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C-Heterochromatin and chiasma terminalization in the jerboas *Allactaga* and *Jaculus* (Rodentia : Dipodidae)

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ABSTRACT. C-heterochromatin and chiasma distribution patterns of meiotic chromosomes were studied in the dipodids *Allactaga tetradactyla*, *Jaculus jaculus jaculus* and *Jaculus orientalis* and chiasma terminalization was discussed. Darkly stained C-band located at the centromeric region of some bivalents was observed in all species at diakinesis and metaphase I. Of the occurrence of C-heterochromatin in the 24 bivalents, *J. orientalis* exhibited the highest percentage of absence of the C-blocks, where it was 68.8%, compared to 18.8% in *A. tetradactyla* and 14.6% in *J. j. jaculus*. Analysis of variance of the means of relative distances of interstitial and terminal chiasmata from the centromere in the larger bivalents no. 1 and 2 of each species at diakinesis and metaphase I showed that the interstitial chiasmata are stable in their positions at the two stages and do not move to the chromosome termini, while the terminal chiasmata scored at diakinesis are in fact achiasmatic terminal associations and some of them gradually terminalize at metaphase I. Therefore, it is concluded that C-heterochromatin pattern of meiotic chromosomes is quite similar to that of mitotic chromosomes except the pair no. 1 in *A. tetradactyla*, stability of interstitial chiasmata at the two stages might negate the idea of chiasma terminalization and C-heterochromatin has not any role in the distribution of chiasmata.

KEY WORDS : C-heterochromatin, chiasma terminalization, Jerboas, Dipodidae, *Allactaga tetradactyla, Jaculus* spec.

INTRODUCTION

At the cytological level, heterochromatin is far known to vary in its amount, position, and type (for recent reviews, see CRAIG & BICKMORE, 1993; CARVALHO et al., 2001; EISSENBERG & ELGIN, 2000; PARK & KURODA, 2001). Closely related species may differ not only in the amount of heterochromatin in their genomes, but also in the number of heterochromatic bands, their location and their staining properties (SUMNER, 1990; ARTONI & BERTOLLO, 2001; KAVALCO et al., 2004). This variation has been attributed either to transformation of euchromatin into heterochromatin or *vice versa* (KING, 1980, 1991; CUEVAS & FORMAS, 2003; SHAHIN & ATA, 2004), duplication or deletion of heterochromatic segments (WHITE, 1973; SHAHIN & ATA, 2004), variation of euchromatin content and its correlation with the chromosome size and rearrangement of heterochromatin (SHAHIN & ATA, 2004); euchromatic translocation (WARCHAŁOWSKA-ŚLIWA et al., 1994) or to tandem translocation (HSU et al., 1975).

Since the first finding of chiasma by JANSSENS (1909, 1924), the chiasma frequency per cell and its position on bivalents have been considered two useful cytological parameters for the analysis of crossing-over and ultimately of genetic recombination in a population. Chiasma frequency per cell reveals the frequency of gene shuffling, while its distribution on bivalents provides information on the location of crossing-over points on chromosomes (for review, see JOHN, 1990; WADA & IMAI, 1995; IMAI et al., 1999). IMAI et al. (1999) assumed that interstitial chiasmata at diakinesis are distributed randomly and almost uniformly along bivalents except for the centromere and telomer regions and the size of these chiasma blank regions is consistently 0.8% of the total length of the haploid autosomes in all chromosomes, while terminal chiasmata are mostly telomere-telomere associations. Moreover, they added that variation of chiasma frequency among species is linearly proportional to the haploid chromosome number and would be evolution-adaptive because gene shuffling is dependent upon chromosome numbers.

Centromeric heterochromatin, the common pattern of heterochromatin in many organisms, is suggested to play a role in sister chromatid cohesion and proper segregation of chromosomes during cell division (for more details, see BERNARD et al., 2001). However, its role as a triggering factor of chiasma formation and terminalization remains doubtful and needs further investigations. JOHN & MIKLOS (1979) found that chiasma formation is inhibited in centromeric heterochromatin. NAVAS-CASTILLO et al. (1985) pointed out that heterochromatin variation among homologue chromosomes, which an effect of loss or addition of heterochromatin, leads to chiasma redistribution within the affected bivalents, independently of its position. However, SUJA et al. (1994) reported that chiasma redistribution within the bivalents is independent on the nature of the segment (heterochromatic/euchromatic ones). Moreover, BIDAU (1993) and TORREZAN & POGLIARINI (1995) demonstrated that chiasma frequency and terminalization might be affected by many factors, such as the heterochromatin regions, structural rearrangement, mutagens, etc. TORREZAN & POGLIARINI (1995) mentioned that there is an increase in chiasma frequency,

with a predominance of interstitial chiasmata, in euchromatin during diplotene stage, while there is a reduction in chiasma frequency in euchromatin during diakinesis as a result of consequent increase in the amount of heterochromatin. Further, they suggested that the chiasmata localized in euchromatin appear to move to the region of heterochromatin. The heterochromatin, however, seems to serve as a barrier against terminalization since terminalization is not observed beyond the heterochromatin bands in any heteromorphic bivalent.

On the other hand, it has been established on the basis of karyotypic analysis (SHAHIN & ATA, 2001) that all the dipodid species occurring in Egypt have a diploid number of 2n=48 chromosomes and a fundamental number (FN) of 95 in males and 96 in females. Of the 48 chromosomes, the X chromosome is submetacentric, while the Y is telocentric (acrocentric) in all species. In addition, *A. tetradactyla* has six subtelocentrics (pairs no. 2, 4, 5, 6, 7, and 9), while the remainders are submetacentrics, except the pairs no. 10, 11, 18, and 19, which are metacentrics. Nevertheless, *J. orientalis*, and *J. j. jaculus* have only three subtelocentrics (pairs no. 2, 21, and 22) and the others are submetacentrics, except the pair no. 18 in *J. orientalis* and 20 in *J. j. jaculus*, which are metacentrics. These morphological variations amongst karyotypes of the three species have been interpreted by ATA & SHAHIN (1999) on the basis of G-banding analysis as pericentric inversions occurred during karyotype evolution. However, they attributed the G-banding heterogeneity in the similar chromosomes to variations in the heterochromatin content and its correlation with the chromosome size.

Following this approach, the present study was basically undertaken after the findings of ATA (2000) and ATA et al. (2001) and the postulation of chiasma graph analysis by WADA & IMAI (1995) and the assumption that the so-called terminal chiasmata should be excluded when chiasma frequency is estimated. This assumption is basically assumed because terminal chiasmata are in fact mostly achiasmatic terminal associations (telomere-telomere associations) and are cytologically functional for ensuring the normal disjunction of bivalents at anaphase, but genetically non-functional for gene shuffling that is primarily the main function of interstitial chiasmata in addition to binding of bivalents (ATA, 2000; ATA et al., 2001; WADA & IMAI, 1995; IMAI et al., 1999).

The main aims of this study were 1) to describe and compare the distribution of heterochromatin in meiotic chromosomes with that of the somatic metaphase chromosomes (SHAHIN & ATA, 2004), 2) to analyze the chiasmata distribution and terminalization in the light of principles of the chiasma graph method, and 3) to examine the effect of C-heterochromatin distribution on chiasma frequency and terminalization.

MATERIAL AND METHODS

Three males of each of the dipodids *Allactaga tetradactyla* Lichtenstein, 1823, *Jaculus jaculus jaculus* Linnaeus, 1758, and *Jaculus orientalis* Erxleben, 1777 were captured in Egypt from Al Salum, Abu Rawash, and Mersa Matruh, respectively, either with the use of butterfly nets or with live traps placed in tracks made in sand. The animals were intraperitoneally injected with 0.05% colchicine solution (0.01 ml/g body weight) and one and half hour later killed with chloroform. The testes were excised and dissected gently into small pieces in 0.9% sodium chloride solution. The cell suspension was then centrifuged at 1000 r.p.m. for five min at room temperature. Subsequently, the cell pellet was treated with a hypotonic solution of 1% sodium citrate for 20 min at 37°C. Then, the suspension was recentrifuged as mentioned above and the cell pellet was fixed in 3 :1 ethanol :acetic acid at room temperature. Meiotic chromosome spreads were prepared by the flame drying technique using the method of EVANS et al. (1964), with a slight modification (unpublished data)[1]. C-bands were obtained according to the standard protocol of SUMNER (1972), with major modifications (SHAHIN & ATA, 2004). Chromosome spreads from each animal were examined and good spreads (about 10-15) from each species were scored and photographed using Olympus BX 51 microscope with a C-4040 zoom digital camera. Chromosomes were classified according to the method of LEVAN et al. (1964), with some modifications (SHAHIN & ATA, 2001).

Chiasmata were nomenclated following WHITE (1973) and as described by ATA et al. (2001), while the different bivalents were classified and identified at diakinesis and metaphase I according to the procedure of IMAI & MORIWAKI (1982) and as described by ATA (2000) and ATA et al. (2001). Chiasma distribution, both interstitial and terminal, of a total of 200 chromosome arms of the larger bivalents no. 1 and 2 obtained from 20-30 cells at both of diakinesis and metaphase I was scored in each species. Then, using C-heterochromatin as a marker, the distance of interstitial and of terminal chiasma from the centromere in both of the short and long arms of each bivalent pair in each cell was calculated at each stage using the Soft Imaging System (SIS) analysis program (version 3.0) edited in 1999 by Soft Imaging System GmbH, Germany. Afterwards, the mean value and relative distance of each chiasma from the centromere in relation to the arm length of each bivalent pair were calculated. Data were tested for normality using Anderson-Darling test prior to further statistical analysis. In case of normally distributed data, two-sample T-test was used to compare between the position of both the interstitial and distal chiasmata at diakinesis and metaphase I, while Mann-Whitney *U* test, as a non-parametric test, was used in case of not normally distributed data. All of these statistical analyses were carried out using the MINITAB software, version 13.13 (MINITAB, State College, Pennsylvania Area, USA, 2002).

Bivalents no. 1 and 2 were only chosen herein for accurate and perfect analysis of chiasmata distribution amongst the three species because of their relatively large size in comparison to other bivalents sizes and their large amount of centromeric heterochromatin. The remainder bivalents, however, were either relatively smaller that they cannot be accurately measured or some of them having no centromeric heterochromatin in one or more species.

[1] ATA, A.M., (1988). *Cytological studies on rodents*. M.Sc. Thesis, Minia Univ., Egypt.

RESULTS

C-heterochromatin variation : The karyotype of the dipodid species examined consists of a total of 24 normal bivalents, which are characterized by the presence of a relatively small amount of constitutive heterochromatin located at the centromeric region of some bivalents in all species at diakinesis and metaphase I (Figs 1-3). The bivalents are identified herein according to the karyotype previously cited by SHAHIN & ATA (2001). Of the 24 bivalents, only five pairs and the Y chromosome of the XY bivalent (22.9%) possess C-bands in all taxa, 18 (75%) pairs also have C-bands, but exhibit intertaxon variation, and only one chromosome (2.1%), the X of the XY bivalent, is entirely devoid of C-bands. *J. orientalis*, in this regard, has the highest percentage of absence of C-blocks, where it is 68.8%, compared to 18.8% in *A. tetradactyla* and 14.6% in *J. j. jaculus*. The following is a detailed description of the C-heterochromatin distribution among bivalents of each species at diakinesis and metaphase I.

Allactaga tetradactyla :. All bivalents at diakinesis and metaphase I have C-bands except the pairs no. 4, 5, 6, 8, and the X chromosome of the XY bivalent, which are nearly devoid of heterochromatin. Of these C-banding stained bivalents, a large centromeric C-band is observed only in the bivalent no. 1, while the remainder pairs and the Y chromosome of the XY bivalent possess a small centromeric C-band (Figs 1a, b).

***Jaculus jaculus jaculus* :** Three bivalents no. 9, 16, and 23 and the X chromosome of the XY bivalent have no C-bands at both diakinesis and metaphase I, while the other bivalents and the Y chromosome of the XY bivalent have a dark centromeric C-band (Figs 2a, b).

***Jaculus orientalis* :** The bivalents of this species exhibited a species-specific C-banding pattern at both diakinesis and metaphase I, which is quite different from the other two species. Sixteen bivalents and the X chromosome of the XY bivalent are completely devoid of C-bands; however, centromeric C-bands are found in the remainder seven pairs and in the Y chromosome of the XY bivalent (Figs 3a, b).

Chiasma distribution patterns : The data on the distribution of interstitial and terminal chiasmata in both of the short and long arms of each of the bivalents no. 1 and 2 in each species at both diakinesis and metaphase I are given in Tables 1 and 2. A summary of the results is as follows :

Interstitial chiasmata : In the three species, as a rule, the interstitial chiasmata distribute as a whole randomly and almost uniformly on the arms of each bivalent type at both diakinesis and metaphase I except at the centromere and telomere regions in which chiasma formation is suppressed. Generally in all species, the short arms of the bivalents no 1 and 2 exhibit a rather fewer number of interstitial chiasmata per cell than the long arms (Figs 1-3). Hence, the analysis employed herein includes only the chiasmata of the long arms (Table 1).

In *A. tetradactyla*, it is noteworthy to mention that no interstitial chiasmata are recorded at all in the short arms of the bivalents no. 1 and 2 neither at diakinesis nor at metaphase I (Figs 1a, b). In the long arms, however, the mean relative distances of interstitial chiasmata from the centromere at diakinesis and metaphase I are 1.65 ± 0.08 (range = 1.13-2.08) and 1.51 ± 0.10 (range from 1.08 to 2.36) in the bivalent no. 1, compared to means of 1.59 ± 0.22 (range = 0.85-2.36) and 1.86 ± 0.16 (range = 1.29-2.89) in the bivalent no. 2. Analysis of variance between the matrices of relative distance means of chiasmata in each bivalent at both stages using T-test showed no significant differences between their positions at diakinesis and metaphase I ($T = 1.01$, $P = 0.324$, $df = 20$, $P > 0.05$ for bivalent no. 1 and $T = -1.00$, $P = 0.331$, $df = 16$, $P > 0.05$ for bivalent no. 2; Table 1).

In *J. jaculus*, the mean relative distance of interstitial chiasmata from the centromere in the bivalent no. 1 is 1.71 ± 0.07 (range = 1.64-1.77) at diakinesis and 1.84 ± 0.09 (range = 1.75-1.92) at metaphase I, while it is 1.01 ± 0.47 (range = 1.53-1.84) and 1.69 ± 0.08 (range = 1.53-1.78) at the two stages in the bivalent no. 2. Likewise in *A. tetradactyla*, no significant differences are found between the chiasmata positions at the two stages ($T = -1.21$, $P = 0.438$, $df = 22$, $P > 0.05$ for bivalent no. 1 and $T = 1.11$, $P = 0.468$, $df = 20$, $P > 0.05$ for bivalent no. 2; Table 1).

In *J. orientalis*, the means are 1.47 ± 0.15 (range = 0.94-2.30) at diakinesis and 1.55 ± 0.10 (range = 1.02-2.14) at metaphase I in the bivalent no. 1, compared to mean values of 1.58 ± 0.08 (range = 1.24-2.02) and 1.40 ± 0.28 (range 1.18-2.57) at the two stages in the bivalent no. 2. Likewise in *A. tetradactyla* and *J. jaculus*, there are no significant differences between the localizations of chiasmata at the two stages ($T = -.0.43$, $P = 0.67$, $df = 15$, $P > 0.05$ for bivalent no. 1 and $T = 0.59$, $P = 0.567$, $df = 20$, $P > 0.05$ for bivalent no. 2; Table 1).

Terminal chiasmata : Terminal chiasmata also distribute randomly on the arms of each bivalent, but they richly distribute on the long arms than on the short arms and their number is higher in *J. orientalis* than in the other two species (Figs 1-3). Terminal chiasmata exhibit significant differences in their distribution on the short arms of the bivalents no. 1 in both of *J. jaculus* and *J. orientalis* and no. 2 in *A. tetradactyla* and on the long arms of the bivalents no. 1 in both of *A. tetradactyla* and *J. orientalis*. Nevertheless, non-significant differences in the distribution of terminal chiasmata are observed at diakinesis and metaphase I in the short arms of the bivalent no. 1 in *A. tetradactyla* and no. 2 in *J. orientalis* and on the long arms of the bivalents no. 1 and 2 in *J. jaculus* and the bivalent no. 2 in both of *A. tetradactyla* and *J. orientalis* (for more details, see Table 1).

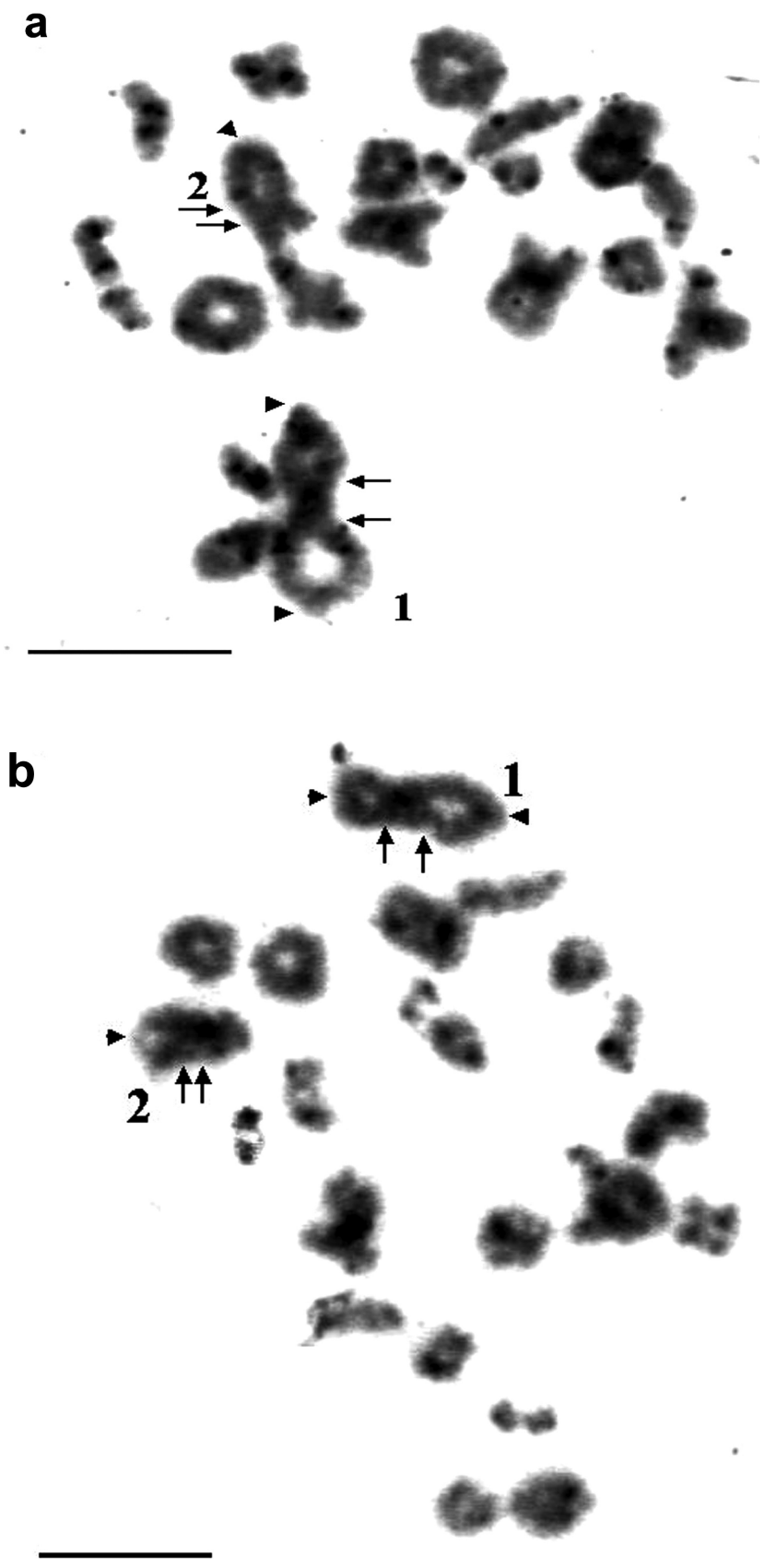

Fig. 1. – C-heterochromatin and chiasma distribution pattern of *Allactaga tetradactyla*. a. Diakinesis stage. b. Metaphase I stage. Scale bar = 10 μm. Arrows and arrowheads in this and the following figures refer to the interstitial chiasmata and terminal chiasmata, while the numbers refer to the bivalents no. 1 and 2.

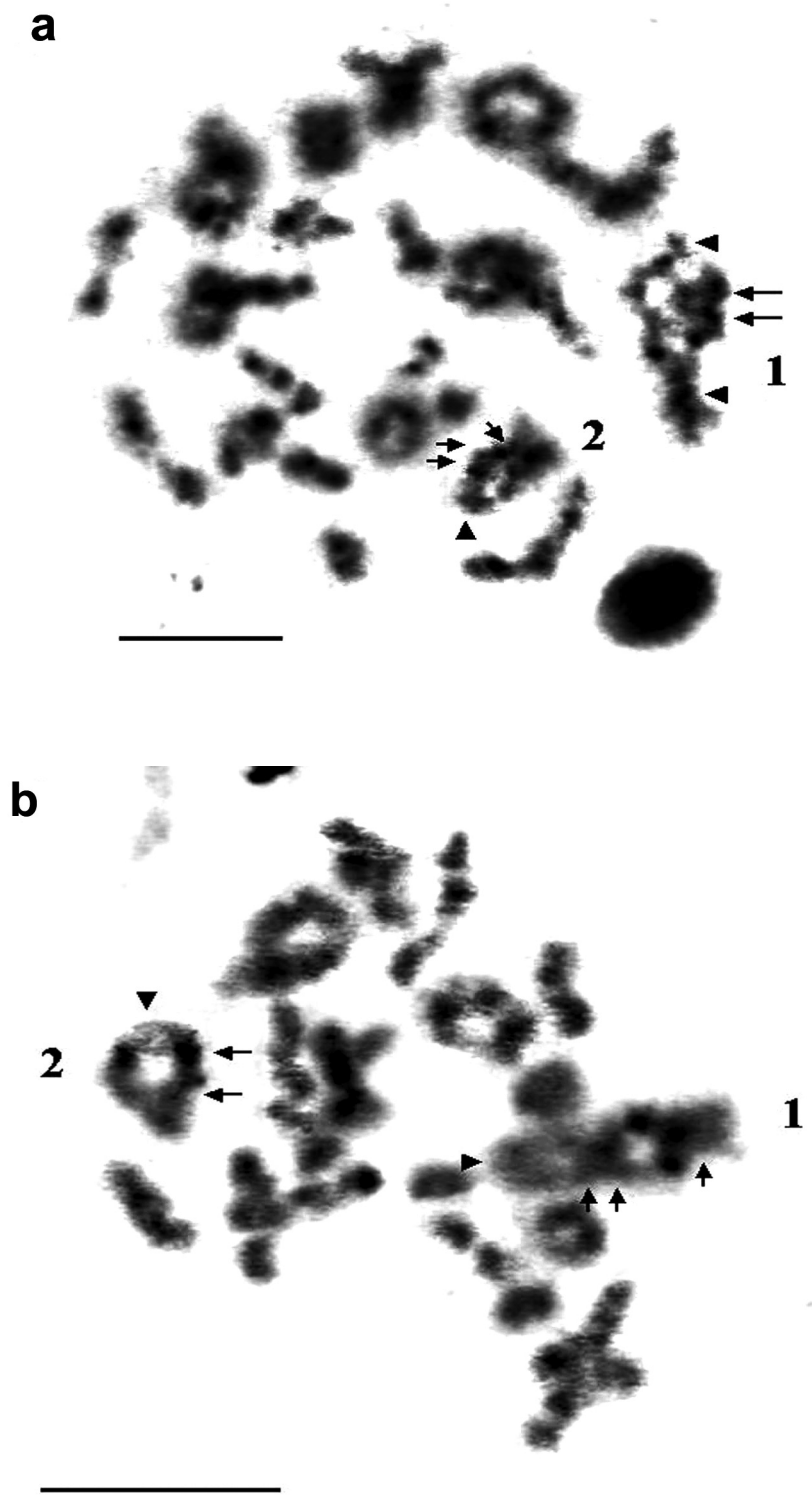

Fig. 2. – C-heterochromatin and chiasma distribution pattern of *Jaculus jaculus jaculus*. a. Diakinesis stage. b. Metaphase I stage. Scale bar = 10 μm.

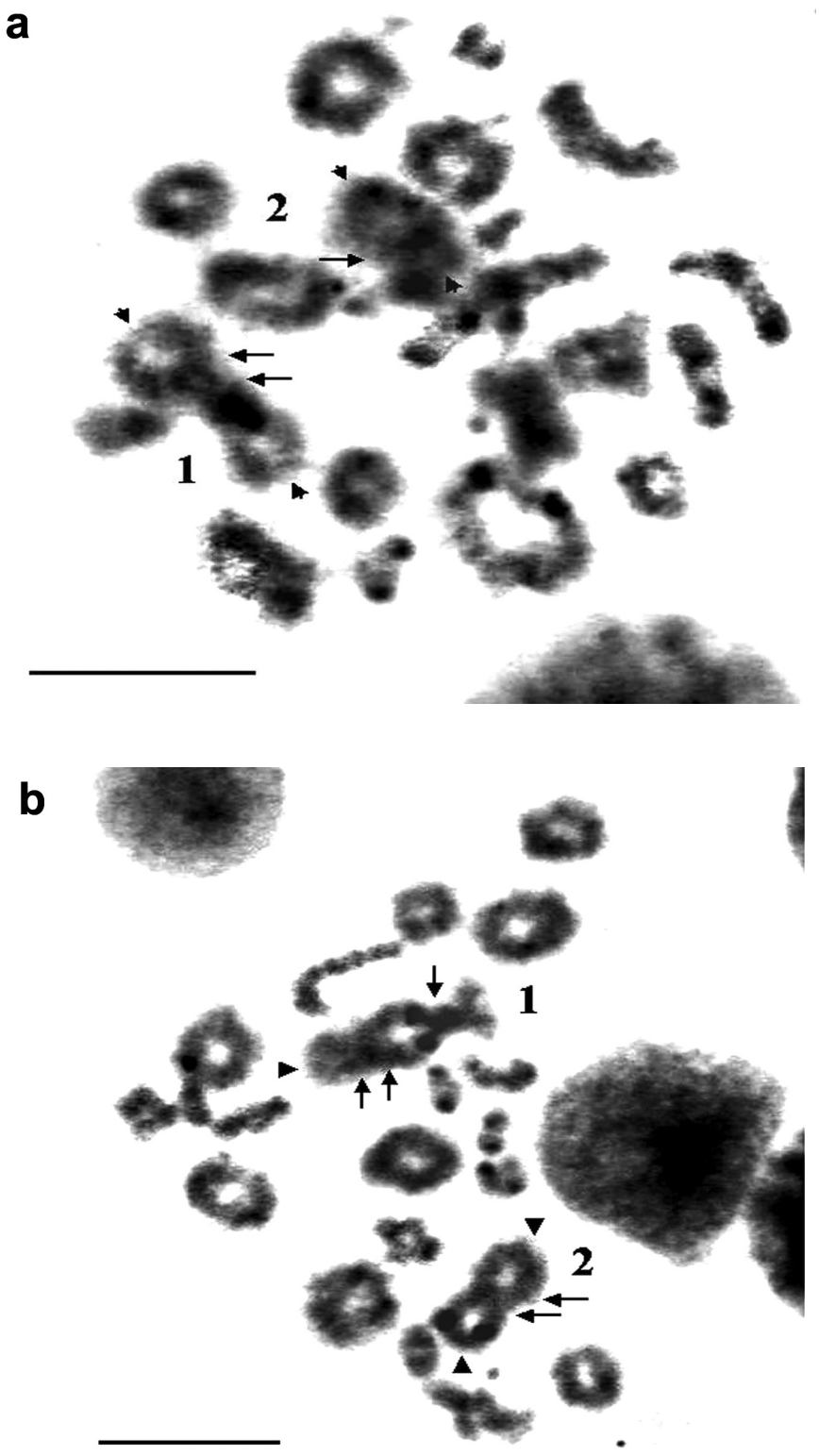

Fig. 3. – C-heterochromatin and chiasma distribution pattern of *Jaculus orientalis*. a. Diakinesis stage. b. Metaphase I stage. Scale bar = 10 μm.

TABLE 1

Mean relative distance values of the distribution of interstitial chiasmata on the long arms of the bivalents no. 1 and 2 in the three dipodid species examined. Values are in micrometers (μm)

Species			***A. tetradactyla***		***J. jaculus***		***J. orientalis***	
Stages			*Diakinesis*	*Metaphase I*	*Diakinesis*	*Metaphase I*	*Diakinesis*	*Metaphase I*
Mean relative distance of interstitial chiasmata ± SE of mean (range)	Bivalent no. 1		1.65 ± 0.08 (1.13-2.08)	1.51 ± 0.10 (1.08-2.36)	1.71 ± 0.07 (1.64-1.77)	1.84 ± 0.09 (1.75-1.92)	1.47 ± 0.15 (0.94-2.30)	1.55 ± 0.10 (1.02-2.14)
		T and (P)* values	1.01 (0.324)*		1.21 (0.438)*		-0.43 (0.670)*	
	Bivalent no. 2		1.59 ± 0.22 (0.85-2.36)	1.86 ± 0.16 (1.29-2.89)	1.01 ± 0.47 (1.53-1.84)	1.69 ± 0.08 (1.53-1.78)	1.58 ± 0.08 (1.24-2.02)	1.40 ± 0.28 (1.18-2.57)
		T and (P)* values	-1.00 (0.331)*		1.11 (0.468)*		0.59 (0.567)*	

* P values are non-significant (P>0.05).

TABLE 2

Mean relative distance values of the distribution of terminal chiasmata on the long and short arms of the bivalents no. 1 and 2 in the three dipodid species examined. Values are in micrometers (μm)

Species			***A. tetradactyla***		***J. jaculus***		***J. orientalis***	
Stages			*Diakinesis*	*Metaphase I*	*Diakinesis*	*Metaphase I*	*Diakinesis*	*Metaphase I*
Mean relative distance of terminal chiasmata ± SE of mean (range)	Bivalent no. 1	Short arm	0.06. ± 0.00 (0.05-0.06.)	0.05 ± 0.00 (0.04-0.06)	0.06 ± 0.00 (0.04-0.06)	–	0.06 ± 0.00 (0.05-0.06)	0.01 ± 0.01 (0.00-0.06)
		T and (P) values	0.36 (0.732)***		18.73 (0.000)**		6.00 (0.001)**	
		Long arm	2.13 ± 0.34 (0.06-3.18)	–	2.16 ± 0.08 (1.89-2.45)	2.31 ± 0.09 (1.98-2.64)	2.67 ± 0.15 (1.88-3.33)	0.70 ± 0.46 (0.00-3.00)
		T and (P) values	6.25 (0.000)**		-1.19 (0.278)***		(0.0204)*	
	Bivalent no. 2	Short arm	0.06 ± 0.00 (0.05-0.06)	–	–	–	–	0.02 ± 0.01 (0.05-0.06)
		T and (P) values	30.98 (0.000)**		–		1.58 (0.175)***	
		Long arm	0.94 ± 0.66 (0.06-3.97)	2.09 ± 0.77 (1.51-2.50)	2.29 ± 0.09 (1.89-2.48)	2.71 ± 0.15 (2.30-3.17)	2.55 ± 0.10 (2.17-2.91)	2.81 ± 0.19 (2.08-3.39)
		T and (P) values	1.49 (0.197)***		-2.24 (0.066)***		-1.07 (0.333)***	

No terminal chiasmata were found.

* Mann-Whitney test is significant at the values given in the Table.

** P values are significant (P≤ 0.05) and non-significant (***) at P>0.05.

DISCUSSION

As regards the occurrence of interstitial and distal chiasmata amongst karyotypes of the three species examined, ATA (2000) pointed out that the number of bivalent types in *A. tetradactyla* is ten, while it is only eight in both of *J. jaculus* and *J. orientalis* (ATA et al., 2001). Furthermore, it has been found that only the larger bivalent of these bivalent types has two patterns (2I.2D and 2I. 1D) at diakinesis and metaphase I in both of *J. jaculus* and *J. orientalis* (ATA et al., 2001), while in *A. tetradactyla* it has two patterns for each stage; 3I.2D and 2I.2D at diakinesis and 3I.1D and 2I.1D at metaphase I (ATA, 2000). The other bivalents, on the contrary, have only one pattern with different frequencies at diakinesis and metaphase I in all species (ATA, 2000; ATA et al., 2001). Therefore, the latter authors, following ZICKLER & KLECKNER (1999), attributed the differences in the number of bivalent types to the relative variation of the genome length, DNA quantity and the genetic background which may play an important role in pairing, synapsis and subsequently in chiasma formation and distribution between the two genera *Allactaga* and *Jaculus*. Nonetheless, they suggested that the variation in the number of bivalent forms of the pair no. 1 between the two genera is due to that one of the two distal chiasmata at diakinasis is more stable or not terminalized at metaphase I. Further, ATA et al. (2001) reported that there are significant differences in the mean frequency of interstitial chiasmata between the three dipodid species at both diakinesis and metaphase I, while no significant differences are found within each species. On the contrary, they added that the mean frequency of distal chiasmata is significantly different at the two stages not only among individuals of the same species, but also among the three species. The non-significant variations observed in the mean frequency of interstitial chiasmata from diakinesis to metaphase I in each of the three dipodid species has been attributed to the fact that all of the chiasmata recorded are interstitial and nothing is terminal (for review, see ATA et al., 2001).

In the present investigation, the non-significant differences observed in the distribution of interstitial chiasmata on the larger bivalents no. 1 and 2 of each species at both diakinesis and metaphase I means that these chiasmata

are fixed in their positions, *viz*. they do not move or change their positions at the two stages. If the interstitial chiasmata move or terminalize toward the ends of chromosomes, then all chiasmata should appear terminally in position, i.e. they form terminal (or distal) chiasmata, at metaphase I. Thus, the interstitial chiasmata could not terminalize to the ends of chromosomes during meiosis. These findings contradict the hypothesis of chiasma terminalization by DARLINGTON (1932) and strongly confirm the assumption of JONES (1978; 1987), KANDA & KATO (1980), IMAI & MORIWAKI (1982), JOHN (1990), WADA & IMAI (1995), IMAI et al. (1999), ZICKLER & KLECKNER (1999) and ATA et al. (2001).

On the other hand, the significant differences appeared in the distribution of terminal chiasmata on both of the short and long arms of the bivalents no. 1 and 2 at the two stages in one or more of the species examined suggest that these chiasmata scored at the diakinesis are achiasmatic terminal associations resulting from the telomere-nuclear membrane association (HRAI et al., 1996). These achiasmatic terminal associations serve for binding the bivalents during crossing-over, and then they gradually disappear or terminalize as crossing-over ceases at metaphase I.

Moreover, specific variations in the distribution of C-heterochromatin are observed among bivalents of the three species. These variations could be attributed, as described by SHAHIN & ATA (2004), either to transformation of heterochromatin into euchromatin or *vice versa*, deletion of heterochromatic segments resulting from pericentric inversions, or to variation of euchromatin content and its correlation with the chromosome size and arrangement of heterochromatin. A comparison of the occurrence of C-bands in both of the meiotic chromosomes surveyed in this study and mitotic chromosomes (SHAHIN & ATA, 2004) shows a close similarity of the amount and pattern of C-heterochromatin in the mitotic and meiotic chromosomes of the three species except the chromosome pair no. 1 in *A*. *tetradactyla*. This pair appears herein having a large dark block of C-heterochromatin, while it is completely devoid of heterochromatin in the mitotic metaphase chromosomes (SHAHIN & ATA, 2004). This heteromorphic feature could be due to the transformation of euchromatin into heterochromatin and subsequently duplication of the amount of heterochromatin needed for silencing nearby genes (for more details, see AVRAMOVA, 2002 and refs. therein).

As regards the distribution of both C-heterochromatin and interstitial chiasmata in the 24 bivalents and in particular the larger bivalents no. 1 and 2, no noteworthy relation could be found between C-heterochromatin and chiasma formation. This is firstly because C-heterochromatin in the species examined is located in the centromeric region and both kinds of chiasmata are basically distributed in the euchromatin regions. Secondly, as reported by ATA et al. (2001), the frequency of interstitial chiasmata is not significantly different in each species at diakinesis and metaphase I. This interpretation is inconsistent with the conclusions of BIDAU (1993) and TORREZAN & POGLIARINI (1995) who mentioned that there is an inverse relation between chiasma frequency and terminalization and the amount of heterochromatin and the latter seems to serve as a barrier against terminalization since terminalization beyond the C-bands is not observed in any bivalent.

A conclusion of this study is 1) the meiotic chromosomes of the three species examined have C-heterochromatin pattern and amount similar to the mitotic chromosomes (SHAHIN & ATA, 2004) except the pair no. 1 in *A*. *tetradactyla*, which has a large darkly stained C-band, 2) the interstitial chiasmata are stable in their positions in the euchromatin regions at diakinesis and metaphase I and they do not terminalize to the chromosomes termini, and 3) the centromeric C-heterochromatin in the chromosomes of the species examined does not affect the distribution and frequency of interstitial chiasmata during meiosis.

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