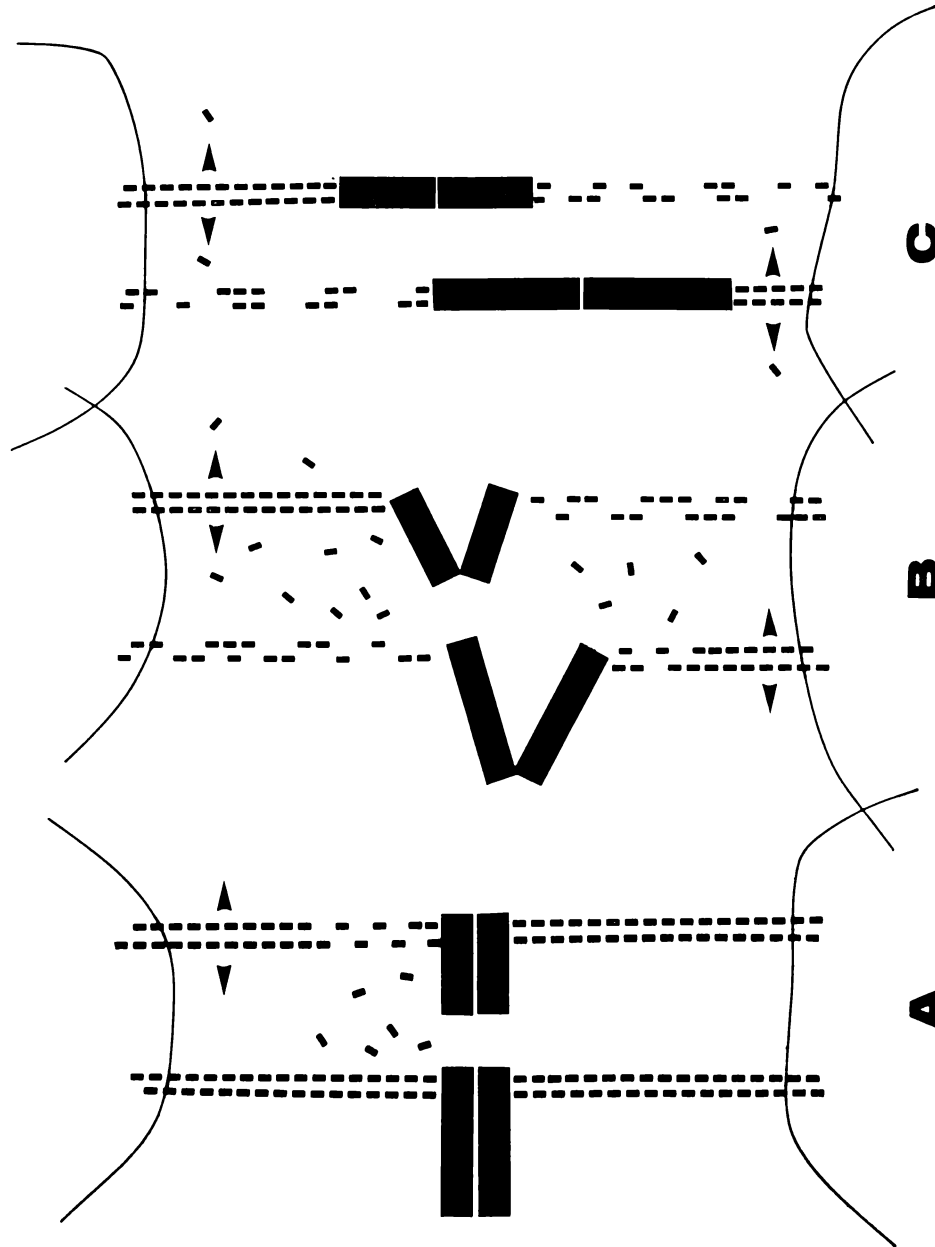


FIG. 5. *Omophoita albicollis* Fabr. 880X. Top: M I. Distance sex bivalent to the left. Bottom: A I. Simultaneous disjunction of the sex chromosomes with the autosomes.



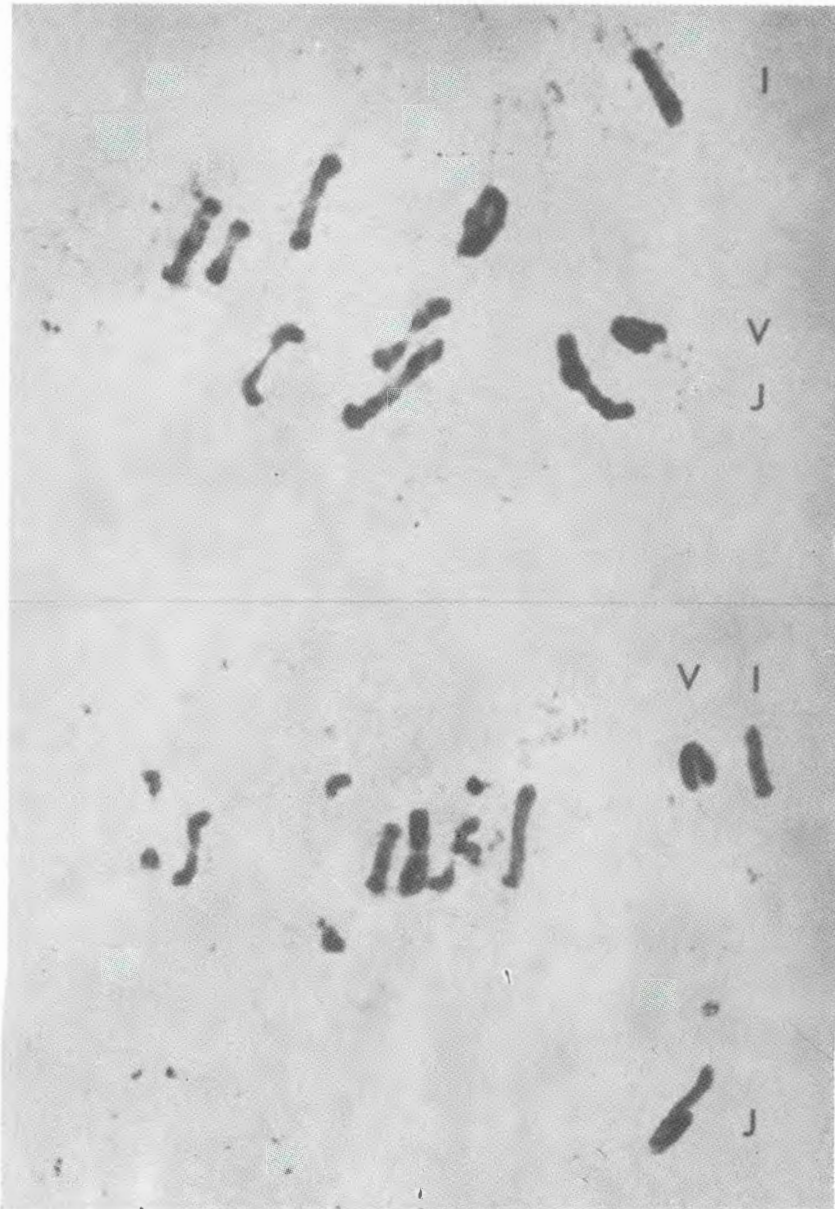


FIG. 6. *Omophoita clerica* Erichson. 1500X. Top: Premetaphase I. Position of the sex chromosomes (J, V, I) still variable. Bottom: Full M. I. Orientation $\frac{J}{I + V}$ established.

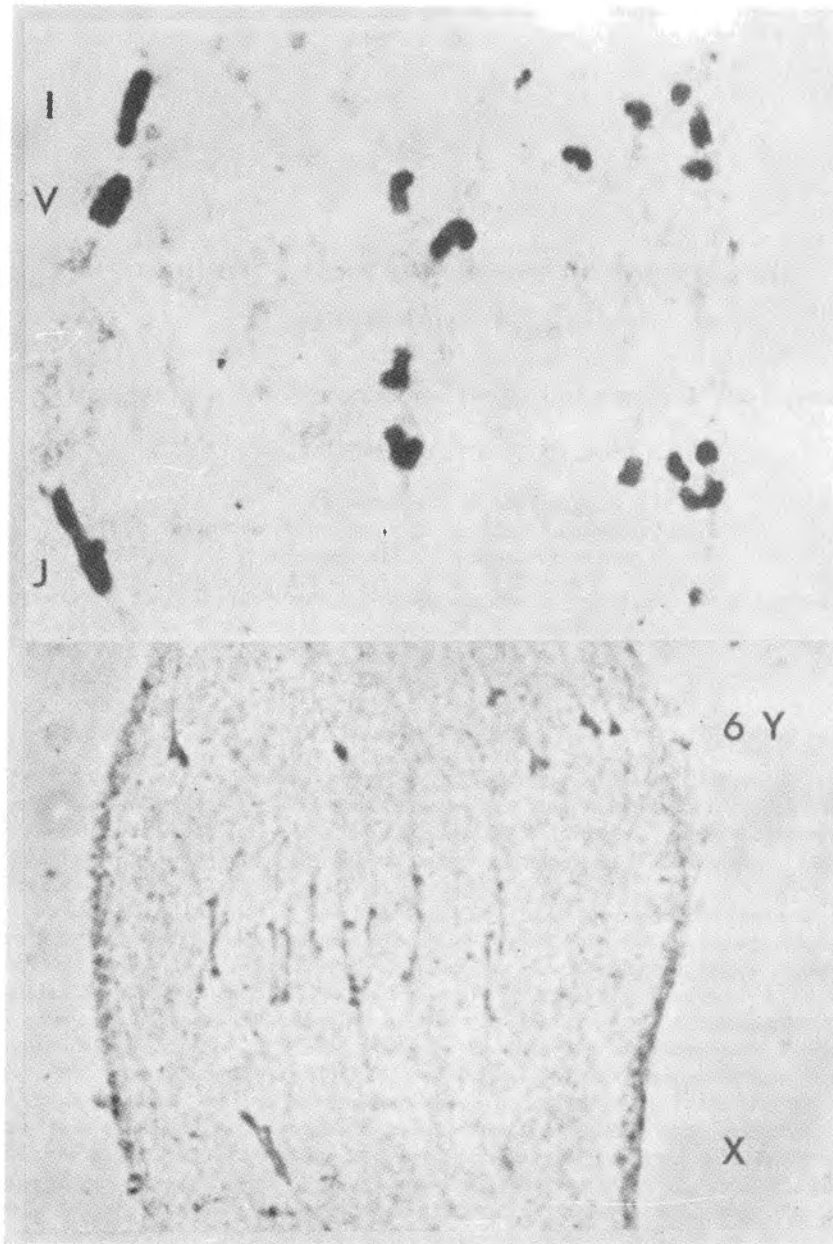


FIG. 7. Top: *Omophoita clerica* Erichson. 1500X. A I, showing that disjunction follows the pattern of orientation. Bottom: *Asphaera daniela* Bech. 850X. M I showing distance

$$\text{multivalent } \frac{X}{Y_1 + Y_2 + Y_3 + Y_4 + Y_5 + Y_6}$$