Hereditas 134: 245–254 (2001)

# Synapsis in Robertsonian heterozygotes and homozygotes of *Dichroplus pratensis* (Melanoplinae, Acrididae) and its relationship with chiasma patterns

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**Martí, D. A. and Bidau, C. J. 2001**. Synapsis in Robertsonian heterozygotes and homozygotes of *Dichroplus pratensis* (Melanoplinae, Acrididae) and its relationship with chiasma patterns.—*Hereditas 134*: 245–254. Lund, Sweden. ISSN 0018-0661. Received May 10, 2001. Accepted October 4, 2001

*Dichroplus pratensis* has a complex system of Robertsonian rearrangements with central-marginal distribution; marginal populations are standard telocentric. Standard bivalents show a proximal-distal chiasma pattern in both sexes. In Robertsonian individuals a redistribution of chiasmata occurs: proximal chiasmata are suppressed in fusion trivalents and bivalents which usually display a single distal chiasma per chromosome arm. In this paper we studied the synaptic patterns of homologous chromosomes at prophase I of different Robertsonian status in order to find a mechanistic explanation for the observed phenomenon of redistribution of chiasmata. Synaptonemal complexes of males with different karyotypes were analysed by transmission electron microscopy in surface-spread preparations. The study of zygotene and early pachytene nuclei revealed that in the former, pericentromeric regions are the last to synapse in Robertsonian trivalents and bivalents and normally remain asynaptic at pachytene in the case of trivalents, but complete pairing in bivalents. Telocentric (standard) bivalents usually show complete synapsis at pachytene, but different degrees of interstitial asynapsis during zygotene, suggesting that synapsis starts in opposite (centromeric and distal) ends. The sequential nature of synapsis in the three types of configuration is directly related to their patterns of chiasma localisation at diplotene-metaphase I, and strongly supports our previous idea that Rb fusions instantly produce a redistribution of chiasmata towards chromosome ends by reducing the early pairing regions (which pair first, remain paired longer and thus would have a higher probability of forming chiasmata) from four to two (independently of the heterozygous or homozygous status of the fusion). Pericentromeric regions would pair the last, thus chiasma formation is strongly reduced in these areas contrary to what occurs in telocentric bivalents.

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*Dichroplus pratensis* is a South American grasshopper, the geographic distribution of which covers most of Argentina, Uruguay and southern Brazil (BIDAU et al. 1991). A complex system of eight polymorphic and polytypic Robertsonian (Rb) fusions that involves the six large autosomes (L1–L6) is superimposed upon the standard telocentric chromosome complement ($2n = 18 + X♂$, $18 + XX♀$). Meiotic studies of a large number of Argentinian populations, demonstrated that the Rb fusions strongly affect chiasma frequency and distribution and thus, potential genetic recombination and meiotic orientation and segregation (BIDAU 1990, 1991, 1993, 1996; BIDAU et al. 1991; MIROL and BIDAU 1991, 1992, 1994; TOSTO and BIDAU 1991; BIDAU and MARTÍ 1995, 1998; MARTÍ and BIDAU 1995, 1998). An adaptive role of the fusions as potential reservoirs of coadapted supergenes through the creation of recombination-free chromosomal regions, has been proposed (BIDAU 1990, 1993, 1996; BIDAU and MARTÍ 1995; MARTÍ and BIDAU 1995). This hypothesis could also explain the central-marginal distribution of the Rb polymorphisms and their behaviour in hybrid zones (BIDAU 1991, 1996; TOSTO and BIDAU 1991; MARTÍ and BIDAU 1998).

To explain the decrease in chiasma frequency and the repatterning of chiasmata produced by the fusions, involves the displacement of cross-over events to distal ends of the involved chromosomes in all heterozygotes and homozygotes for the eight different fusions (BIDAU 1990; BIDAU and MARTÍ 1995; MARTÍ and BIDAU 1995). A mechanistic model has been put forward which accounts for the parallel chiasma repatterning of both classes of Rb configurations (BIDAU 1993): in grasshoppers pairing usually starts at chromosome ends attached to the nuclear envelope and assuming that chiasmata are formed more readily in regions that pair first and remain paired longer (JONES 1987), a Rb fusion (homozygous or heterozygous) instantly reduces the early pairing ends from four to two, the distal ones,

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Table 1. *Chiasma characteristics of the L chromosomes of the D. pratensis males (N = 28) from Manantiales including those studied in this paper (only the autosomes involved in the Robertsonian variation of this population are represented). St = standard telocentric; Het = Robertsonian heterozygote; Hom = Robertsonian homozygote; P = proximal; I = interstitial; D = distal; n = number of analysed cells*

| L chromosome | Status | Position of chiasmata (%) | | | Chiasma frequency | n |
|---|---|---|---|---|---|---|
| | | P | I | D | | |
| L1 | St | 20.0 | 0 | 80.0 | 1.00 | 10 |
| | Het | 0 | 2.90 | 97.1 | 1.00 | 70 |
| | Hom | 1.5 | 5.0 | 93.5 | 1.00 | 200 |
| L3 | St | 57.5 | 5.5 | 37.0 | 1.15 | 110 |
| | Het | 1.1 | 10.0 | 88.9 | 1.00 | 90 |
| | Hom | 2.1 | 6.3 | 91.3 | 1.00 | 80 |
| L4 | St | 58.1 | 8.0 | 33.9 | 1.13 | 110 |
| | Het | 1.1 | 10.0 | 88.9 | 1.00 | 90 |
| | Hom | 1.3 | 11.4 | 87.3 | 0.98 | 80 |
| L6 | St | 75.0 | 0 | 25.0 | 1.20 | 10 |
| | Het | 0 | 21.4 | 78.6 | 1.00 | 70 |
| | Hom | 2.6 | 16.3 | 81.1 | 0.98 | 200 |

thus decreasing the probability of proximal chiasma formation that occur at high frequencies in non-fused telocentric bivalents.

In this paper, we analysed meiotic chromosome pairing through the observation of synaptonemal complexes of *D. pratensis* males with different Rb karyotypes by transmission electron microscopy in surface-spread preparations, in order to test the above mentioned hypothesis.

## MATERIAL AND METHODS

This paper is based on four male specimens of *D. pratensis* collected at Manantiales (33°32'S/63°20'W Córdoba province, Argentina) whose testes were processed following two parallel protocols. One testis was fixed in methanol-glacial acetic acid (3:1) and conventional meiotic preparations were performed by squashing a few follicles in propionic haematoxylin or lacto-propionic orcein in order to determine the karyotype. Two males were heterozygous for the 1/6 and 3/4 fusions (Het 1/6, Het 3/4), one was a 1/6 heterozygote (Het 1/6) and one, 1/6 homozygote (Hom 1/6). The other testis was processed for the observation of synaptonemal complexes by transmission electron microscopy as follows: Gonads were deposited in 0.5 ml of TC 199 medium with 2 mM EDTA and 0.1 % seroalbumin. Fat tissue was carefully removed. A cell suspension was then obtained by maceration in a 1.5 ml glass plunger. A drop of this suspension was placed on an acetate coated slide and two or three drops of swelling medium (10 ml 0.1 M EDTA + 10 ml 0.06 M phosphate buffer + 3 ml 1 % Triton X-100 + 77 ml distilled water; pH was adjusted to 7.5 with 1N NaOH) were added. After 18 min exposure of the cells, they were fixed with 4 % paraformaldehyde in a 1.7 % sucrose solution (pH 8.9). Slides were dried at 60°C for 6 hours and then washed thoroughly for two min in distilled water. Staining was performed with 50 % $AgNO_3$ adjusted to pH 3.1–3.2 with formic acid at 60°C and selected zygotene and pachytene nuclei were transferred to TEM grids. Observations were performed in a Jeol JEM 1010 TEM. Measurements of SCs were done on photographic enlargements with the aid of a cartographic curvimeter.

Chiasma frequency and distribution was studied in 10 metaphase I cells of each of 28 males collected at Manantiales.

## RESULTS

Table 1 indicates the localisation of chiasmata in the relevant Rb configurations studied and Table 2 summarises the behaviour of synaptonemal complexes of 14 complete zygotene-pachytene nuclei of *D. pratensis* males with different Robertsonian karyotypes. To establish the precise chronology of the zygotene-pachytene transition, we decided to use as the sole criterion for the progression of stages, the total length of the axial elements either synapsed (SCs) or not synapsed as shown in Table 2.

It is clear from our results, that the different types of chiasma localisation observed in fused (mainly

Table 2. *Pairing patterns in 14 zygotene-pachytene nuclei of different Robertsonian karyomorphs of D. pratensis. Total length of SC's is expressed in μm. N = Nucleus number; K = Karyotype; TLSC = Total length of Synaptonemal Complexes of the autosomal complement; P = Percentage of homologous pairing; TAS = Asynapsis of Robertsonian trivalents expressed as a percentage of the total length of the synapsed autosomal complement; BAS = Asynapsis of Robertsonian bivalents expressed as a percentage of the total length of the synapsed autosomal complement; TeAS = Asynapsis of telocentric L and S bivalents, except the megameric (S7) bivalent expressed as a percentage of the total length of the synapsed autosomal complement. MAS = Asynapsis of the S7 bivalent expressed as a percentage of the total length of the synapsed autosomal complement; NORAS = Asynapsis of the S8 bivalent (NOR carrier) expressed as a percentage of the total length of the synapsed autosomal complement. Results in parentheses correspond to percentages of asynapsis of the involved chromosomes*

| N | K | TLSC | P | TAS | | BAS | TeAS | MAS | NORAS |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 1/6 | 3/4 | | | | |
| 1 | Hom 1/6 | 623.13 | 55.99 | – | – | 29.02 (42.34) | 9.67 (36.76) | 4.25 (85.72) | 1.06 (25.00) |
| 2 | Het 1/6 | 398.53 | 98.40 | 1.59 (5.00) | – | 0 | 0 | 0 | 0 |
| 3 | Het 1/6, Het 3/4 | 328.48 | 96.15 | 1.28 (4.04) | 2.56 (8.09) | 0 | 0 | 0 | 0 |
| 4 | Het 1/6, Het 3/4 | 288.10 | 92.23 | 3.28 (9.73) | 4.48 (12.50) | 0 | 0 | 0 | 0 |
| 5 | Het 1/6, Het 3/4 | 279.05 | 95.89 | 1.95 (4.53) | 2.15 (8.16) | 0 | 0 | 0 | 0 |
| 6 | Het 1/6, Het 3/4 | 266.64 | 97.02 | 1.88 (4.95) | 1.09 (2.50) | 0 | 0 | 0 | 0 |
| 7 | Het 1/6, Het 3/4 | 256.41 | 91.15 | 3.93 (11.03) | 4.91 (12.66) | 0 | 0 | 0 | 0 |
| 8 | Hom 1/6 | 238.68 | 100 | – | – | 0 | 0 | 0 | 0 |
| 9 | Hom 1/6 | 237.12 | 100 | – | – | 0 | 0 | 0 | 0 |
| 10 | Het 1/6, Het 3/4 | 229.91 | 95.36 | 2.89 (7.72) | 1.74 (4.76) | 0 | 0 | 0 | 0 |
| 11 | Hom 1/6 | 226.59 | 98.54 | – | – | 0 | 0 | 0 | 1.46 (39.60) |
| 12 | Hom 1/6 | 201.24 | 100 | – | – | 0 | 0 | 0 | 0 |
| 13 | Hom 1/6 | 185.64 | 100 | – | – | 0 | 0 | 0 | 0 |
| 14 | Het 1/6, Het 3/4 | 178.53 | 86.37 | 6.11 (16.50) | 3.15 (6.72) | 0 | 0 | 3.62 (70.01) | 0.74 (17.39) |

distal) and non-fused (proximal-distal) L-autosomes, is not dependent on incomplete or restricted synapsis, since those nuclei showing the shortest length of SCs tended to display almost full synapsis of all relevant autosomal configurations. Only four nuclei displayed 100 % synapsis (Table 2); significantly, they did not carry heterozygous Rb configurations. Nuclei with shorter SC total length also tend to show very clear bouquet configurations although these can also be observed in earlier nuclei (Fig. 2). The only observed exceptions to this behaviour seem to be the S7 (megameric) and S8 (NOR carrier) bivalents which are never involved in Robertsonian fusions; their differential pairing behaviour is probably a consequence of their special properties (see below).

The most regular pairing behaviour observed was that of the standard telocentric L-autosomes which, although in most nuclei, were fully synapsed, nucleus N° 1 clearly shows that bivalents (Fig. 1) show large asynaptic interstitial regions, while proximal and distal portions are completely paired. Note that in this nucleus, the longest telocentric bivalent (L2), has a larger asynaptic region than the shortest one (L3); the other two L bivalents (L4 and L5) are completely synapsed.

In the same nucleus, the Robertsonian metacentric bivalent (L1.L6) has a large pericentromeric non-synapsed region (Fig. 1, Table 2). In more advanced nuclei of 1/6 homozygotes, this Robertsonian bivalent was always seen completely synapsed (Table 2).

Robertsonian trivalents show the most variable synaptic behaviour. In all analysed nuclei of simple and double heterozygotes, both trivalents (1/6 and 3/4) showed variable degrees of asynapsis (Table 2) that always involved the pericentromeric region of the trivalent (Fig. 2, 3 and 4a,b). No significant correlation exists between the extent of pericentromeric asynapsis of the two trivalents, nor between total SC length and extent of trivalent pairing. It is interesting to note that in two nuclei, associations

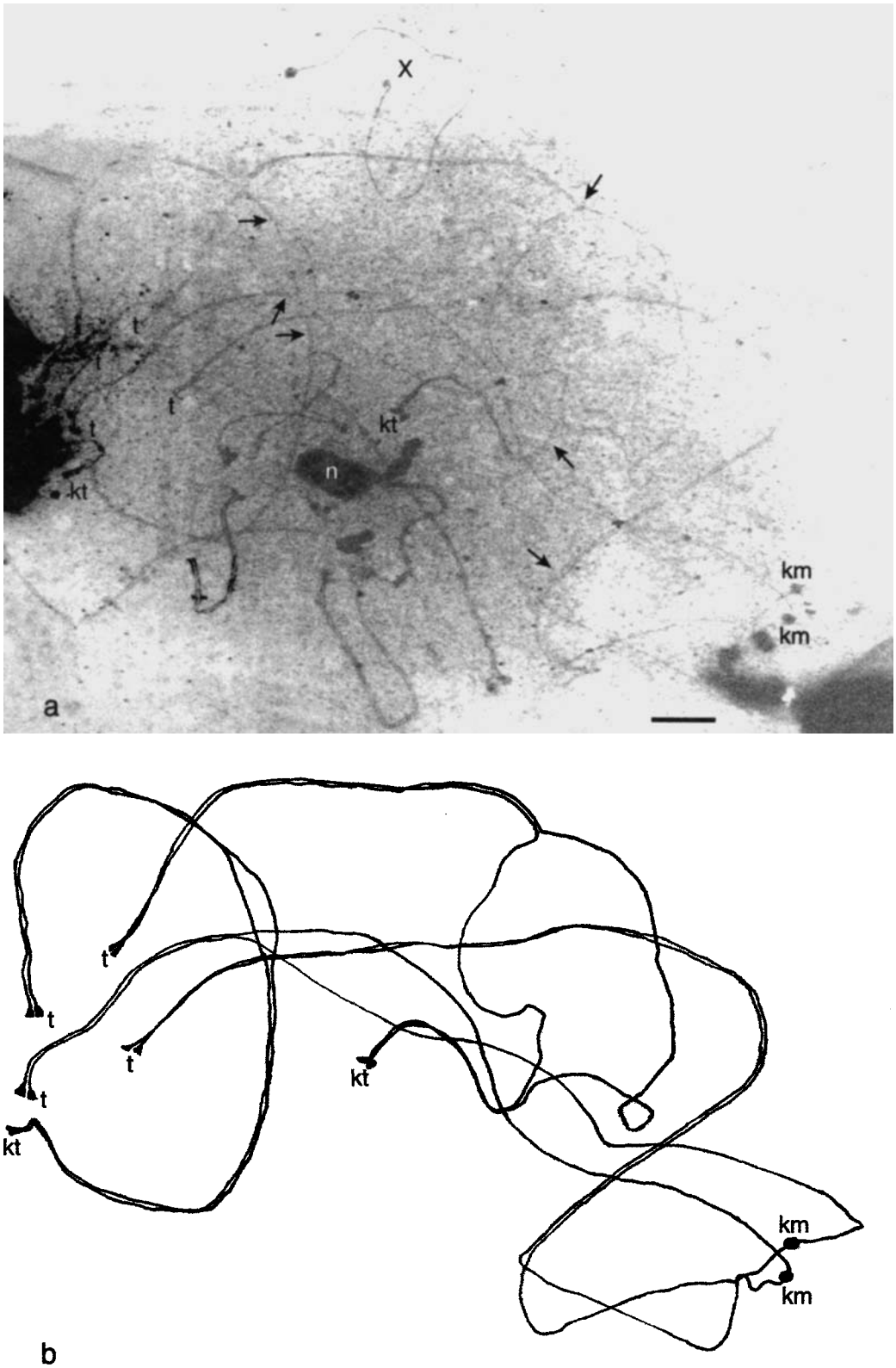


**Fig. 1a and b.** **a** Zygotene-Early Pachytene nucleus from a 1–1.6–6 structural homozygote of *D. pratensis*. Synapsis has occurred along the proximal and distal portions of telocentric bivalents L2 and L3 leaving relatively large interstitial unsynapsed regions. The metacentric bivalent also shows a large pericentromeric unsynapsed region. The bar indicates 2.5 μm. **b** Schematic representation of the relevant configurations shown in Fig. 1 (a) km: kinetochore of the metacentric bivalent; kt: terminal kinetochores of telocentric bivalents; n: nucleolus; t: distal telomere; X: univalent X chromosome.

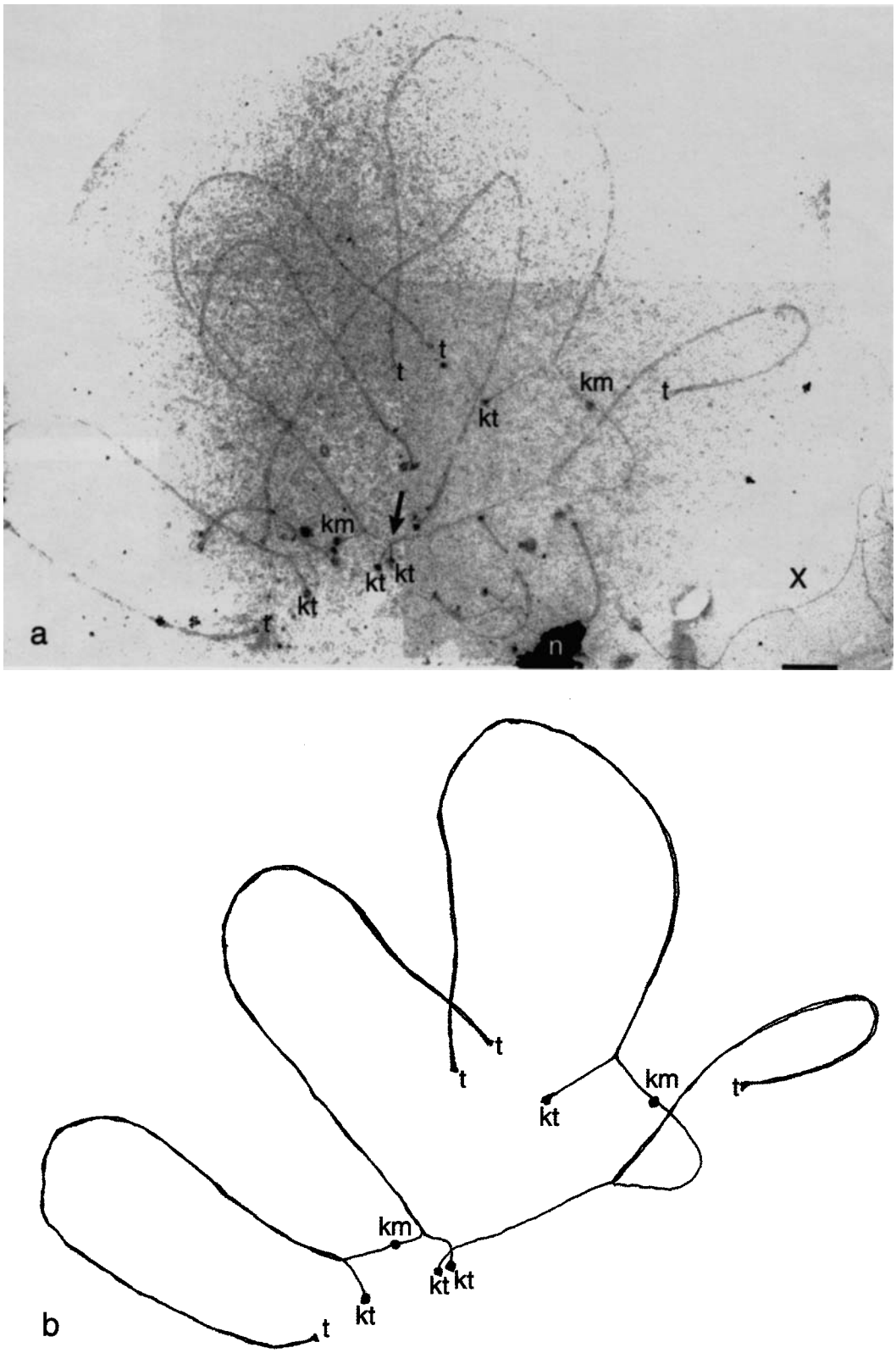


**Fig. 2a and b.** **a** Pachytene nucleus of a double 1–1.6–6 and 3–3.4–4 structural heterozygote of *D. pratensis*. The arrow indicates the centromeric association between two non-homologous telocentric chromosomes belonging to both trivalents present in this nucleus. Note the lack of proximal synapsis in both trivalents. The bar indicates 2.5 μm. **b** Schematic representation of the relevant configurations shown in Fig. 2 (a) km: kinetochore of the metacentric bivalent; kt: terminal kinetochores of telocentric bivalents; n: nucleolus; t: distal telomere; X: univalent X chromosome.

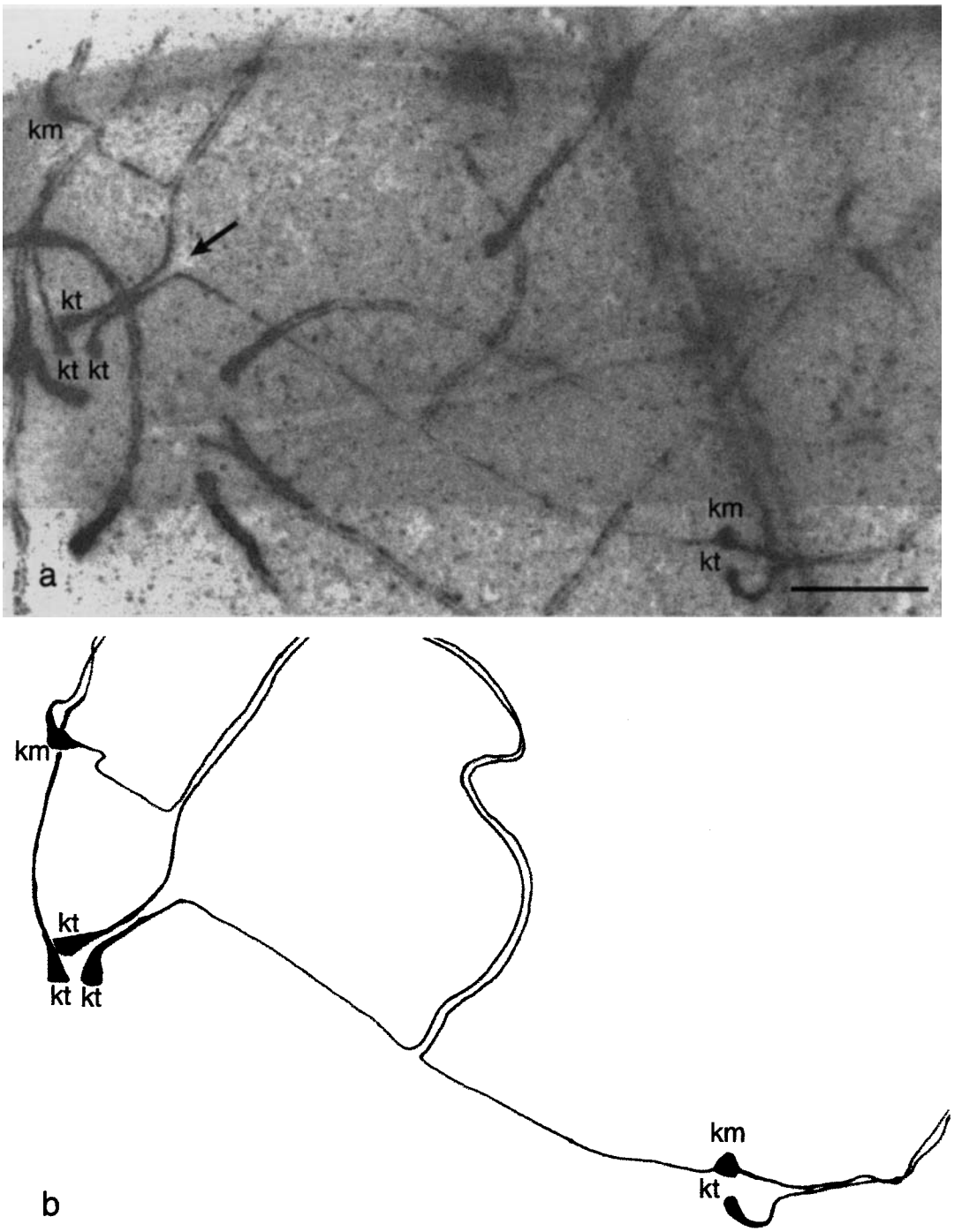


**Fig. 3a and b.** **a** Late pachytene nucleus of a 1–1.6–6 y 3–3.4–4 structural heterozygote of *D. pratensis*; the arrow indicates a region of paracentromeric heterosynapsis between telocentric chromosomes belonging to different trivalents. The bar indicates 2.5 μm. **b** Schematic representation of the relevant configurations shown in Fig. 3 (a) km: kinetochore of the metacentric bivalent; kt: terminal kinetochores of telocentric bivalents.

between the free centromeric ends of the asynapsed telocentric members of two different trivalents, were observed (Fig. 2 and 3).

The three S bivalents tended to show a very regular pairing behaviour and were completely synapsed in most nuclei. However, S7 (the megameric bivalent) showed large asynaptic regions in two nuclei: in one case, the asynaptic region involved the proximal and a large interstitial portion of the bivalent with short distal and interstitial zones with fully formed SCs

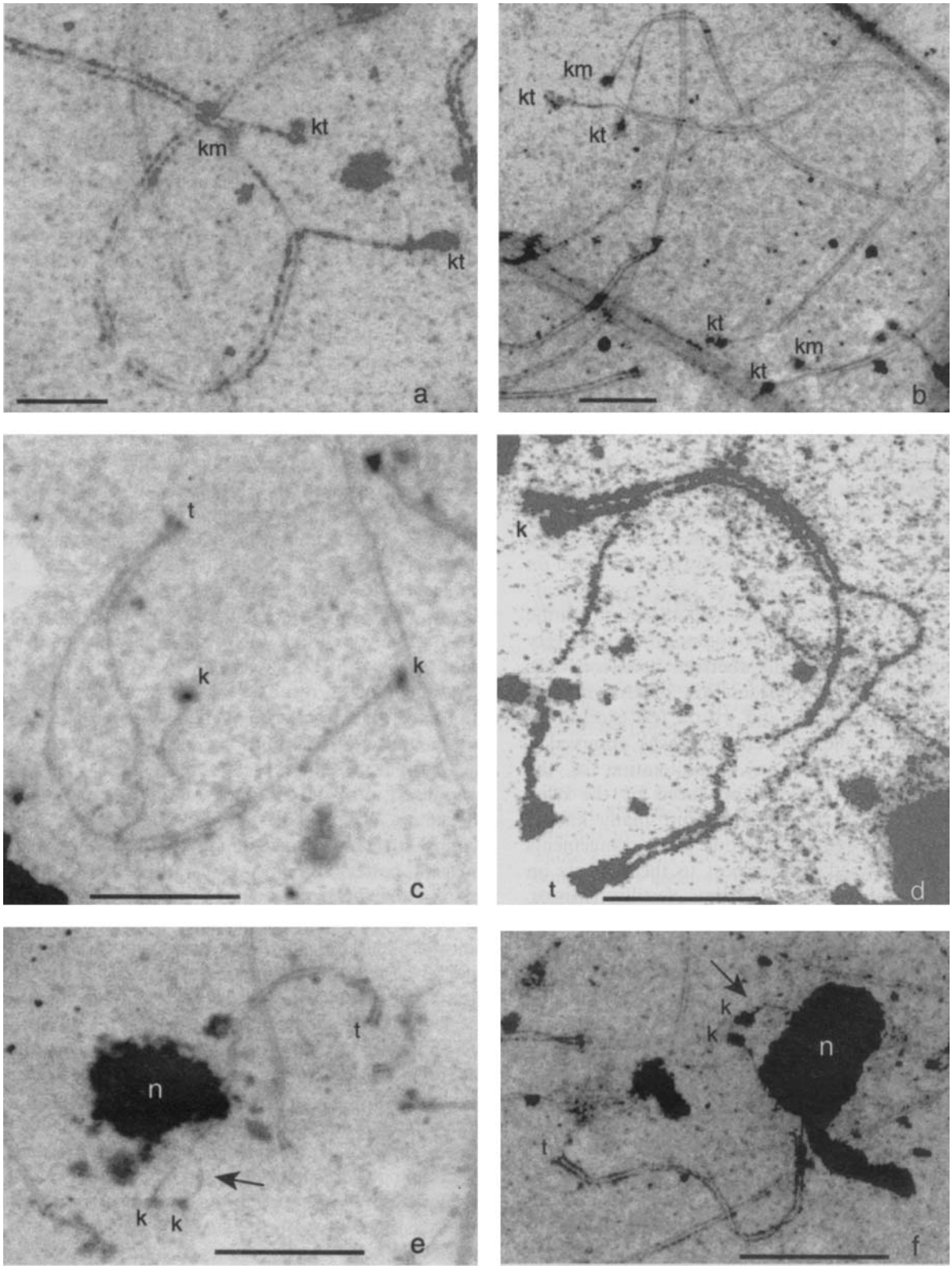


**Fig. 4a–f. a and b** Robertsonian trivalents of *D. pratensis* showing asynapsis in the centromeric region. **c and d** The megameric bivalent showing its typical precocious synaptic behaviour. **e and f** The S8 bivalent, carrier of the single NOR of the species. Note that the presence of the nucleolus impedes synapsis in the proximal region (arrows). k: kinetochore; t: distal telomere; km: kinetochore of the metacentric bivalent; kt: terminal kinetochores of telocentric bivalents. The bars indicate 2.5 μm.

(Fig. 4c). In the other case, only the interstitial region showed lack of synapsis (Fig. 4d). S8, which carries the single standard NOR of the species, showed variable degrees of proximal asynapsis in three nuclei (Table 2; Fig. 4e and f).

The X chromosome displayed a typical Acridid behaviour: it was always seen as a more or less folded single axis with a prominent terminal kinetochore and usually located at the periphery of the nucleus.

## DISCUSSION

It is well known that a frequent consequence of chromosomal rearrangement is the modification of cross-over patterns that are a basic component of the genetic system of a species. These effects have been extensively documented in a wide range of animals and plants and involve all known types of spontaneous and polymorphic chromosomal mutations (JOHN 1990; BIDAU and MARTÍ 1995). Chromosomal rearrangements have also been the subject of a very long debate related to their impact on speciation (KING 1993). The debate has mostly been centered on the negatively heterotic effects of heterozygous rearrangements, mainly based on the aberrant meiotic behaviour of heterozygous configurations. In a very large number of cases, this aberrant behaviour was inferred without any consideration of true meiotic behaviour. Furthermore, and with a few exceptions, when anomalous meiotic behaviour was observed it was evaluated without any consideration of the change in chiasma patterns produced by the rearrangements. The reverse is also true: many known cases of chiasma remodelling due to rearrangements were never analysed with respect to their effects on chromosomal segregation and thus, fertility (MIROL and BIDAU 1992).

Robertsonian variation is widespread in natural populations. Classical cases are those of *Mus musculus domesticus* (REDI and CAPANNA 1988) and *Sorex araneus* (SEARLE 1988) among mammals, several grasshopper species (including *D. pratensis*) among insects and the *Commelinaceae* (JONES 1990) in the case of plants. Quantitative studies on chiasma pattern variation related to Robertsonian change are however, very scarce.

In *D. pratensis*, homozygotes and heterozygotes for its eight fusions, have a significant modification of chiasma frequency and distribution in the chromosomes involved. Standard L telocentrics of both sexes have a proximal-distal (P/D) chiasma distribution with occasional formation of interstitial (I) chiasmata (although females have lower total chiasma frequencies than males). However, all fused chromosomes have significantly fewer total and P chiasmata than standards, showing a shift to distal positions; there are no significant differences between fusion bivalents and trivalents, nor between sexes. The effects of all fusions are intra-chromosomal but total reduction in chiasma frequency depends on the telocentrics involved and on sex; the effects of the fusions are more marked in longer than in shorter telocentrics and in males than in females. The fusions have an homogenising effect, producing the same chiasma frequency and distribution in all Rb chromosomes and combinations (about one D chiasma per arm) in both sexes thus, males and females with the same karyotype have indistinguishable chiasma patterns and frequencies except for the X bivalent of females which has a typical P/D pattern). Thus, several independent fusions show the same meiotic behaviour and the same set of properties that account for it and this probably permitted the establishment of such a complex and widespread Rb polymorphism (BIDAU and MARTÍ 1995). Chiasma repatterning seems to be the most important component of the *D. pratensis* system since it facilitates normal disjunction and produces pericentric recombination-free regions in all metacentrics, whether homozygous or heterozygous (BIDAU 1990; MIROL and BIDAU 1992).

A simple hypothesis has been put forward to explain these parallel behaviours (BIDAU 1993) based in part on previous results of MOENS et al. (1989) in another grasshopper species. If, in standard telocentrics homologous chromosome ends are attached to the nuclear envelope near one another at early prophase I, providing initiation point of synapsis and chiasmata occur more probably in regions that synapse first and remain synapsed longer, then a P/D chiasma pattern is expected. In the case of a Rb fusion either heterozygous or homozygous, the number of effective chromosome ends involved in synaptic initiation is halved. Thus P chiasmata will be rare and a large pericentromeric recombination-free region will be created instantaneously independently of the telocentrics involved.

The results presented in this paper give support to the previous hypothesis. It appears that telocentric bivalents have basically two points of pairing initiation corresponding to their distal and proximal ends which, as it is clear from the bouquet organisation at zygotene-pachytene, are attached to the inner nuclear envelope. Thus, synapsis progresses from both ends towards the center of the bivalent until it is completed. However, interstitial chiasmata are very rare thus, chiasma formation and pairing initiation must in some way be connected. The observations on Rb trivalents and bivalents also support this view. In both types of configuration, two points of pairing initiation seem to occur corresponding to the distal

ends of both arms; the centromeric region in these cases does not seem to play a role in initiating synapsis. Again, the distal ends are attached to the nuclear membrane and the patterns of chiasma distribution are those expected according to this pairing behaviour.

The relationship between synapsis and recombination is controversial and a number of recent papers have reviewed the subject (LOIDL 1990; KLECKNER 1996; MAREC 1996; SCHWARZACHER 1997, 1999; ZICKLER and KLECKNER 1998; SANTOS 1999; SYBENGA 1999). Two opposite views exist: the traditional one, that considers SC formation as a prerequisite for crossing-over initiation (SANTOS 1999), and the view from yeast, that states that the stage of commitment to crossing-over might precede or accompany the formation of the SC (ZICKLER and KLECKNER 1998). For the first view, there is abundant albeit indirect evidence (see SANTOS 1999 for a review): many cases of chiasma localisation in several species of animals and plants, are associated with localised synapsis that is, if no SC is formed no chiasmata are produced. These examples include Orthopteran species such as *Chloealtis conspersa* (MOENS et al. 1989; MOENS 1994), *Neocurtilla hexadactyla* (SPYROPOULOS et al. 1989), *Stetophyma grossum*, and several Tetrigidae, other invertebrates (i.e. *Mesostoma ehrenbergi*) and plants (i.e. *Rhoeo spathacea*) (DEL CERRO and SANTOS 1997). In the case of *D. pratensis*, although synapsis is eventually complete, there is a close correlation between SC formation and chiasma localisation in the different Rb configurations analysed. This is relevant since it supports our hypothesis about the establishment of polymorphic Rb rearrangements in *D. pratensis*: changes in the initiation sites of synapsis produced by the fusions may produce an instantaneous rearrangement of the chiasma pattern in the involved chromosomes thus increasing the probabilities of disjunctional trivalent segregation by the elimination of proximal chiasmata (BIDAU 1993). This simple model could explain the independent establishment of very different polymorphic fusions within the range of the same species, without recurring to orthoselective mechanisms that may progressively shift chiasmata to distal ends of chromosome arms or increase interference across the centromere.

In our material, other conditions than Rb rearrangements were seen to affect synapsis of homologous chromosomes in the cases of the S7 and S8 bivalents. In the case of the megameric pair, it is probable that the effect is due to the large heterochromatic interstitial block present in this chromosome; this is also probably the cause of the location of the single chiasma which is almost always proximal, less frequently distal but never interstitial. In the case of the NOR carrier, asynapsis was observed associated with the nucleolar mass which suggests that the organisation of the nucleolus probably can impair synapsis in this region.

A further point deserves mention: the unsynapsed centromeric ends of telocentrics belonging to trivalents sometimes were seen to associate in a non-homologous fashion (Fig. 2 and 3). This situation can be tentatively correlated to previous results obtained by MIROL and BIDAU (1994) in the same species where, in multiple Rb heterozygotes, the frequencies of non-disjunctional orientation of trivalents were higher than expected. It is at least possible that non-homologous centromeric associations could impede stable disjunctional orientation when several trivalents are present in the same cell; thus, if one trivalent tends to orientate linearly, it could drive others to which it is associated, to the same kind of orientation. This behaviour however, would not significantly affect the fertility of the heterozygous carrier.

## ACKNOWLEDGEMENTS

We wish to thank very especially Dr. Juan Luis Santos (Universidad Complutense de Madrid, Spain) in whose laboratory and through his generosity, the main part of this work was done. We are also very grateful to Ms. Carmen Hernández López for expert technical assistance. Our dear friend and collaborator Lic. Cecilia Lanzone provided useful and critical comments on the manuscript. DAM is indebted to Liliana, Emiliano and Franco for unlimited support. CJB dedicates this paper to Mabel. Thanks are also due to Dr Anssi Saura and an anonymous reviewer whose comments substantially improved the manuscript. Both authors acknowledge the constant support of CONICET. The work included in this paper was partially financed through Grant 0022 (Res. 2851/98; CONICET) to CJB.

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