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Cytogenetic studies on Siberian spiders

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Karyotypes are reported for 24 spider species, of which 1 is represented by juveniles, from Western Siberia (environs of Novosibirsk). Chromosome counts (2n) are as follows: Lycosidae — *Pardosa agrestis*, *P. lugubris*, *P. palustris*, and *P. plumipes*, 28 (males); *Hygrolycosa rubrofasciata*, 20 (males) and 22 (females); *Xerolycosa miniata* and *X. nemoralis*, 22 (males). Thomisidae — *Misumenops tricuspidatum* and *Xysticus* sp., 23 (males). Linyphiidae — *Erigone atra*, *Bolyphantes alticeps*, *Helophora insignis*, and *Taranucnus setosus*, 24 (males); *Neriene clathrata*, 25 (males). Tetragnathidae — *Pachygnatha clercki*, 24 (males) and 26 (females); *P. listeri*, 24 (males). Clubionidae — *Clubiona stagnatilis*, 24 (males). Araneidae — *Singa hamata*, 24 (males). Theridiidae — *Steatoda grossa*, 22 (males) and 24 (females). Some uncommon peculiarities were observed: (1) one specimen of *P. lugubris* showed the region-specific chromatin decondensation visible at diakinesis only; (2) tetraploid pachytene and diakinetic cells were found in a male *Xysticus sp.*; (3) all nuclei of *P. listeri* contained two trivalents. An analysis of the synaptonemal complexes of three species (*Pardosa sp.*, *Tibellus sp.*, and *Steatoda grossa*) was also performed.

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Up to now, karyotypes of about 300–330 spider species, mainly from Europe, India, Japan and N-America, have been described (HACKMAN 1948; MADDISON 1982; DATTA and CHATTERJEE 1988; COKENDOLPHER 1989; TUGMON et al. 1990; TSURUSAKI et al. 1993; etc.). Karyotypes of species occurring in Russia are not known excluding SOKOLOV's data (1960, 1962) on 15 species. This study adds karyotypic data for 19 additional identified and 1 non-identified (juveniles) species collected from Siberia.

In some spider species polymorphism for chromosomal variants, e.g., Robertsonian fusions, have been reported (MADDISON 1982; ROWELL 1990, 1991). That is why we also attempted to search for the chromosomal polymorphism within species.

There are only a few papers devoted to surveying of the spider synaptonemal complexes (SC) (e.g., BENAVENTE and WETTSTEIN 1980; WISE 1983; ROWELL 1991). Obviously, such studies are very effective, not only for the karyotype description, but also for an examining of the chromosome rearrangements. So, in all species we tried to analyze both meiotic chromosomes and the SCs. The three successful cases are reported.

Materials and methods

A total of 80 males and 10 females were examined. Most specimens were adults. Twenty species of seven families have been studied (see Table 1). Spider specimens were collected during June–November 1994 in the neighborhood of Novosibirsk (W-Siberia). Numbers of species and specimens studied are given in Table 1.

Meiotic chromosome preparations have been made by use of the air-dry method proposed by COKENDOLPHER and BROWN (1985), with some modifications; no colchicine was used. For the SC preparations, the procedure was as follows:

(1) 3–5 drops of 0.1 M saccharose solution were placed on a slide and allowed to dry at room temperature; (2) Dissected in 0.75 % KCl solution, spider testis was transferred onto a dry saccharose layer and carefully distributed (using dissecting needle) along all the saccharose surface; (3) 2–5 min later, 200–300 μl of paraformaldehyde fixative (4 g per 100 ml of distilled water) were added onto a preparation; (4) Slides were allowed to dry at the room temperature; (5) SCs were stained

Table 1. Karyotypes of 19 spider species

Species	Diploid number		Sex determining mechanism		Peculiarities
	Male	Female	Male	Female	
LYCOSIDAE					
Pardosa agrestis	28 (2/21)	–	XXO		
P. plumipes	28 (1/15)	–	XXO		
P. lugubris	28 (10/96)	–	XXO		In one specimen stage- and chromosome-specific chromatin decondensation was observed
P. palustris	28 (7/10)	–	XXO		
Xerolycosa miniata	22 (2/7)	–	XXO		
X. nemoralis	22 (2/8)	–	XXO		
Hygrolycosa rubrofasciata	2/ (2/8)	22 (2/5)*	XXO	XXXX	
THOMISIDAE					
Misumenops tricuspidatum	23 (1/20)	–	XO		
Xysticus sp.	23 (1/10)		XO		50% of cells are tetraploid; satellites are seen near the ends of one bivalent
LINYPHIIDAE					
Erigone atra	24 (3/17)		XXO		
Bolyphantes alticeps	24 (2/14)		XXO		
Neriene clathrata	25 (20/100)		XXXO		
Helophora insignis	24 (2/6)		XXO		
Taranucnus setosus	24 (1/18)		XXO		
TETRAGNATHIDAE					
Pachygnatha clercki	24 (8/30)	26 (1/3)	XXO	XXXX	
Pachygnatha listeri	24 (6/27)		XXO		At diakinesis 9 bivalents and 2 trivalents are observed
CLUBIONIDAE					
Clubiona stagnatilis	24 (2/15)		XXO		
ARANEIDAE					
Singa hamata	24 (3/12)		XXO		
THERIDIIDAE					
Steatoda grossa	22 (5/70)	24 (7/21)	XXO	XXXX	

* The numbers of specimens/nuclei are given in parentheses

using 60% silver nitrate solution at 60°C and high humidity during 40 min.

After staining, SCs become visible and suitable for analysis through a light microscope.

To carry out the electron microscopic analysis, the preparations were covered with a plastic film (1 g of plastic petri dish per 100 ml of chloroform). Using a light microscope, cells with clearly visible SCs were selected and suitable sites of preparation were cut out. To remove a site from the glass, a drop of HF was placed around the edges of the site and then the slide was put into a vessel of water. The site cut emerged and was transferred onto the electron microscopic grid. The electron microscopic analysis was performed under 4000× magnifying.

Results and discussion

General remarks

Diploid chromosome counts in males range from 20 to 28 among these species. Only acrocentrics have been recognized in the species studied, with differences in the chromosome lengths, being rather significant (an average length of bivalents ranges from 14 μm in *Pardosa lugubris* to 3 μm in *Taranucnus setosus*). In all cases when karyotypes of both sexes have been studied, chromosome counts in females were equal to that of males plus the number of sex chromosomes. So, all the females presently studied showed two sex chromosomes more than the males. This kind of the sex determining mechanism has been reported to be

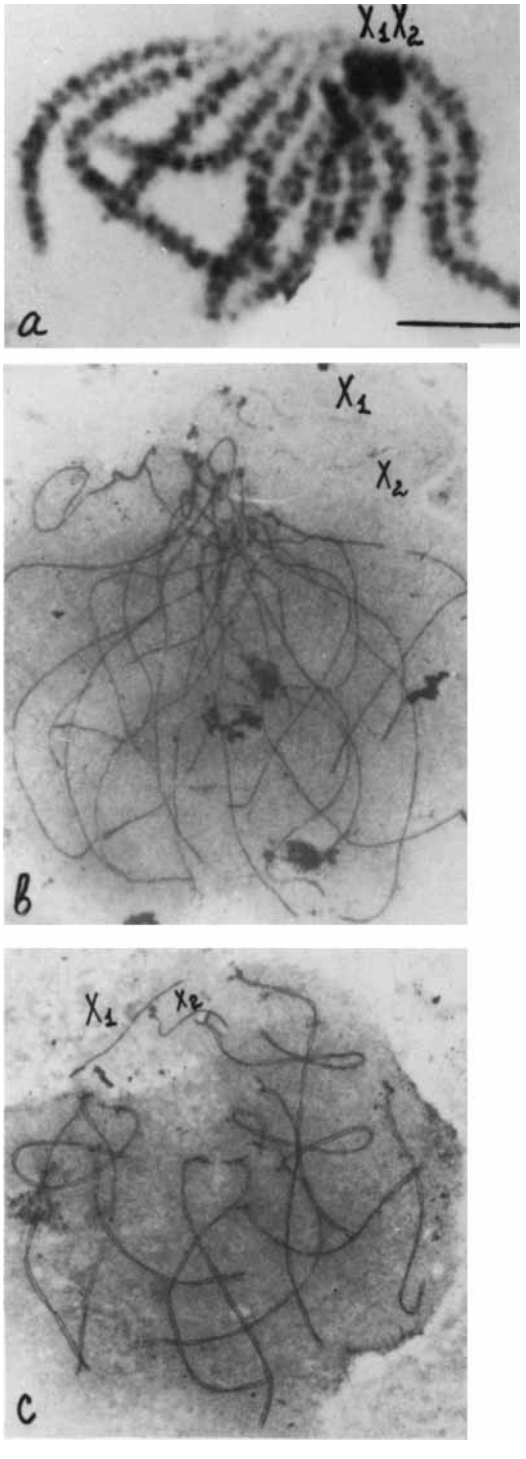

Fig. 1a–c. Bouquet-like structure in spiders' pachytene cells. **a** Pachytene cell of a male *Tibellus* sp. (Philodromidae). **b** Unpaired lateral elements of synaptonemal complexes at early pachytene in a male *Tibellus* sp. **c** Synaptonemal complexes of a male *Pardosa* sp.

common among spiders (HACKMAN 1948; SUZUKI 1950; SOKOLOV 1960, 1962; MITTAL 1966a,b; DATTA and CHATTERJEE 1988; COKENDOLPHER 1989; TUGMON et al. 1990; etc.), with all spiders appearing to be XO, XXO, XXXO and XXXXO, or even XXXY (see MADDISON 1982) in the males. Our results reported below showed the same consistency, except for the two latter cases, which have not been found among the examined Siberian species.

Analysis of SCs

We encountered a lot of difficulties when trying to perform an analysis of synaptonemal complexes in adult individuals. However, it turned out to be successful in subadult males. Unfortunately, to determine exactly to which species a subadult specimen belonged, was not possible in most cases. For this reason only one species of three in which SCs were studied (*Pardosa* sp., *Tibellus* sp. and *Steatoda grossa*) was identified faithfully.

The SCs in all the species showed the usual morphology. The sex chromosomes formed single lateral elements and never conjugate. In most cells sex chromosomes lay in the periphery of nuclei, with the autosomal SCs being usually directed by one of their ends to this region. This specific bouquet-like structure was observed in almost all cells examined (Fig. 1).

Description of karyotypes

Fam. Lycosidae

According to GOWAN (1985, cited by TUGMON et al. 1990), approximately 62 species of wolf spiders have been cytologically studied, with diploid counts usually ranging from 22 to 30 and the male XXO sex determining mechanism being the most common. Our findings agree with these data except for *Hygrolycosa rubrofasciata*, which showed $2n = 20$ in males, i.e., the lowest count for the Lycosidae.

Genus Pardosa. — Four species of *Pardosa* genus, namely *P. palustris* (Linnaeus 1758), *P. agrestis* (Westring 1861), *P. plumipes* (Thorell 1875), and *P. lugubris* (Walckenaer 1802) were studied. All of

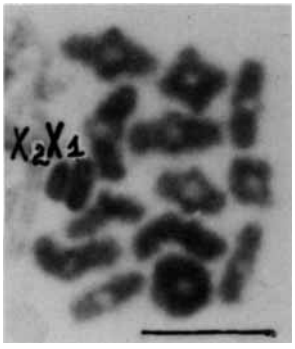

Fig. 2. Diakinetic chromosomes of a male *Pardosa palustris* (Lycosidae). Sex chromosomes are marked. Scale = 10 μm.

them possessed the same karyotype: at diakinesis 13 bivalents and two heteropycnotic sex chromosomes were observed. There was usually either a single chiasma on a bivalent, or two ones (more seldom) (Fig. 2).

A single specimen of *P. lugubris* out of 9 studied showed three uncommon peculiarities:

(1) At diakinesis in all cells, one of the Xs appeared as normal, but instead of the second X there was a pair of separated fragments being approximately of equal length and situated near the normal X (Fig. 3a,b,c). The gap between the fragments sometimes could be poorly visible, but it was always present.

(2) About a half of cells at diakinesis contained two small autosomal fragments lying near the ends of one of the longest bivalents. In other diakinetic cells there is no orientation of the fragments towards chromosomes (Fig. 3a,b,c).

(3) In addition, some 33 % of all the diakinetic cells were found to contain a small, probably subcentromeric, fragment of another bivalent. In some cells the fragment was situated near the centromere of one of the bivalents (Fig. 3c).

In the same specimen at pachytene only a few cells showed a small opening situated halfway along one of the Xs (Fig. 3d). There were two ordinary sex chromosomes in most pachytene cells. About 6 spermatogonial mitotic cells were analysed, with no cell containing fragments or other abnormalities (Fig. 3e). The M2 cells were also analyzed, 3 cells of them containing 15 bivalents, the other 2, 13 chromosomes. There were no fragments at this stage; all the chromosomes look normal (Fig. 3f).

How have the fragments in question arisen? If there were fragments indeed, then we should believe that they emerge at late pachytene — early diplotene (since the fragments are absent in spermatogonial mitosis and most pachytene cells) and turn into normal X again after the first meiotic division is completed (since there is no fragment at M2). We suppose that the fragments observed resulted from region-specific stage-specific chromatin decondensation, with DNA probably being intact so that connections between fragments in (1) and between fragments and autosomes in (2) and (3) were retained. This may account for the orientation of fragments towards autosomes. Chromatin in these regions has condensed before the second meiotic division began; thus chromosomes at M2 stage look normal. We do not know the mechanism of the decondensation. Nor is it clear why these particular regions underwent the decondensation. Since the decondensation was only observed at meiosis, but not at mitosis, one can suggest that the mechanisms of chromatin condensation at meiosis and mitosis should be quite different, at least in the regions discussed.

Genus Xerolycosa. — Karyotypes of two species studied, *Xerolycosa nemoralis* (Westring 1861) and *X. miniata* (C. L. Koch 1834), did not differ, as both showed 2n = 22 and two sex chromosomes in males.

In males of *Hygrolycosa rubrofasciata* (Ohlert 1865) at mitosis 20 chromosomes were seen, while there were 22 chromosomes at this stage in females. So, it is safe to conclude that there are two sex chromosomes in the species, with male XXO sex determining mechanism.

Fam. Thomisidae

Male XO sex determining mechanisms have been reported to be uncommon in spiders (10% of about 300 species studied) (see COKENDOLPHER 1989). However, this rare condition is apparently normal for the crab spiders, as all species examined here (see Table 1) and most of those reported in the relevant literature (about 13 species) (HACKMAN 1948; SOKOLOV 1960, 1962; MITTAL 1966a) showed a male XO sex determining system, with three exceptions where haploid numbers were either 11 + XX (two cases), or 11 + XXX (one case).

At diakinesis 11 autosomal bivalents and one X-chromosome were observed in the male *Misumenops tricuspidatum* (Fabricius 1775) (Fig. 4). Most of the bivalents formed a single chiasma, but some of them carried two chiasmata.

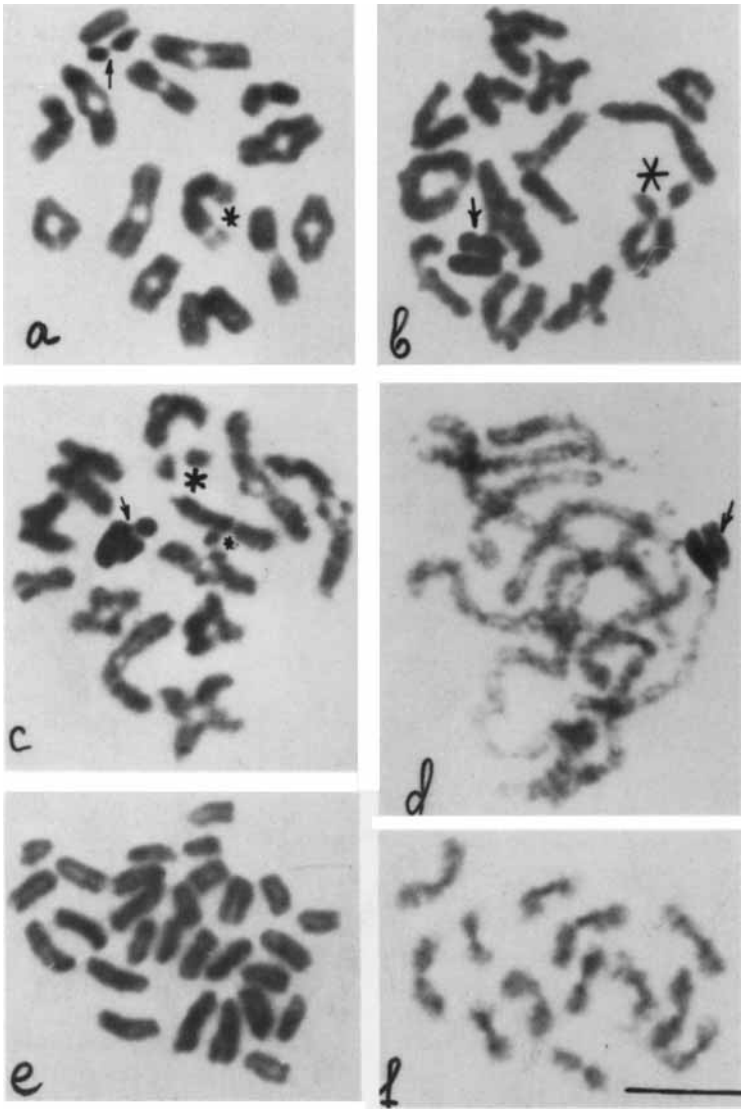

Fig. 3a–f. Unusual karyotype of a male *Pardosa lugubris*. **a** Diakinesis. Marked with an arrow is X, consisting of two fragments; with asterisk, subtelomeric fragments in one of the autosomes. **b** Diakinesis. Subtelomeric fragments are marked with large asterisk, fragmented X, with an arrow. **c** Diakinesis. Marked with large asterisk are subtelomeric fragments, with small asterisk, subcentromeric fragment; fragmented X is indicated by an arrow. **d** Pachytene cell. One of the Xs shows a poorly visible opening marked with an arrow. **e and f** Spermatogonial mitosis and M2 with no abnormality seen. Scale = 10 μm.

Xysticus sp. — A specimen studied showed two types of the pachytene and diakinetic cells. The first pachytene type is characterized by a single heteropycnotic sex chromosome as shown in Fig. 5a, while the pachytene cells of the second kind are approximately twice as large as the former ones and contain two heteropycnotic sex chromosomes closely spaced and identical in length (Fig. 5b). These two types of cells occurred in equal ratio. As for the diakinetic cells, the situation was similar to

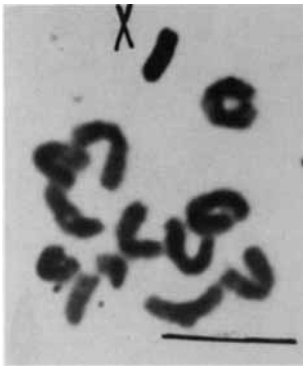

Fig. 4. Diakinesis of a male *Misumenops tricuspidatum* (Thomisidae). Marked is the single sex chromosome. Scale = 10 μm.

that for the pachytene cells. About half the diakinetic cells contained 11 autosomal bivalents and a single sex chromosome [one of the autosomal bivalents was heteromorphic, with one of the homologous chromosomes carrying a satellite (Fig. 5c)]. Another half of the diakinetic cells contained 22 autosomal bivalents and two adjacent sex chromosomes (Fig. 5d).

Most probably, these two types of cells differ in their ploidy, the first type being diploid and the second, tetraploid. A similar phenomenon has been found in some Salticidae species (SUZUKI 1954). It is of interest that neither Suzuki nor we observed tetravalents in these cells. For this reason, one can suppose spiders to develop a special genetic system which suppresses tetravalent formation. Such systems have been found in polyploid wheat (RILEY et al. 1966).

It is believed that these tetraploid cells seem to result in two kinds of gametes: haploid and diploid. Unfortunately, only a few cells at the M2 stage were observed, thus we could not ascertain if diploid gametes have indeed been formed. (In the M2 cells we have invariably found two acrocentric chromosomes, of which one chromatid carried a satellite (Fig. 5e). These chromosomes have obviously resulted from crossing over between centromeres and satellites.) We also failed to examine gametes, because there were no spermatozoa in the subadult male specimen we studied. However, if the diploid gametes actually arise in the species, triploid and tetraploid individuals probably should occur in the same population. It is a common knowledge that the tetraploid individuals are generally twice as large as diploid ones. In this respect, one can suggest that wild populations of *Xysticus* sp. should possess both the types of male individuals: (1) small, and (2) large (twice as large as 1).

The facts that quite large size variations among the spider individuals in a given population are the rule rather than the exception and that a size range from 1 to 2 is not exceptional, are widely recognized (e.g., JOCQUE 1981; VOLLRATH 1987; etc). This phenomenon is routinely explained as being due to ecological factors, like temperature, humidity, photoperiod, feeding rate, etc., with genetic variations being usually neglected. Our findings, as well as those made by SUZUKI (1954), enable us to assume that differences in ploidy could also be taken into consideration for the size variations in spiders.

Fam. Linyphiidae

Four out of five species examined, *Erigone atra* (Blackwall 1833), *Bolyphantes alticeps* (Sundevall 1832), *Helophora insignis* (Blackwall 1841), and *Taranucnus setosus* (O. P.-Cambridge, 1863) (Fig. 6a), possessed 11 bivalents and two sex chromosomes in males, while *Neriene clathrata* (Sundevall 1829) showed 11 bivalents and 3 sex chromosomes (Fig. 6b,c).

Fam. Tetragnathidae

All known cytologically investigated species of the Tetragnathidae, mainly from the genera *Tetragnatha* and *Meta* (HACKMAN 1948; SOKOLOV 1962; MITTAL 1966b; DATTA and CHATTERJEE 1988) showed 2n = 24, with the male XXO sex-determining mechanism, the only exception of *Meta segmentata* having an unique, XXXXO type. Our data for two species of *Pachygnatha* karyotyped here for the first time agree with those obtained previously for other genera.

Genus Pachygnatha. — We have karyotyped 6 males of the species *Pachygnatha listeri* (Sundevall 1829). At mitosis, 24 chromosomes can be seen (Fig. 7a). At diakinesis 9 normal bivalents and two trivalents were seen (Fig. 7b), all the specimens studied showing the same chromosome arrangement. One of the trivalents probably consisted of two sex chromosomes and a small univalent. Another trivalent included two chromosomes appearing as an ordinary bivalent, one of the homologues juxtapositioning with a univalent which is a little

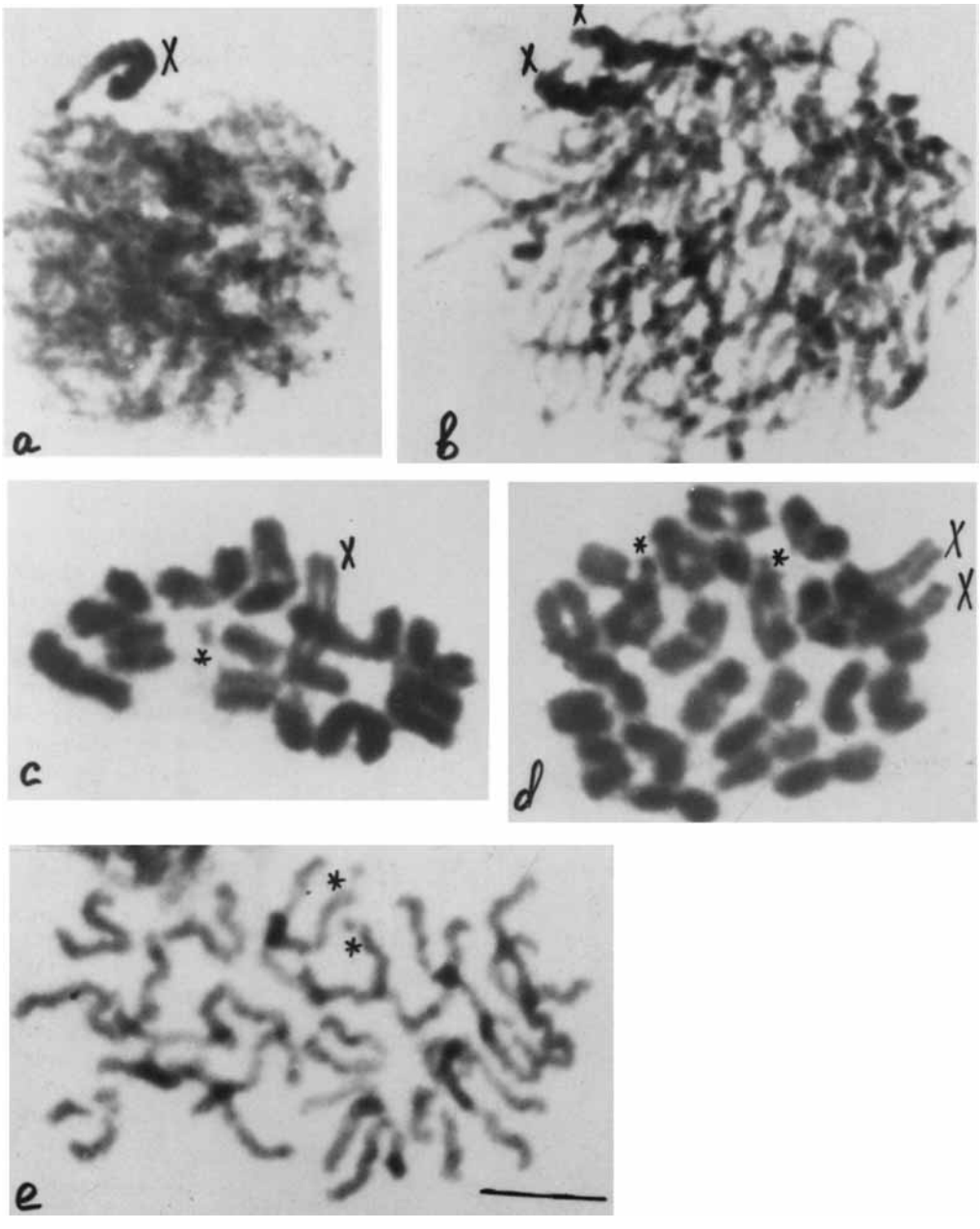

Fig. 5a–e. Meiotic chromosomes of a male *Xysticus* sp. (Thomisidae). **a–d** Two types of pachytene and diakinetic cells. **a and b** diploid and tetraploid pachytenes. **c and d** Diploid and tetraploid diakinetic cells. Heteromorphic bivalents, one homologue of which carries a satellite, are marked with asterisk. **e** M2 cell. Two recombinant chromosomes, one chromatid of which shows a satellite, are marked with asterisks. Marked are sex chromosomes. Scale = 10 μm.

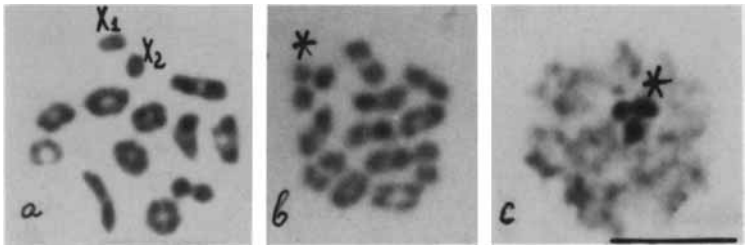

Fig. 6a–c. Chromosomes of species of the family Linyphiidae. **a** Diakinesis of a male *Taranucnus setosus*. Marked are sex chromosomes. **b and c** Diakinetic and pachytene cells of males *Nerine clathrata* (Linyphiidae). Three sex chromosomes are marked with asterisks. Scale = 10 μm.

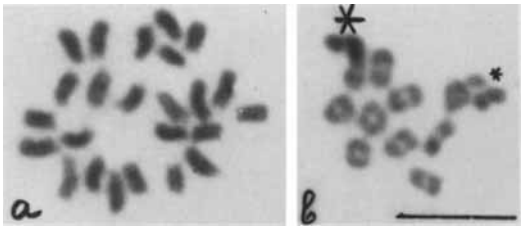

Fig. 7a and b. a Spermatogonial mitosis of a male *Pachygnatha listeri* (Tetragnathidae). **b** Diakinesis of a male *P. listeri*. Autosomal trivalent is marked with large asterisk, while one composed of sex chromosomes and autosomal univalent, with small asterisk. Scale = 10 μm.

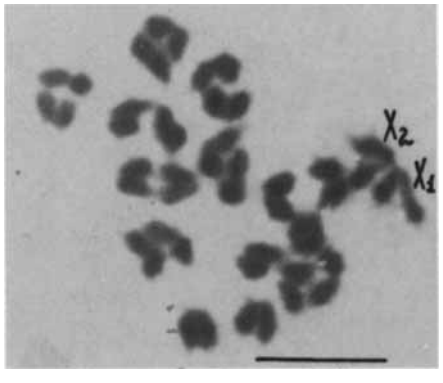

Fig. 8. Early anaphase of a male *Singa hamata* (Araneidae). All bivalents are separated into homologues, the majority of which lie close to each other. Sex chromosomes are marked. Scale = 10 μm.

larger than that lying near the sex chromosomes. A possible way by which these fragments could arise is here supported to be as follows. One of the autosomal bivalents appeared to break up into univalents, with one of them lying always near the sex chromosomes and the other near one of the autosomal bivalents. In this regard, an analysis of the SCs in this species should be of great importance to solve the problem and we are going to perform the analysis as soon as possible.

In females of *P. clercki* (Sundevall 1823), 26 chromosomes at mitosis have been found. At metaphase 1, males showed 11 autosomal bivalents and 2 sex chromosomes.

Fam. Clubionidae

At mitosis, 24 chromosomes were seen in males of *Clubiona stagnatilis* (Kulczyński 1897).

Fam. Araneidae

As counted by DATTA and CHATTERJEE (1988: tables 1 and 2), a total of 55 araneid species have been chromosomally studied to the moment, with the 2n number ranging from 14 to 46. The chromosome number of *Singa hamata* is reported here for the first time.

Studies of *Singa hamata* (Clerck 1758) male meiosis show 22 autosomal acrocentrics and two sex chromosomes at early anaphase 1 (Fig. 8). So, the species typified the family's modal number that was regarded to be 13 (11 + XX; 2n = 24) (DATTA and CHATTERJEE 1988).

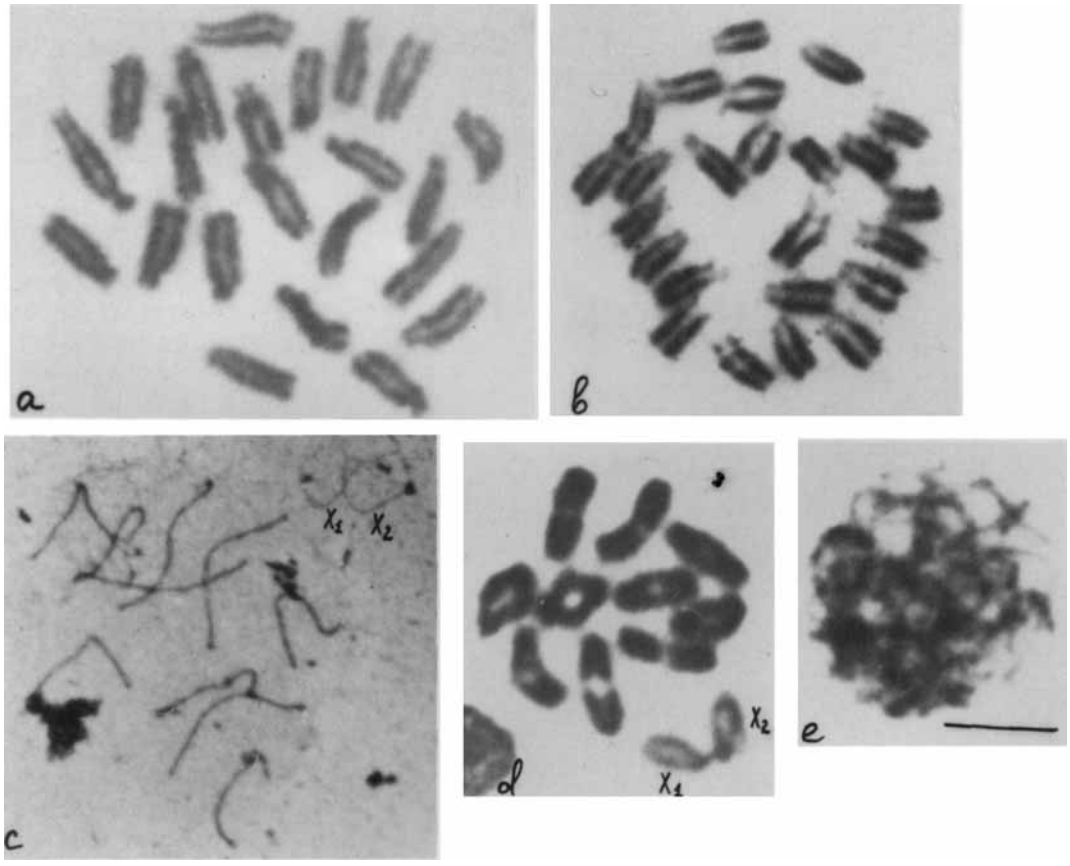

Fig. 9a–e. Chromosomes of *Steatoda grossa* (Theridiidae). Spermatogonial mitosis. **b** Oogonial mitosis. **c** SCs of a male. Lateral elements of sex chromosomes are marked. **d** Diakinesis. Sex chromosomes (marked) demonstrate negative heteropycnosis. **e** Pachytene cell. No heteropycnosis of sex chromosomes is present. Scale = 10 μm.

Fam. Theridiidae

To the moment, eight genera and 13 species of the Theridiidae have been karyotyped (TUGMON et al. 1990), all of them except *Chrysso venusta* having 10 autosomal pairs and an XXO-XXXX sex determining mechanism. *Steatoda grossa* karyotyped here for the first time typified this pattern as well (see Table 1).

At mitosis 22 chromosomes in males and 24 in females of *Steatoda grossa* (C. L. Koch, 1838) have been observed (Fig. 9a,b). The light microscopic analysis of the SCs showed that at the meiotic prophase there were 10 double SCs, probably corresponding to autosomes, and the sex chromosomes were seen here as a pair of single lateral elements located in the periphery of nuclei (Fig. 9c). At diakinesis we have also found 10 autosomal bivalents and two sex chromosomes lying close to each other in the periphery of nuclei and demonstrating negative heteropycnosis (Fig. 9d). In the pachytene nuclei we have never seen heteropycnotic chromosome elements that could be interpreted as the sex chromosomes (Fig. 9e).

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