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Meiotic behaviour of holocentric chromosomes: orientation and segregation of autosomes in *Triatoma infestans* (Heteroptera)

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The meiotic behaviour of the holocentric chromosomes of the heteropteran species *Triatoma infestans* has been analysed by means of orcein staining and C-banding on squashed spermatocytes. We have focused our analysis on chromosome 3, which shows a large distal heterochromatic band at one of the ends of both homologues. At metaphase I, and independently of the chiasma position, two alternative orientations have been observed: either the heterochromatic or the euchromatic ends of both homologues are directed to opposite poles. At anaphase I, the kinetic activity is restricted to the same chromosome end (euchromatic or heterochromatic) of each homologue. The frequencies of these two alternatives are not random and differ significantly among the five individuals analysed. However, the euchromatic ends present kinetic activity at a higher frequency than the heterochromatic ends. At metaphase II, half-bivalents also show the kinetic activity restricted to either of the chromosome ends (euchromatic or heterochromatic). The frequencies of each alternative are inverted in anaphase II compared with those scored in anaphase I. Accordingly, those ends that present kinetic activity at anaphase I segregate reductionally during the first meiotic division and equationally during the second meiotic division. These results provide sound evidence on the meiotic behaviour of holocentric chromosomes, as regards the absence of chiasma terminalization and the modes of orientation and segregation.

Key words: chiasma terminalization, chromosome segregation, Hemiptera, holocentric chromosomes, meiosis, *Triatoma infestans*

Introduction

Two main categories of chromosomes, as regards the microtubule–centromere interactions and the mitotic anaphase progression, have been defined: monocentric and holocentric chromosomes. Monocentric chromosomes are those in which the spindle microtubules attach to a discrete centromere region of the chromosome. Since, during anaphase, the kinetic activity is restricted to that region, they exhibit a 'monokinetic' movement. Holocentric chromosomes are those in which the spindle microtubules interact with most of the chromatid length, i.e. they present a non-localized centromere. During mitotic anaphase, their sister chromatids separate in parallel and exhibit a 'holokinetic' movement (for review, see White 1973). Two terms have been used synonymously for holocentric chromosomes: polycentric and holocentric. Ultrastructurally, holocentric chromosomes show continuous microtubule attachment sites along the entire or almost the entire length of the chromosome (Buck 1967, Comings & Okada 1972). Polycentric chromosomes are those with many discrete regions of microtubule attachment distributed along the poleward surfaces of chromosomes (Braselton 1971), although their precise organization is still controversial (Bokhari & Godward 1980). Nonetheless, since both kinds of chromosomes coincide in their anaphase 'holokinetic' behaviour, we will employ the term holocentric to designate both of these categories. A wide range of animal and plant species possess holocentric chromosomes, although they are particularly well represented in insects (John & Lewis 1966, Pimpinelli & Goday 1989, John 1990), including heteropteran species (Ueshima 1979).

Holocentric chromosomes present some common characteristics during mitosis: (i) no primary constrictions are detectable, although kinetochore structures are observed; (ii) at metaphase, each chromosome is oriented with its long axis parallel to the equatorial plate; (iii) spindle fibres attach all along the chromatid length; and (iv) at anaphase, the chromatids move polewards with their long axes parallel to the spindle equatorial plate (John 1990). Moreover, chromosome fragments produced by radiation are able to divide (Hughes-Schrader & Schrader 1961).

During meiosis, holocentric chromosomes show a variable behaviour not only in different species but

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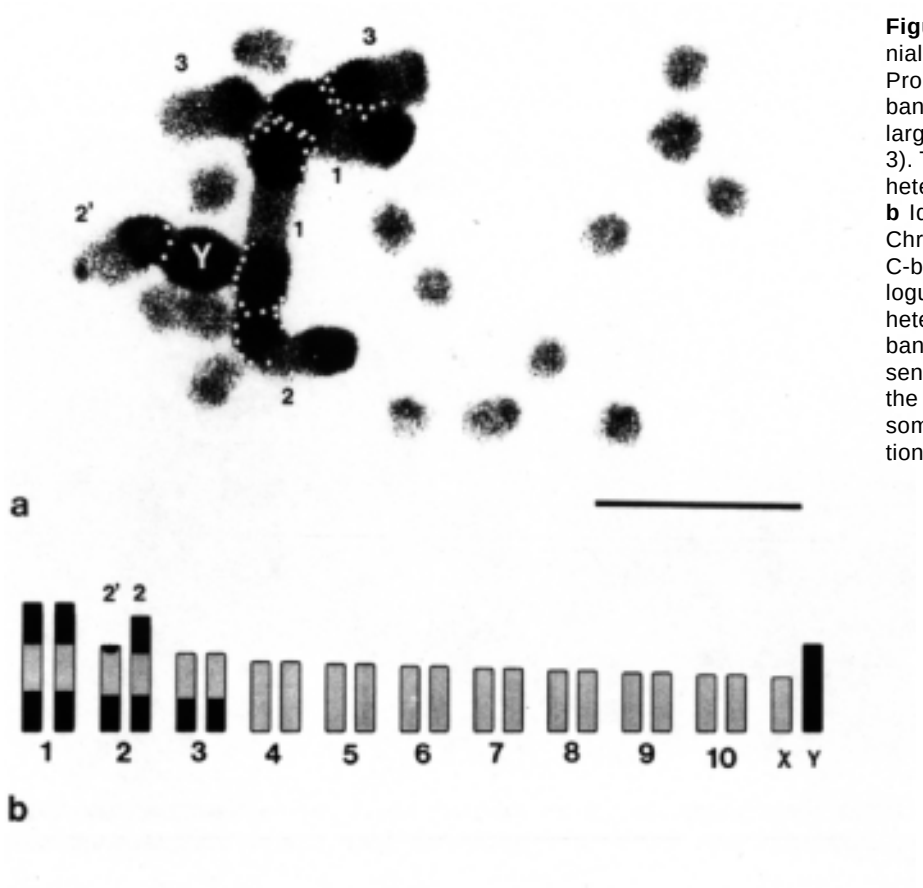


Figure 1. a C-banded spermatogonial prometaphase of *T. infestans*. Prominent distal heterochromatic bands are only present in the three larger chromosome pairs (1, 2 and 3). The Y chromosome is completely heterochromatic. Scale bar = 5 μm. **b** Idiogram of the plate shown in **a**. Chromosome 1 presents prominent C-bands in both ends of both homologues. Chromosome 2 (2 and 2′) is heterozygous for one of the distal bands. Chromosome 3 only presents the distal bands in one of the chromosome ends. The chromosome sizes are not depicted proportionally.

also between the chromosomes of a given complement (e.g. sex chromosomes vs. autosomes) (see John & Lewis 1966, White 1973, John 1990). Four peculiar features have been attributed to the chromosomes of heteropteran species during meiotic divisions: (i) no kinetochore structures are present (Buck 1967, Comings & Okada 1972, Motzko & Ruthman 1984, Rufas & Giménez-Martín 1986, Wolf 1996); (ii) kinetic activity is restricted to the chromosome ends (Schrader 1935, 1940, Hughes-Schrader & Schrader 1961, González-García *et al*. 1996) (iii) chiasmata terminalization is presumed to occur (John & King 1985), although there are reports that argue against this assumption (Jones 1987, Solari & Agopian 1987); and (iv) the first meiotic division is reductional for the autosomes and equational for the sex chromosomes. This sequence of meiotic segregation is well sustained for the sex chromosomes, which are easily identified (see González-García *et al*. 1996). However, this sequence is rather speculative for the autosomes in which chromosome markers have rarely been revealed.

This paper presents a conclusive analysis on the meiotic behaviour of the autosomes in the hemipteran bug, *Triatoma infestans*. The analysis takes advantage of the clear difference between the chromosomes ends on chromosome 3, since one end presents a positive heterochromatic C-band (Panzera *et al*. 1992).

Materials and methods

Triatoma infestans (Hemiptera: Reduviidae) is the main vector of Chagas' disease in South America. This disease is caused by *Trypanosoma cruzi* and is almost exclusively present in domestic and peridomestic habitats. Adult males of *T. infestans* were collected from natural populations in Uruguay under the auspices of the National Programme of Chagas' disease.

Testes were removed, fixed in an ethanol–glacial acetic acid mixture (3:1) and stored at −20°C. For orcein staining, small pieces of the testes were squashed in a drop of lactopropionic orcein. For C-banding, squashes were made in a drop of 50% acetic acid. Coverslips were then removed after freezing in liquid nitrogen and the slides were air dried. Slides were treated with 1 N HCl at room temperature for 15 min, rinsed in tap water and incubated at room temperature in saturated (5%) $Ba(OH)_2$ for 10 min. Slides were rinsed in tap water and incubated in 2 × saline sodium citrate (SSC) (1 × SSC: 0.15 M NaCl, 0.015 M sodium citrate) at 60°C for 20 min and then thoroughly rinsed in tap water. They were then stained with 5% Giemsa for about 5 min, rinsed in tap water, air dried and mounted with Eukitt.

Results

Chromosome complement and C-banding pattern

The chromosome complement of *T. infestans* is composed of 20 autosomes plus two sex chromosomes (XX

in females and XY in males) (Schreiber & Pellegrino 1950). Chromosomes appear as a continuous chromatin mass in spermatogonial mitotic metaphases. However, in spermatogonial prometaphases each chromosome is easily distinguishable. They do not show any obvious primary constriction, so they can be considered as holocentric chromosomes. Orcein staining reveals positive heteropycnotic regions in the chromosome ends of the three larger autosomal pairs. C-banding shows large bands in those same regions (Figure 1). These bands are located at both ends of chromosome 1 and 2 and at only one end of chromosome 3. One of the distal bands of chromosome 2 is polymorphic and, when it is not present, it appears as a dot (Panzera *et al*. 1992) (Figure 1). Additionally, the Y chromosome is completely positive to C-banding in contrast with the X chromosome, which does not show any C-positive region (Figure 1).

Meiotic behaviour

Prophase I nuclei present a single or double chromocentre that involves the three larger bivalents and the sex chromosomes. The chromocentre is formed by the lateral association of the X and Y chromosomes, which are surrounded by the three autosome pairs closely attached by their heterochromatic regions (Figure 2a & b). In later stages, these associations must have been lost, since at metaphase I the autosomal bivalents and the sex chromosomes are individualized (Figure 2c & d).

Autosomal bivalents invariably present a single chiasma that may occupy interstitial or proximal positions as regards one of the chromosome ends (Figure 2b). These chiasmatic configurations are maintained from diplotene (Figure 2b) up to metaphase I (Figure 2c & d), so that chiasmata terminalization is not apparent.

At anaphase I, half-bivalents show a kinetic activity restricted to one of the chromosome ends giving rise to V-shaped chromosomes (Figure 5c & d). During the first meiotic division, whole chromosomes, not chromatids, migrate to opposite poles.

At prometaphase II, the chromatids of each half-bivalent are associated along most of their length, thus lying parallel (Figure 2e). However, during the transition between prometaphase II and metaphase II, a change in their association takes place so that they appear only associated by their ends in metaphase II cells (Figure 2f). At anaphase II, the kinetic activity is also restricted to one of the ends of each chromatid.

The sex chromosomes follow a different mode of segregation. At metaphase I, they are individualized and do not form a true bivalent, since a chiasma between them is absent. Their long axes appear perpendicular to the equatorial plate (Figure 2c). Chromatids of each sex chromosome migrate to opposite poles in anaphase I, thus showing an equational segregation. The sex chromatids are observed individualized at prometaphase II (Figure 2e); however, they present an end-to-end association in metaphase II with their long axes perpendicular to the equatorial plate (Figure 2f & g). During anaphase II, sex chromatids segregate to opposite poles. During both meiotic divisions, these chromosomes also show a kinetic activity restricted to one of the chromosome/chromatid ends (see Figure 5).

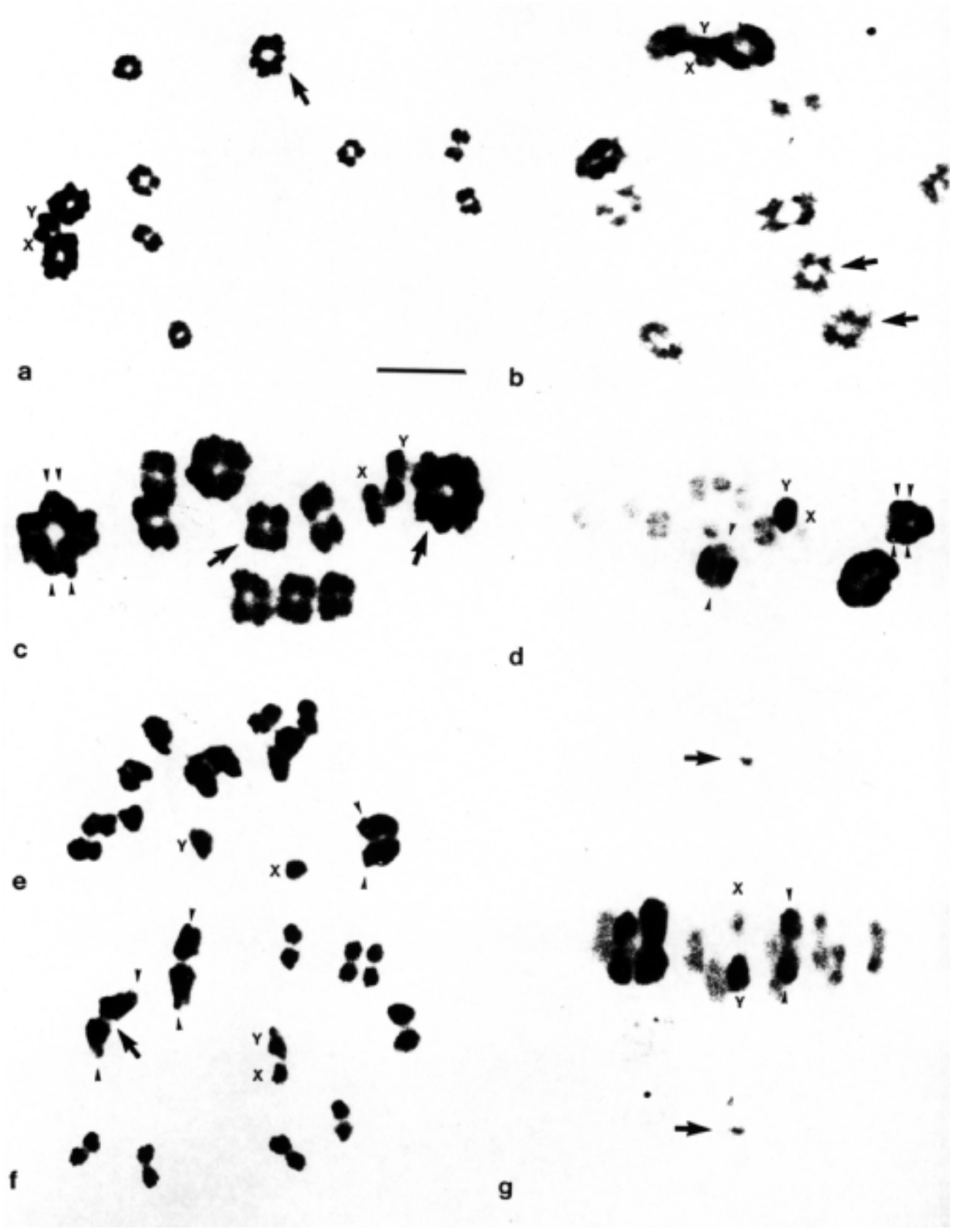
Autosome orientation and segregation

C-banding provides reliable chromosome markers in some autosomes to analyse their behaviour during both meiotic divisions (Figure 1). Particularly, the presence of a band at only one of the ends of chromosomes 3 allows us to differentiate the involvement of both ends (euchromatic or heterochromatic) in the kinetic behaviour of these chromosomes.

At metaphase I, this bivalent shows two alternative orientations: either the euchromatic (Figures 2d, 3b, 3d, 3f & 5b) or the heterochromatic (Figures 3a, 3c, 3e & 5a) ends of each homologue are directed towards the poles. This difference allows us to distinguish, in fact, six alternatives, if the position of the single chiasma is taken into account (Figure 3). Although these same possibilities are observed for the heterozygous bivalent 2 (Figures 2d, 3a & 3c), we only centred our analysis on bivalent 3.

At anaphase I, we have observed the expected segregation of each alternative for the bivalent 3. Therefore, the V-shaped half-bivalents of this autosome pair show the kinetic activity located in either the euchromatic or the heterochromatic ends (Figures 4 & 5). We have never observed a segregation in which the kinetic activity resides in the euchromatic end of one homologue and the heterochromatic end of the other homologue.

In order to test whether the kinetic activity of both ends is a random process, we scored the bivalent and half-bivalent configurations in five individuals. Results show that in every case more than 50% of the metaphase I cells show the bivalent 3 with a kinetic activity restricted to the euchromatic end (Table 1). However, these frequencies show significant differences among the five individuals ($\chi^2 = 23.88$, $P < 0.01$, d.f. $= 4$). At metaphase/anaphase II, we have also observed the kinetic activity restricted to the euchromatic or the heterochromatic ends. Interestingly, the frequencies scored for each alternative in each individual are inverted if compared with those obtained in metaphase I (Table 1). This result clearly suggests that the chromosome end that is active during the first meiotic division becomes inactive during the second one (see Figure 4). That is, for a given chromosome, this function is carried out by opposite ends during both meiotic separations. The frequencies scored in three of the individuals analysed (1, 2 and 3) fit this prediction, since a contingency test does not reveal significant differences (see Table 1).


a
b
c
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g
X
Y

Table 1. Frequencies of metaphase I and metaphase II cells showing the kinetic activity restricted at the euchromatic or the heterochromatic ends of chromosome 3

Individual	1 (%)	2 (%)	3 (%)	4(%)	5 (%)
Metaphase I					
Bivalents with kinetic activity at the euchromatic ends	42 (66.7)	133 (79.6)	72 (82.8)	82 (60.3)	89 (63.1)
Bivalents with kinetic activity at the heterochromatic ends	21 (33.3)	34 (20.4)	15 (17.2)	54 (39.7)	52 (36.9)
Total	63	167	87	136	141
Metaphase II					
Half-bivalents with kinetic activity at the euchromatic ends	27 (30.0)	45 (22.2)	22 (23.1)	60 (25)	94 (27.7)
Half-bivalents with kinetic activity at the heterochromatic ends	63 (70.0)	158 (77.8)	73 (76.9)	180 (75)	245 (73.3)
Total	90	203	95	240	339

In each case the percentage of each alternative is indicated between brackets.

Discussion

Autosome orientation and segregation

Several reports have provided evidence that, during the meiotic divisions of Heteroptera, the kinetic activity is restricted to the chromosome ends in both autosomes (Hughes-Schrader & Schrader 1961) and sex chromosomes (Schrader 1935). These authors observed that, during both meiotic metaphases, the chromosomes appeared with their long axes parallel to the equatorial plate. However, during both meiotic anaphases only their ends were kinetically active leading the chromosome/chromatid segregation to opposite poles. This restriction of kinetic activity in autosome bivalents is obvious in every case analysed (Ueshima 1979), while to ascertain whether this process affects both chromosome ends or only one of them is more debatable. Camacho *et al.* (1985) reported that, in monochiasmatic bivalents of *Nezara viridula*, only the end that is further from the position of the chiasma presents kinetic activity. On the contrary, our results on the behaviour of bivalent 3 in *T. infestans* clearly show that the kinetic activity is restricted at the same end of each homologue, and that both ends (heterochromatic or euchromatic) can show kinetic activity (Figure 4 & Table 1). When an interstitial chiasma is present, two heterochromatic and two euchromatic ends, as defined by C-banding, are clearly discerned. The analysis of the metaphase I orientations and anaphase I segregations demonstrates that both ends may show kinetic activity. Moreover, even the ends near the chiasma may show kinetic activity. These observations demonstrate that both ends may show kinetic activity independently of the chiasma position.

We have also determined that in bivalent 3 of *T. infestans* the restriction of the kinetic activity affecting both chromosome ends is not a random process. In the five individuals that we have analysed, the frequencies of kinetic activity at each chromosome end during the first meiotic division are significantly different but depart from a 50% expectation. The percentages of active euchromatic ends vary between 60.3% and

Figure 2. Spermatocytes at different stages. **a**, **c**, **e** & **f** Orcein staining. **b**, **d** & **g** C-banding. **a** Diakinesis. The sex chromosomes (X, Y) appear associated with two of the larger bivalents. Each autosomal bivalent shows a single chiasma. One bivalent presenting an interstitial chiasma is arrowed. Scale bar = 5 μm. **b** Diplotene. C-banding reveals that chromosome pairs 1 and 2 are associated to the sex univalents (X, Y) forming a chromocentre. Each autosomal bivalent shows a single interstitial (arrows) or distal chiasma. **c** Metaphase I. Sex univalents (X, Y) are associated but a true chiasma between them does not exist. Autosomal bivalents maintain a single chiasma as those shown in earlier stages. One medium and one large bivalent with an interstitial chiasma are arrowed. Kinetic activity seems to be restricted to the chromosome ends of each homologue (arrowheads). **d** Metaphase I. C-banding allows differentiation of the chromosome end possessing kinetic activity. Kinetically active euchromatic ends (single arrowheads) in bivalent 3 and heterochromatic ends (double arrowheads) in bivalent 2 are marked. **e** Prometaphase II. Ten autosomal half-bivalents and the unassociated sex chromatids (X, Y) are visible. Some of the half-bivalents show kinetic activity at the same end in both chromatids (arrowheads). **f** Metaphase II. Chromatids of each half-bivalent show kinetic activity at one of their ends (arrowheads) but are joined at the opposite end (arrow). The sex chromatids (X, Y) appear associated and co-oriented. **g** Metaphase II. The kinetic activity is restricted to one of the ends (arrowheads) of each chromatid. Cell poles are marked by arrows.

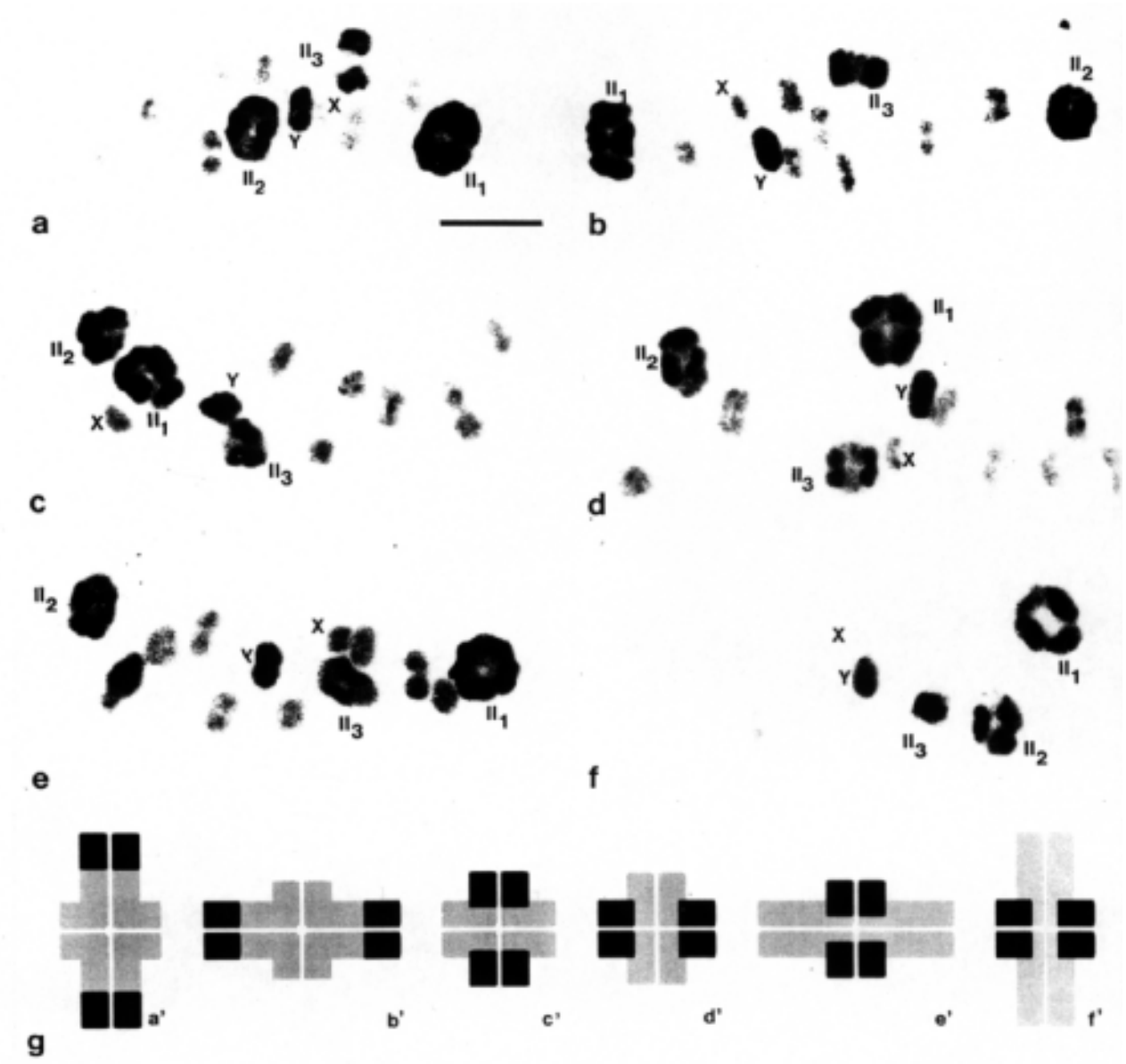

Figure 3. Different metaphase I configurations of bivalent 3 after C-banding. Three distinct locations of the single chiasma with respect to the distal C-band were found: distal (**a** & **b**), interstitial (**c** & **d**) and proximal (**e** & **f**). **g** Since the kinetic activity is localized in either of the chromosome ends, we have observed up to six alternatives, which are indicated (**a**'–**f**'). This circumstance may be found in the other bivalents. Compare, for instance, the distinct orientation of the heterozygous bivalent 2 in **c** & **f**. Bivalents 1 (II_1), 2 (II_2), 3 (II_3) and the sex chromosomes (X, Y) are marked. Scale bar = 5 μm.

82.8% and, correspondingly, those of heterochromatic ends vary between 39.7% and 17.2%. Moreover, we have obtained results that strongly support the hypothesis that for a given chromosome the kinetic activity is restricted to a chromosome end during the first meiotic division and to the opposite end during the second one (Nokkala 1985). Thus, the percentages of kinetic activity shown by the chromosome ends in chromosome 3 are inverted during both divisions in every individual analysed (Table 1). During the second meiotic division, the higher percentages of kinetic activity correspond to the heterochromatic ends. Moreover, a contingency test does not yield significant differences between the frequencies scored in three individuals (1, 2 and 3) during both meiotic divisions. These results suggest that, although individuals may show particular frequencies, as a general rule the euchromatic ends direct the segregation in anaphase I, while the heterochromatic ends carry out this function in anaphase II. We have never detected half-

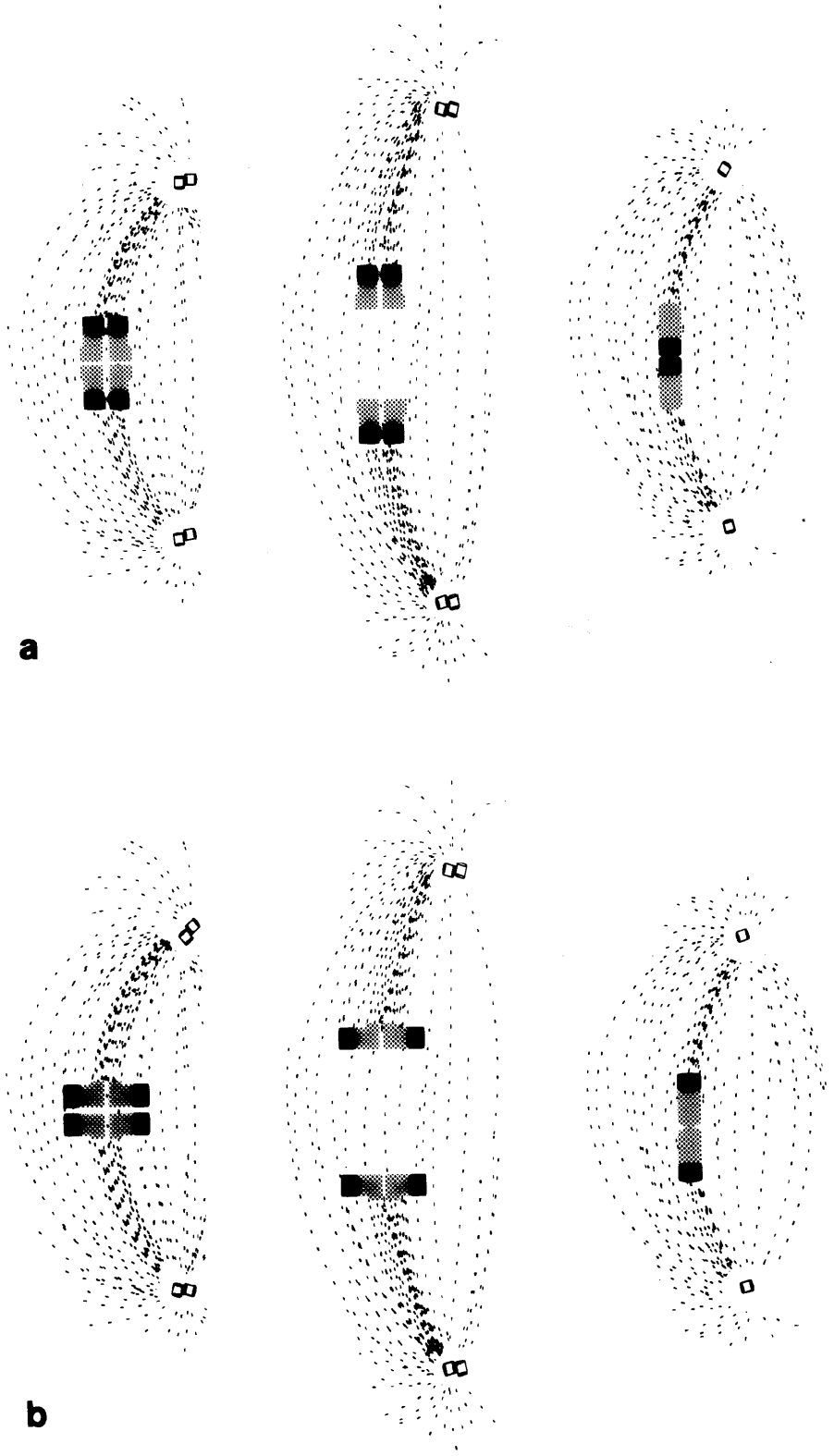

Figure 4. Diagrams illustrating the two expected alternative orientations of bivalent 3 with a single distal chiasma with respect to the C-band and throughout both meiotic divisions. Left, metaphase I; middle, anaphase I; and right, metaphase II. **a** We depict the alternative observed in Figure 3a and schematized in Figure 3g (a′) in which the heterochromatic ends possess the kinetic activity during the first meiotic division. As stated in the Results section, it is expected that during anaphase II, the euchromatic ends of the chromatids of the half-bivalent will present kinetic activity. **b** We indicate the alternative observed in Figure 3b and schematized in Figure 3g (b′) in which the euchromatic ends are those showing kinetic activity during the first meiotic division. In this case, it is expected that during anaphase II, the heterochromatic ends will show kinetic activity. In both alternatives, the presumed microtubule interaction with the chromosome/chromatid ends is also depicted. Compare these diagrams with the plates shown in Figure 5.

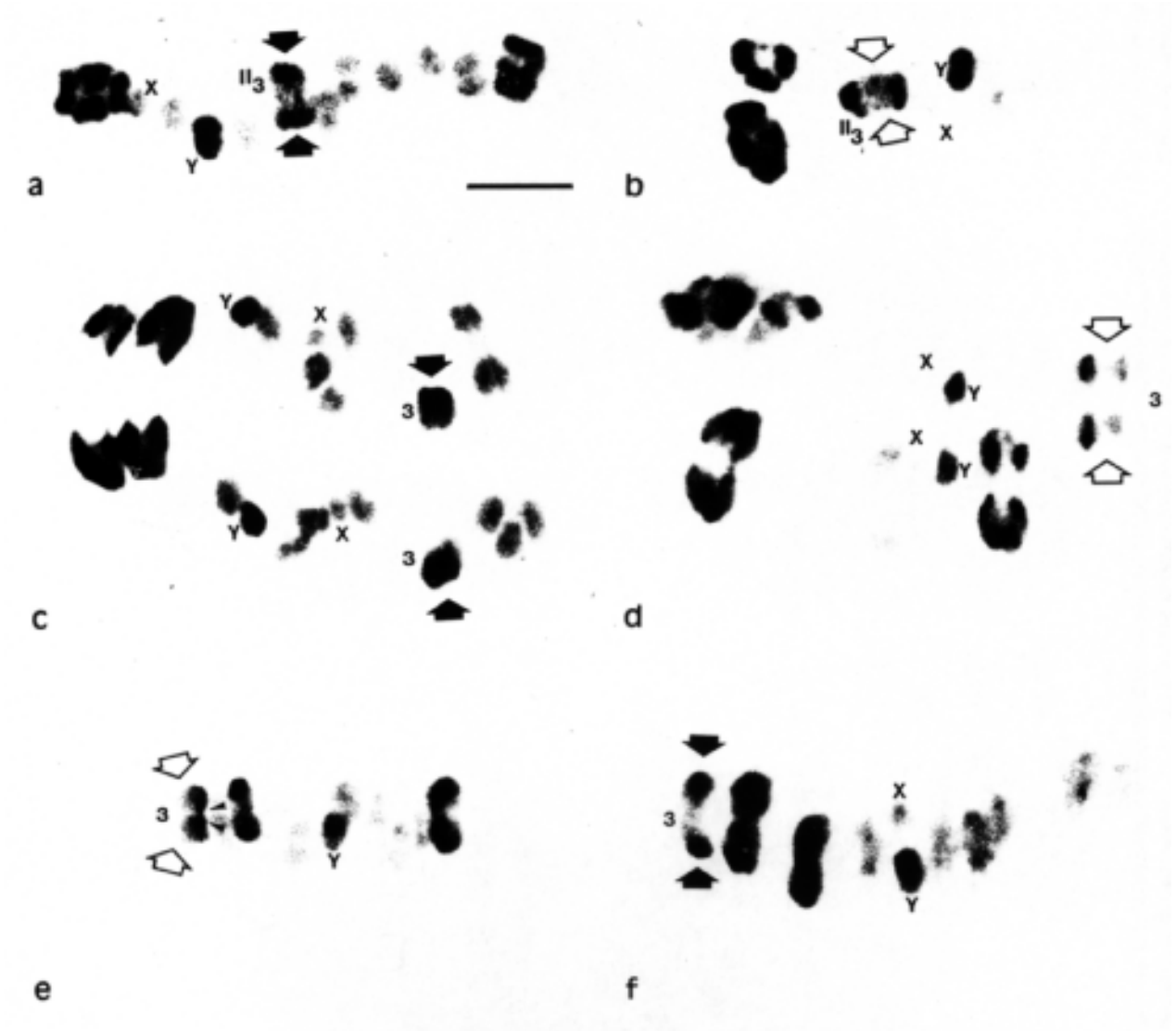

Figure 5. Kinetic activity in chromosome 3. **a**, **c** & **e** A sequence of the expected behaviour of bivalent 3 (II_3) in which the kinetic activity is located in the heterochromatic ends during the first meiotic division is presented. The bivalent orientation at metaphase I (**a**) shows the heterochromatic ends (arrows) of both homologues directed to the poles. Scale bar = 5 μm. At anaphase I, these ends direct the movement of the homologues to opposite poles (**c**). At metaphase II, the kinetic activity is restricted to the euchromatic ends (empty arrows), while the heterochromatic ends (arrowheads) are located in the association place between both chromatids (**e**). Note the parallel disposition of half-bivalent 3 (3) (**e**). **b**, **d** & **f**. Sequence of the expected behaviour of bivalent 3 (II_3) when the kinetic activity is located in the euchromatic ends (empty arrows) at metaphase I (**b**) and anaphase I (**d**). At metaphase II, the kinetic activity is located in the heterochromatic end (arrows) of each chromatid of the half-bivalent (**f**). Note that the long axis of half-bivalent 3 is parallel to the spindle axis (**f**). Sex chromosomes (X, Y) follow the inverted meiotic sequence. At metaphase I, they appear as univalents (**a** & **b**) and segregate their chromatids independently at anaphase I (**c** & **d**). At metaphase II, both sex chromatids associate to form a pseudobivalent (**e** & **f**) to segregate to opposite poles posteriorly.

bivalents 3 at metaphase II with distal associations between the euchromatic and the heterochromatic ends. Such orientation would be expected, if kinetic activity at metaphase II was independent of that observed during the first meiotic division.

The observation that kinetic activity is restricted to a chromosome end during the first meiotic division and to the opposite end during the second one raises the question of how the ends acquire their kinetic capacity. This is an interesting and unusual situation, since in most heteropteran species there is no decondensation stage between the first and second meiotic divisions, i.e. interkinesis does not exist, and the cell begins the second division just after telophase I. Thus, it remains to be explained how the microtubule-dependent motor proteins located at one chromosome end, and required

for its kinetic activity, lose functionality or relocate during the transition between both meiotic divisions, and how the opposite end achieves the capacity to direct the chromosome movement during the second one. In any case, it is clear from our results that constitutive heterochromatin is not an obstacle for the location of motor proteins rendering kinetic activity.

Chiasmata terminalization in heteropteran species

The chiasma terminalization hypothesis implies that a chiasma could move during late prophase I from its site of origin to reach the bivalent end at metaphase I (Darlington 1932). This hypothesis, while canonically held over the years, has been questioned for systems with monocentric chromosomes (see Jones 1987). However, it has been repeatedly claimed that chiasma terminalization is a regular feature of meiosis in organisms with holocentric chromosomes, such as heteropteran species (see John & King 1985). Although we have not carried out an extensive analysis of chiasma distribution in the bivalents of *T. infestans*, our results analysing the configurations of bivalent 3 allowed us to determine the real chiasmata position owing to both its large size and the possibility of discriminating the two ends. Thus, interstitial vs. the two different distal chiasmata could be easily detected at metaphase I. These observations are in agreement with the results obtained by Solari & Agopian (1987) on surface spreads of pachytene spermatocytes of *T. infestans*. These authors found that recombination nodules, considered to be a morphological expression of recombinational processes (von Wettstein *et al*. 1984), may be found all along the bivalent length. The appearance of interstitial chiasmata and the observation of bivalents with their long axes parallel to the equatorial plate undoubtedly suggest that, at least in *T. infestans*, chiasma terminalization does not occur. We think that the chiasma terminalization claimed to occur in other heteropteran species could also be considered as pseudoterminalization cases (Jones 1978, 1987). The presence of subterminal chiasmata in bivalents composed of small-sized and highly packaged chromosomes, such as those present in most heteropteran species (White 1973), may lead to the interpretation of terminalization, whereas this is not the case. Thus, it would be interesting to find chromosome markers in these species to test this assumption.

Following our results, it is tempting to speculate on the existence of at least two different groups of heteropteran species regarding the meiotic behaviour of their chromosomes. The first group would include most previously analysed heteropteran species and would be characterized by the tendency to present pseudoterminalized chiasmata, i.e. chiasmata near the chromosome ends. In some species, bivalents with two apparent chiasmata congress to the metaphase I plate showing a holokinetic behaviour, but then one chiasma resolves before anaphase (Mola & Papeschi 1993). As a result, all the monochiasmate bivalents at late metaphase I present their long axes perpendicular to the metaphase plate. Another feature that is present in most heteropteran species is that the chromosome end showing kinetic activity during the first meiotic division is that not engaged in the chiasmatic association between the homologues (Camacho *et al*. 1985). The second group of species, in which *T. infestans* would be included, would present chiasmata all along the bivalent, not showing terminalization or pseudoterminalization. In these species, the presence of a distal chiasma would not abolish the ability of the nearest end to show kinetic activity, and consequently, both chromosome ends could show kinetic activity.

The inverted meiotic sequence

First meiotic division in monocentric systems is characterized by the bipolar orientation of the bivalents with the two sister kinetochores of each homologue facing the same pole. Therefore, the first meiotic division is reductional for sister kinetochores. Subsequently, during the second meiotic division, sister kinetochores of a half-bivalent orient to opposite poles and segregate equationally. This sequence, which is considered standard, is not followed by all species. In most heteropteran species, this meiotic sequence is inverted for the sex chromosomes (González-García *et al*. 1996). Sex univalents segregate equationally during the first meiotic division and reductionally during the second one. Whether this sequence is also followed by autosomes has been poorly analysed and results are based on speculative observations.

Our observations on the meiotic behaviour of the sex chromosomes of *T. infestans* corroborate that described for the sex chromosomes of other heteropteran species. By contrast, the autosomes do not follow the same inverted meiotic sequence that characterizes the sex univalents. On the contrary, they behave in a similar manner to monokinetic chromosomes. However, the alternative modes of segregation observed in anaphase I make clear that the classical distinction between reductional and equational segregation (see White 1973, p. 197) is not applicable in this case. Holocentric chromosomes with restricted kinetic activity do not always 'reduce' the same chromosome segment as monokinetic chromosomes indeed do. This depends on which of the two chromosome ends is directing the segregation of half-bivalents at anaphase I.

Finally, it is important to point out that the resulting genetic combinations after both the standard meiotic sequence and that reported here for the autosomes are the same. In this sense, none of them offers an increase in meiotic variability. Thus, some heteropteran species have developed a special meiotic mechanism that produces the same results as those present in species with monocentric chromosomes. In these systems, the chromosome segregation sequence throughout the meiotic divisions is not a fundamental meiotic event. It has

been suggested that the suppression of kinetochore structures in heteropteran meiotic chromosomes is needed to allow chiasmata terminalization (Comings & Okada 1972). Our results indicate that, in *T. infestans*, chiasmata terminalization does not occur, and that two different modes of metaphase I bivalent orientation are present. Thus, the absence of kinetochore structures in holocentric meiotic chromosomes is not fundamentally associated with chiasmata terminalization. The lack of kinetochores at fixed chromosome positions allows two possible bivalent orientations during the first meiotic division. Moreover, this situation allows the alternation of kinetic activity of the two chromosome ends during both meiotic divisions.

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