

# Studies of Synaptonemal Complexes in Farm Mammals—A Review

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**For the last 10 years extensive studies of synaptonemal complexes in farm mammals were carried out. In this article a survey of the obtained results is presented. Studies on synaptic behavior of chromosomes at pachytene substage of meiotic prophase I in carriers of centric fusions (cattle, sheep, goat, pig, and blue fox) showed that the trivalent is rarely involved in an association with the sex bivalent. In carriers of reciprocal translocations (pig and cattle) a wide range of synaptic configurations were found. Besides the expected cross-shaped quadrivalent, the following configurations were observed: open quadrivalent, trivalent plus univalent, and two heteromorphic bivalents. The latter configurations were quite frequently involved in the association with XY bivalent. Studies of synaptonemal complexes in interspecies hybrids (cattle × zebu, river × swamp buffalo, blue fox × silver fox) revealed a wide range of synaptic disturbances. Cases of pericentric inversions, aneuploidy, and chromosomal polymorphisms are also reviewed. This survey shows that synaptonemal complex analysis is a very useful tool in studies on causes of altered fertility in carriers of abnormal chromosome complement.**

Synaptonemal complexes (SCs) are proteinaceous structures which appear along the homologous chromosomes in meiotic zygotene and last until the end of the pachytene substage of meiotic prophase I. This structure consists of two lateral elements, with so-called attachment plaques on both ends, and a central element, localized between the lateral ones. The central element is an overlapping part of transverse elements which are anchored in the lateral elements.

The main aim of SC studies in farm animals is the analysis of the regularity of the pairing process during pachytene substage of meiotic prophase I. Abnormal progress of this process may result in an arrest of gametogenesis or may lead to the production of unbalanced gametes, causing decreased fertility or sterility of an animal. Usually a so-called whole-mount surface spreading technique of meiocytes, followed by observations under transmission electron or light microscopy (Counce and Meyer 1973) or scanning electron microscopy (Barlow et al. 1993) is applied.

Synaptonemal complexes are most often studied in spermatocytes, which can be collected by biopsy, castration, or post-mortem from sexually matured males. Cryogenic preservation of testicular material can also be done (Sudman 1989). In

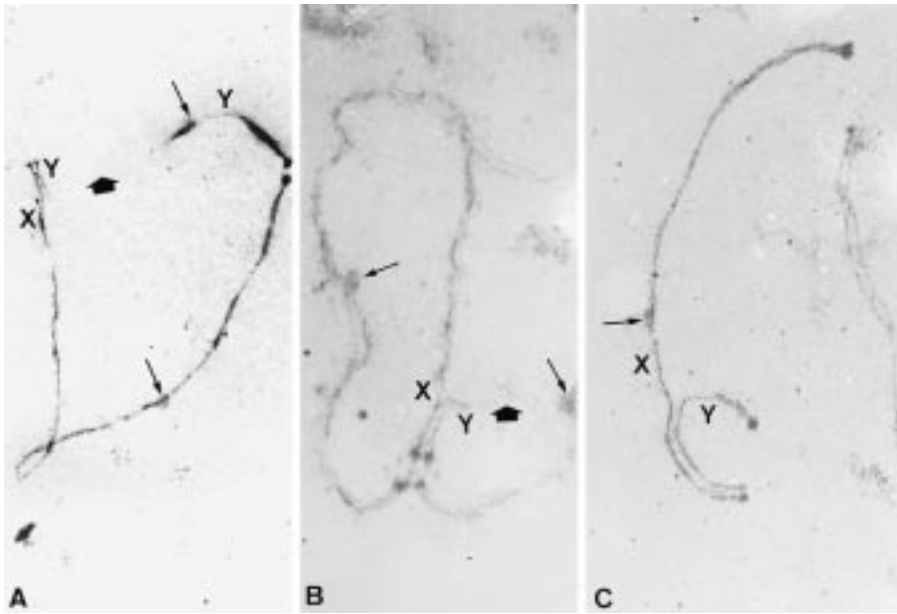
case of oocytes, observations of SCs can be made on material collected from fetal ovaries. Although there are species in which pachytene substage appears in ovaries shortly after birth, that is, the dog (Freixa et al. 1987; Lechniak et al. 1997) and some rodent species (Singh et al. 1993), investigations of chromosome pairing in breeding females are impossible. Only a few studies have been carried out on synaptic behavior in fetal bovine oocytes (Jung 1991; Koykul and Basrur 1994a; Świtoński and Basrur 1992). Oocytes at pachytene stage appeared in bovine fetal ovaries between days 80 and 160 of gestation. It was found that pairing irregularities (asynapsis, desynapsis, and mispairing) were more frequently noted in X chromosome bivalent, especially at the onset of meiosis. The same phenomenon was observed with relatively low frequency in autosome bivalents (Koykul et al. 1997).

## Sex Bivalent

Exceptional synaptic behavior is demonstrated by the sex bivalent (XY) in spermatocytes. Due to size differences between these chromosomes, the tripartite structure of the synaptonemal complex (two lateral elements and a central one in

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**Figure 1.** Synaptonemal complexes of XY bivalent in spermatocytes of (A) bull, early pachytene, (B) bull, mid-pachytene, and (C) boar, early pachytene. Kinetochores are indicated by small arrows and discontinuity of a bull's Y chromosome is indicated by solid arrows. XY bivalent of a bull demonstrates an additional association of free ends of sex chromosomes.

between) is present only along some parts of both chromosomes. The pairing starts from the pseudoautosomal region and may be extended to nonhomologous regions of both sex chromosomes. Un-

paired axes of the different sex chromosomes, which may be stranded or tangled, demonstrate specific behavior. It was shown that the appearance of XY bivalent is a useful tool for substaging of pachy-

tene in humans (Chandley et al. 1984; Solari 1980), cattle (Dollin et al. 1989), pigs (Villagomez 1993), sheep (Dai et al. 1994a), and mink (Koykul and Basrur 1995). At least three main substages of pachytene can be recognized: (1) early pachytene—axes of X and Y chromosomes are not stranded and the chromosomes are partly synapsed (Figure 1A,C), (2) mid-pachytene—axes of sex chromosomes become stranded and pairing can proceed beyond the pseudoautosomal region or additional pairing/associations of free ends can occur (Figure 1B), and (3) late pachytene—sex chromosomes become more stranded or tangled and excrescences appear along the axes.

It is worth mentioning that in some species XY bivalent demonstrates a unique appearance. In cattle for instance, a discontinuous Y chromosome axis is observed (Figure 1A,B) (Świtoński et al. 1987b, 1990).

Due to the unequal length of the chromosome axes of the X and Y chromosomes, the tendency is observed to form an association or synapsis between free fragments of XY bivalent and unpaired autosomal axes at the pachytene substage. This phenomenon is believed to be responsible for a spermatogenic breakdown due to interference with X chromosome inactivation in spermatocytes (Forejt 1996; Lifschytz and Lindsley 1972).

## Structural Chromosome Rearrangements

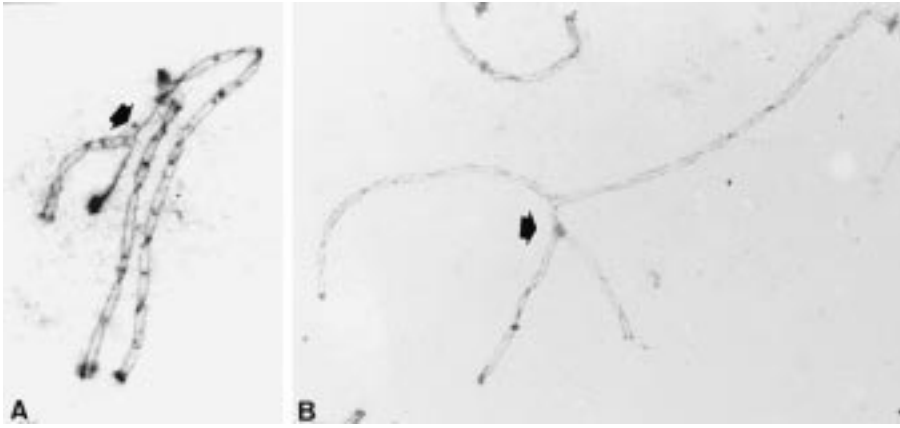
In farm animals, the majority of diagnosed chromosome mutations are balanced ones. Among them the most common are centric fusions (mainly in cattle and blue fox, but also in sheep and goat) and reciprocal translocations (mainly in pigs, but also in cattle and other species).

Synaptonemal complexes of bovine centric fusion carriers have been described in several reports (Table 1). Among them, synaptic behavior of the most common type of bovine Robertsonian translocation—rob(1;29)—was studied in details (Świtoński et al. 1987b). Three main morphological types of the trivalent configuration can be distinguished by the pachytene stage (Świtoński et al. 1988): (1) early pachytene—one or both pericentromeric regions of acrocentric chromosomes are unpaired (Figure 2A), (2) midpachytene—pericentromeric regions of both acrocentrics are nonhomologously synapsed to each other, and (3) mid-late pachytene—both acrocentrics are totally synapsed

**Table 1.** Synaptonemal complex studies of Robertsonian translocation carriers

Robertsonian translocation	Pairing configuration at pachytene	Reference
<b>Cattle</b>		
rob(1;29)	Typical trivalent configuration, XY trivalent association (7%)	Świtoński et al. (1987b)
rob(1;29) <sup>a</sup>	Fully paired bivalent, consisting of two 1;29 chromosomes	Bouvet and Cribru (1990)
rob(1;29) + rob(9;23)	Typical trivalent configurations	Bouvet et al. (1991)
rob(4;8)	Typical trivalent configurations	Bouvet et al. (1989)
rob(5;22)	Typical trivalent configurations, XY trivalent association (3%)	Stota and Świtoński (1992)
rob(8;23)	Typical trivalent configurations	Biluteva et al. (1994)
rob(1;25)	Typical trivalent configurations	Nett et al. (1996)
<b>Sheep</b>		
rob(5;26)	Typical trivalent configurations, XY trivalent association (11%)	Dai et al. (1994b)
rob(8;11)	Typical trivalent configurations, XY trivalent association (10%)	Dai et al. (1994b)
rob(5;26) + rob(8;11)	Typical trivalent configurations, XY trivalent association (7%)	Dai et al. (1994b)
rob(7;25)	Typical trivalent configurations, XY trivalent association (10%)	Dai et al. (1994c)
rob(7;25) + rob(5;26)	Typical trivalent configurations, XY trivalent association (16%)	Dai et al. (1994c)
<b>Goat</b>		
rob(3;7)	Typical trivalent configurations	Jung (1991)
rob(6;15)	Typical trivalent configurations	Jung (1991)
rob(5;15)	Typical trivalent configurations	Amaral and Jorge (1994)
<b>Pig</b>		
rob(13;17)	Typical trivalent configurations	Jidong et al. (1994)
<b>Blue fox</b>		
rob(23;24)	Typical trivalent configurations, XY trivalent associations (2%)	Świtoński and Gustavsson (1991)

<sup>a</sup> This study was performed on spermatocytes of a bull homozygous for centric fusion.



**Figure 2.** Synaptonemal complexes of (A) trivalent (solid arrow) in a spermatocyte of a bull carrier of 1;29 Robertsonian translocation and (B) quadrivalent (solid arrow) in a spermatocyte of a boar carrier of rcp(1;6).

with a translocation chromosome. An association between the sex bivalent and trivalent was found very rarely and thus spermatogenesis in the carriers was not affected. It can be seen that in a vast majority of such spermatocytes, the segregation of chromosomes involved in the trivalent configuration will be balanced. Similar synaptic behavior was found in male goat and blue fox spermatocytes. Surprisingly, in ram spermatocytes, association between the trivalent and the sex bivalent was observed quite frequently—up to 15.6% of spermatocytes in the case of a double carrier of the fusions 7;25 and 5;26 (Dai et al. 1994c). This finding is quite unexpected, as earlier studies reported that carriers of these centric fusions show normal fertility records [for a review see Long (1997)]. It should be mentioned, however, that chromosome 25 is NOR bearing in the terminal part of the q arm.

It can be concluded from the available reports that, in farm animals, centric fusions form typical trivalent configurations which rarely associate with the sex bivalent. So only missegregation of the trivalent at anaphase I can affect gametogenesis by producing chromosomally unbalanced gametes. Pairing behavior of Robertsonian trivalents and the impact on fertility, described in farm animals, is very different from a situation observed in humans. In man-carriers of a Robertsonian translocation, the XY bivalent is quite often associated with the trivalent. This interference is recognized as a main cause of spermatogenic arrest in a carrier (Gabriel-Robez and Rumpler 1996). It seems to be very important to emphasize that the main difference between Robertsonian translocations in humans and those discussed in this article is that the short arms of human acrocentrics bear NORs,

which is not the case in animal acrocentrics involved in centric fusion.

The pairing behavior of chromosomes involved in balanced reciprocal translocations is a more complex issue. First, two types of reciprocal translocations should be considered: autosome-autosome and X-autosome. It is known that the latter one causes male sterility. Second, the size of reciprocally exchanged chromosome fragments and/or the size of chromosomes arising due to the rearrangement seems to have a significant impact on pairing behavior. Also, the type of bands (G-dark or G-light) where the breaks occur was suggested as an important factor (Ashley 1988). Moreover, SC studies of the human reciprocal translocations revealed that involvement of acrocentric chromosomes, bearing nucleolar organizer regions (NORs), in the rearrangements is associated with a high frequency of XY quadrivalent association causing spermatogenic breakdown (Gabriel-Robez and Rumpler 1996).

Until now, numerous cases of autosome-autosome reciprocal translocations were studied in farm animals. In the majority of spermatocytes, a cross-shaped quadrivalent configuration was observed and three main types of it could be recognized (Gustavsson et al. 1988b): (1) lack of pairing around the breakage/rejoining point—early pachytene; (2) complete pairing, up to breakage/rejoining point, along all arms of the quadrivalent—early/mid pachytene; and (3) nonhomologous pairing around the breakage/rejoining point—mid/late pachytene (Figure 2B). Table 2 shows a survey of reciprocal translocations studied until now with the use of SC techniques. Moreover, the breaks described in Table 2 are shown on an ideogrammatic representation of G-banded swine (Figure 3) and bovine (Figure 4) chromosomes. If,

due to a rearrangement, small chromosome fragments arise or small fragments are reciprocally exchanged between chromosomes, unusual pairing configurations such as trivalent + univalent, two bivalents with unequal axes, or open quadrivalent are often observed. Then an unspecific association between XY bivalent and unpaired autosome axes can take place. This can result in the arrest of spermatogenesis due to XY-autosome association and/or increased frequency of unbalanced gametes due to missegregation of small chromosome fragments. There are several such cases described in the literature (Ansari et al. 1993; Villagomez et al. 1993a, 1995a).

A balanced reciprocal translocation—rcp(8q-,13q+)—in an azospermic bull resulted in the occurrence of a minute chromosome fragment, representing a pericentromeric region of chromosome 8 and a distal piece of chromosome 13. Studies of synaptonemal complexes showed that in the majority of spermatocytes an open quadrivalent occurred. Moreover, this configuration was very often (61% of spermatocytes) associated with the sex bivalent. Finally, no sperm was produced by this bull (Ansari et al. 1993).

Another case, rcp(7q+,17q-) in the pig, was reported by Villagomez et al. (1995a). This rearrangement also resulted in a very small chromosome 17-derived pericentromeric fragment, but the pairing behavior and impact on fertility was different. Analysis of synaptonemal complexes revealed that only 39% of spermatocytes demonstrated a typical cross-shaped quadrivalent configuration. In the remaining ones an open quadrivalent or trivalent plus univalent were found. Translocation products were not so often (18.7% of spermatocytes) associated or paired with the sex bivalent. These pairing disturbances resulted in decreased proliferacy and a production of piglets dying soon after birth due to an unbalanced karyotype. One of the offspring, a boar with tertiary trisomy—39,XY+der(17)—survived and the analysis of synaptonemal complexes revealed that in the majority of spermatocytes (75.4%) the marker chromosome, der(17), occurred as a univalent which was often associated or paired with the XY bivalent (Villagomez et al. 1995b).

An interesting rearrangement—rcp(20q-;24q+)—was diagnosed in a subfertile bull by Villagomez et al. (1993a). In this case, a very small distal fragment of chromosome 24 was transferred on chromosome 20 and reciprocally approximate-

**Table 2. Synaptonemal complex studies of reciprocal translocation carriers**

Translocation	Size of exchanged chromosome fragments	Size of the rearranged chromosomes	Type of G-band where breaks occurred <sup>a</sup>	Pairing behavior <sup>b</sup>	Proliferacy	Reference
<b>Pig</b>						
A. (1;7)(q213;q24)	Very small; small	Normal; normal	L/L	Cross q (82%), Open q or two bivalent (18%)	Decreased 50%	Gustavsson et al. (1988b)
B. (7;13)(p13;q21)	Very small; large	Large; small	L/L	Cross q (78%), Open q (22%)	Decreased 40%	Gustavsson et al. (1988b)
C. (15;16)(q26;q21)	Very small; medium	Normal; normal	L/L	Cross q (100%)	Decreased 50%	Gustavsson et al. (1988b)
D. (7;11)(q21;q11)	Large; large	Normal; normal	D/L	Cross q (100%)	Decreased 50%	Gustavsson et al. (1988b)
E. (3;7)(p13;q21)	Large; large	Normal; normal	L/D	Cross q (75%)	ND <sup>c</sup>	Gabriel-Robez et al. (1988)
F. (4;14)(p11;q11)	Large; large	Medium; large	L/D	Two bivalent (25%) Cross q (81%)	ND	Jaafar et al. (1989)
G. (1;18)	Very small; medium	Normal; normal	ND	Two bivalent (19%) Cross q (98%)	Decreased 45%	Villagomez et al. (1991a)
H. (1;6)(Centr;Centr.)	Large; large	Normal; normal	L/L	Two bivalent (2%) Cross q (100%)	Decreased 30%	Yang et al. (1992)
I. (5;14)(p11;p?) + J. (16;17)(q23;q14)	Large; very small	Medium; large	L/?; L/D	Cross q (100%)	ND	Jaafar et al. (1992)
K. (8;14)	Very small; small	Normal; normal	L/L	Cross q (82%) Open q (18%)	Decreased 50%	Ravaoarimanana et al. (1992)
L. (8;13)	Very small; medium	Normal; normal	L/L	Cross q (100%)	Decreased 50%	Ravaoarimanana et al. (1992)
M. (1;10)	Very small; very small	Normal; normal	L/D	Cross q (100%)	Decreased 50%	Ravaoarimanana et al. (1992)
N. (7;8)	Large; very small	Small; large	L/L	Cross q (77%) Open q (23%)	Decreased 50%	Ravaoarimanana et al. (1992)
O. (6;8)(q33;q26)	Medium; very small	Normal; normal	L/L	Cross q (100%)	ND	Ravaoarimanana et al. (1992)
P. (2;14)(p14;q23) <sup>d</sup>	Medium; medium	Normal; normal	D/L	Cross q (72%), Open q (28%)	Decreased 41%	Villagomez et al. (1993b)
R. (7;17)(q26;q11)	Very small; large	Large; very small	L/L	Cross q (39%), Open q (39%), Two bivalent (22%)	Decreased 41% Increased Mortality Of Piglets	Villagomez et al. (1995a)
S. (8;14)(p21;q25)	Medium; medium	Large; medium	L/L	Cross q (100%)	Decreased 25%	Danielak-Czech et al. (1997)
T. (7;13)(q13;q46)	Large; small	Normal; normal	L/D	Cross q (100%)	Decreased 54%	Danielak-Czech et al. (1997)
U. (X;13)(q24;q21)	Small; large	Large; small	L/L	Open q (88%)		
V. (X;14)	Small; medium	Normal; normal	Nd	Trivalent + univalent(12%) Two bivalent (90%), Open q (10%)	Sterile	Gustavsson et al. (1989)
					Sterile	Villagomez et al. (1991b)
<b>Cattle</b>						
A. (1;8;9)(q43;q13;q26)	Small; small; large	Large; normal; small	L/L/L	Hexavalent (74%), Open hexavalent(24%)	Decreased 38%	Kovacs et al. (1992)
B. (8;13)(q11;q24)	Very large; very small	Very large; very small	L/L	Two trival (2%) Cross q (23%) Open q (77%)	Sterile	Ansari et al. (1993)
C. (20;24)(q17;q25)	Medium; very small	Normal; normal	L/L	Cross q (50%), Open q (13%) Trivalent + univalent (5%)	Decreased 17% Teratologic Calves 9%	
D. (X;18)	ND	ND	ND	Two bivalent(32%) Trivalent + univalent (Mostly)	Sterile	Villagomez et al. (1993a) Koykul and Basrur (1994b)
<b>Sheep</b>						
A. (1;20)(p23;q24)	Large, large	Large, large	D/L	Cross q (100%)	ND	Świtoński et al. (1998b)

<sup>a</sup> D = dark G band, L = light G band.

<sup>b</sup> cross q = cross-shaped quadrivalent; open q = open quadrivalent.

<sup>c</sup> ND = no data.

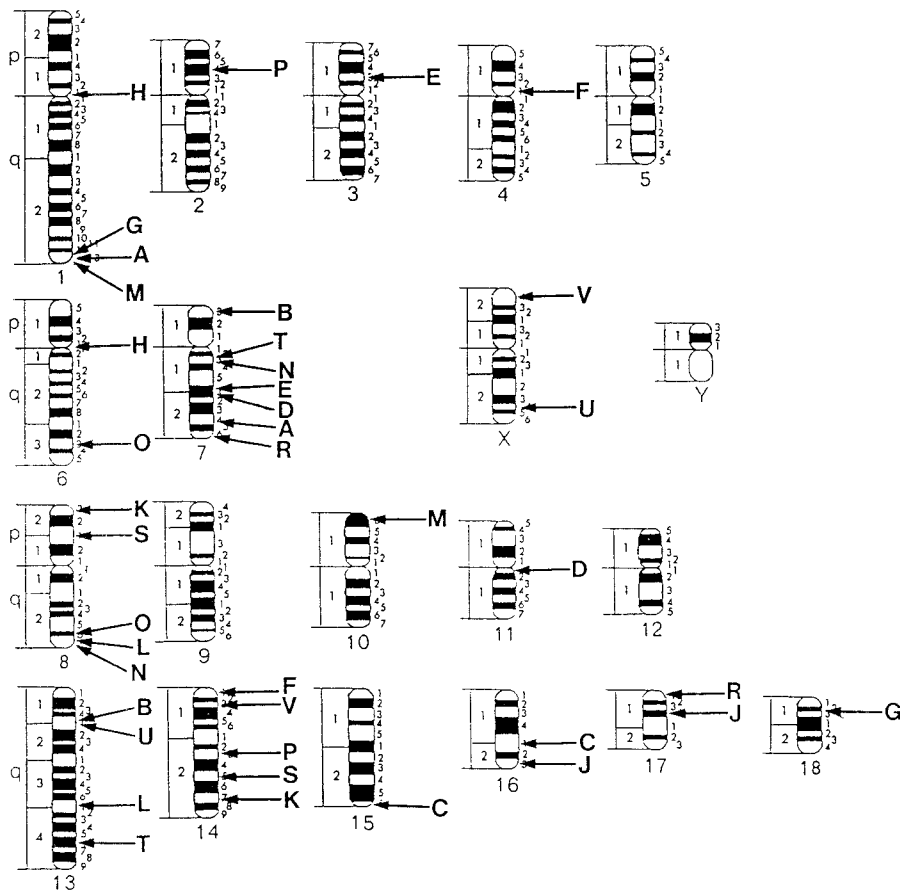
<sup>d</sup> This boar suffered from scrotal inflammation.

ly half of the 20q arm was transferred on chromosome 24. During pachytene, a cross-shaped quadrivalent was found in 50% of spermatocytes, but in the remaining cells other configurations occurred: open quadrivalent (12.5%), trivalent plus univalent (5%), and two bivalents with unequal axes (32.5%). An association between the sex bivalent and the translocation products was found very rarely (4.8%). This bull carrier, apart from a decreased fertility, sired malformed calves

(4.4%) and an increased rate of stillbirth was recorded.

From the reviewed cases of translocations, it is very difficult to draw a simple and clear conclusion on alterations of synaptic behavior in reciprocal translocation carriers (Table 2, Figures 3 and 4). In some cases, where a very small marker chromosome (cases in pigs: B, N, and R; and in cattle: A and B) consisting of a small pericentromeric region of one chromosome and a telomeric region of another

one will arise or very small telomeric fragments are exchanged reciprocally (cases in pigs: A, B, C, G, J, K, L, M, N, O, R, and T; and cases in cattle: A, B, and C) there can appear unusual synaptic configurations (open quadrivalent, trivalent plus univalent, or two heteromorphic bivalents). It seems that such pairing appearance is caused by a lack of crossing over events and subsequently a lack of chiasmata formation in these minute fragments. However, sometimes such alterations



**Figure 3.** Diagrammatic representation of swine G-banded karyotype (Committee for the Standardized Karyotype of the Pig 1988) with indicated breaks (arrows) involved in the reciprocal translocations described in Table 2.

were not observed (cases in pigs: C, J, L, M, O, and T). The above mentioned synaptic configurations may be responsible for increased missegregation at anaphase I and/or unspecific association between translocation products and the sex bivalent and may thus enhance negative effects on fertility of a carrier. It seems that the type of band (G-dark or G-light) where the breaks occur is of minor significance.

Only occasionally, chromosomal inversions were studied with the use of SC technique. There are two reports demonstrating a lack of the pairing loop in a carrier of small paracentric inversion of swine chromosome 8 (Świtoński 1991) and a boar carrier of a pericentric inversion of swine chromosome 1 (Świtoński et al. 1998a). Such synaptic behavior prevents crossing over within the inverted segment due to a lack of synapsis or nonhomologous pairing, and thus unbalanced gametes are not produced by the carrier. From the studies on mice and human carriers of inversions it was suggested that synaptic behavior depends on the type of G-band (dark or light) where the breaks

occurred (Ashley 1988; Gabriel-Robez and Rumpler 1994).

### Aneuploidy

Aneuploidy is rarely identified in breeding animals. There is one report describing synaptonemal complexes in a sterile stallion carrying chromosome 28 trisomy (Power et al. 1992). It was found that the third chromosome was usually associated with the homologous bivalent (75% of spermatocytes) or partially synapsed (23%). In one cell the third chromosome formed a ring univalent. In 50% of the spermatocytes pairing or association between the third chromosome 28 and the sex bivalent was observed. The horse showed azoospermia.

Incidentally, aneuploid spermatocytes were also found in males with a normal karyotype. One such spermatocyte among normal ones, in a Hereford bull, was described by Dollin and Murray (1984). Similar observations were recorded by Świtoński et al. (1991), who found single cells among normal spermatocytes of a bull, a

stallion, and a centric fusion buck carrier. In all three cases mentioned above, the third chromosome was partly synapsed with a homologous bivalent. In the buck's spermatocyte, beside the trisomic trivalent, a centric fusion trivalent was also present. These findings demonstrate that either these animals were mosaics or a missegregation of sister chromatids took place during mitotic cleavages of spermatogonia. Since these males had a normal phenotype, the second possibility seems to be more likely.

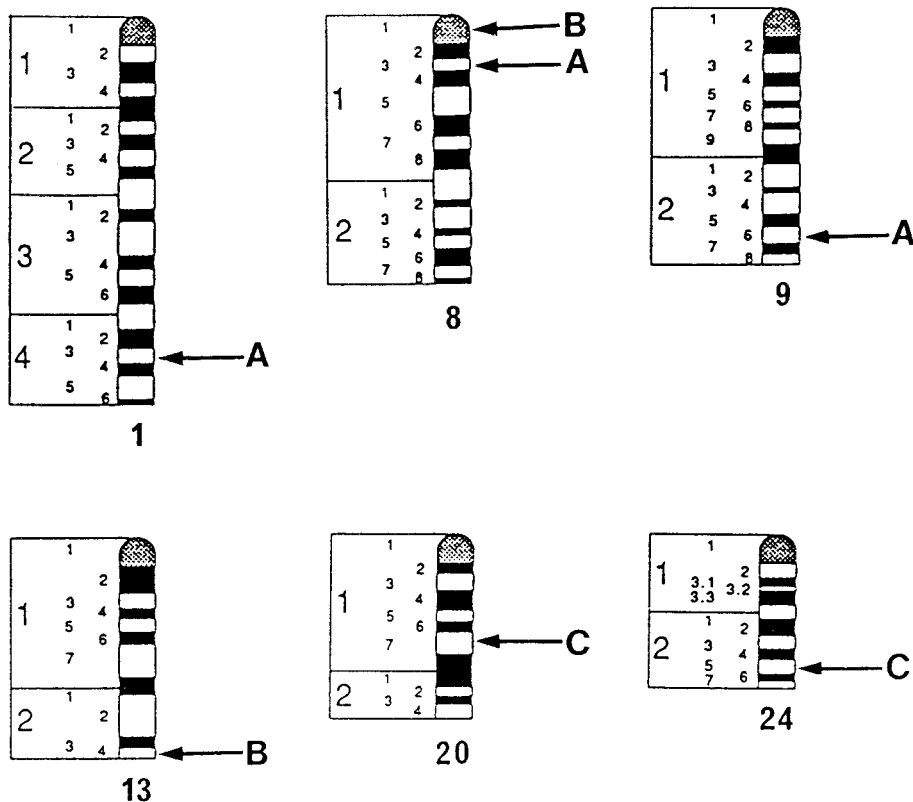
### Karyotype and Chromosomal Polymorphisms

Karyotype polymorphism, caused by the variable number of B chromosomes, was studied by SC techniques in the farm silver fox (*Vulpes fulvus*; Świtoński et al. 1987a) and the captured Chinese raccoon dog (*Nyctereutes procyonoides procyonoides*; Shi et al. 1988). In both studies, synaptic behavior of B chromosomes depended on their number in a spermatocyte. If only one B is present, very often self-pairing of the univalent was observed. When two B's are found, usually a bivalent is formed. In cells with three B's either trivalent or bivalent + univalent is formed. These studies suggest extensive homology between B chromosomes within a species.

Pairing behavior of polymorphic heterochromatic arms in the farm blue fox (*Alopex lagopus*) was studied by Świtoński and Gustavsson (1991). Delayed pairing of heterochromatic arms within a bivalent, especially when distinct length differences between them exist, was observed. In the mid-late pachytene, the heterochromatic arms were completely length adjusted. Very rarely unspecific pairing or associations between nonhomologous heteromorphic pairs or between such a pair and the sex bivalent were found.

### Interspecies Hybrids

There are several examples of interspecies crossbreeds which were included in breeding programs with the aim at improving certain production traits of the hybrids. Unfortunately, the fertility of the hybrids is usually affected. It is known that sterility or decreased fertility of hybrids can be caused by abnormal chromosome pairing at meiotic prophase I or the genotype at so-called *hybrid sterility (Hst)* loci (Forejt 1996). Studies with the use of SC techniques present basic knowledge on the extent of homologous pairing between chro-



**Figure 4.** Diagrammatic representation of selected bovine G-banded chromosomes (ISCNDA 1989) involved in the reciprocal translocations described in Table 2. The breaks are indicated by arrows.

mosomes of two crossbred species and unspecific synaptic behavior during the pachytene substage.

Cattle  $\times$  zebu hybrids were studied by Świtoński et al. (1990) and Dollin et al. (1991a,b). The first study used crosses between native, nondescript, Indian zebu cows and Brown Swiss bulls. In all analyzed cells a normal number of autosome bivalents was observed. However, it was also found that in almost 19% of the analyzed cells at late zygoteny or early pachytene substages one to three bivalents with pericentromerically unequal lateral elements were present. This inequality was considered a result of centromeric C-band polymorphism. As a consequence, in almost 11% of spermatocytes unspecific associations between the sex bivalent and a bivalent with unequal lateral elements (approximately 8%) or between two such bivalents (approximately 3%) were developed. Quite similar observations were described by Dollin et al. (1991a,b) who carried out extensive investigations in Australia on crossbreeds between Hereford (*Bos taurus*) and Brahman (*Bos indicus*) or other zebu breeds. It was found that the most common pairing abnormality was not fully paired bivalents—so-called open bivalents. This phenomenon

was found in approximately 13% of spermatocytes (Dollin et al. 1991a). Such bivalents were associated with the sex bivalent in approximately 6% of the studied cells. These studies showed that in cattle  $\times$  zebu hybrids synaptic behavior is not much altered, and this is mainly due to size differences of pericentromeric heterochromatin (C-band) in some chromosome pairs.

The domestic water buffalo is classified into two types: swamp ( $2n = 48$ ) and river ( $2n = 50$ ). It is known that the difference in the diploid number of chromosomes is caused by a 4;9 tandem fusion translocation (Bongso and Hilmi 1982). Gustavsson et al. (1993) showed that in 34% of spermatocytes, mainly at early and midpachytene, the tandem fusion trivalent was associated with the sex bivalent. Moreover, a conventional analysis of the meiotic second metaphase predicted that roughly 40% of spermatids are chromosomally unbalanced. In the study of Dai et al. (1994d), a very high incidence of associations between the trivalent and the sex bivalent was reported. Almost 41% of the spermatocytes demonstrated such associations. The authors pointed out the role of delayed pairing of the pericentromeric region of chromosome 4 bearing nucleolar

organizer region (NOR). A similar phenomenon is observed in human centric fusion translocations, which involve NOR-bearing acrocentrics and are frequently associated with the sex bivalent. From the above mentioned studies it can be concluded that decreased fertility of river  $\times$  swamp buffalo hybrids is caused by unusual synaptic behavior of the tandem fusion translocation.

Blue fox (*Alopex lagopus*,  $2n = 50$ )  $\times$  silver fox (*Vulpes fulvus*,  $2n = 34 + B$ ) hybrids are occasionally produced on fur animal farms. It is known that the hybrids are sterile. Application of SC techniques revealed that at the pachytene substage of prophase I very complex synaptic configurations are present. Among them multivalents, partly synapsed bivalents, and univalents were identified (Gustavsson et al. 1988a).

The mule (female horse  $\times$  male donkey) and the hinny (female donkey  $\times$  male horse) are the first interspecies hybrids produced by humans. It is well documented that some of mules and hinnies can be fertile [for a review see Allen and Short (1997)], but there are not published results on synaptonemal complexes, however conventional studies of meiosis in spermatocytes of both mules and hinnies was carried out (Chandley et al. 1974).

## Conclusions

The presented survey of SC studies revealed a wide variability of synaptic behavior in spermatocytes carrying the same type of chromosomal abnormality. Distinct differences were found for centric fusion translocations in humans and farm animals. This seems to depend on the involvement of acrocentrics bearing NORs in the human Robertsonian translocations, followed by a negative effect of association between the trivalent and the sex bivalent. This was rarely observed in farm animals.

Certain cases of reciprocal translocations demonstrated unusual synaptic configurations instead of the expected quadrivalent. Reciprocal exchange of very small chromosome fragments may result in a failure of some chiasmata formation, followed by the formation of open quadrivalent, trivalent plus univalent, or two heteromorphic bivalents. The association of these configurations with the sex bivalent was quite frequently observed.

Inversions may form an inversion loop, but lack of synapsis or nonhomologous synapsis can also occur along the inverted

chromosome fragment. Lack of the loop prohibits crossing over within the inverted segment and unbalanced gametes are not formed.

Concluding, one can state that SC techniques are a very useful tool which allows the recognition of causes responsible for a range of fertility alterations in carriers of abnormal chromosome complement.

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