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Sex Chromosomes and Meiosis in Spiders: A Review

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1. Introduction

According to Platnick (2011), the order Araneae possesses 110 families, 3,849 genera, and 42,473 species. It is divided into two suborders: Mesothelae, consisting of only one family (Liphistiidae), and Opisthothelae. The latter suborder is divided into two infra-orders: Mygalomorphae, consisting of spiders with paraxial chelicerae, and Araneomorphae, consisting of spiders with diaxial chelicerae. The latter infra-order is divided into the basal clades (Hypochilidae and Austrochiloidea), Haplogynae, and Entelegynae, which includes the majority of extant spiders (Coddington & Levi, 1991) (Fig. 1).

In the first cytogenetic studies in spiders performed by Carnoy (1885), gonads of male or female individuals were imbedded in paraffin, sectioned, and stained with Heidenhain's iron haematoxylin. Chromosome visualisation and interpretation of cytogenetic analyses were difficult to achieve with this method. Decades later, Sharma et al. (1959) and Beçak & Beçak (1960) were the first researchers to obtain spider chromosomes by the aceto-orcein or aceto-carmin squash methods.

Pinter & Walters (1971) introduced the use of colchicine solution for cytological preparations of spider testes and ovaries. This solution promotes an increase in the number of cells in mitotic and/or meiotic metaphase, the stage in which chromosomes are most easily visualised and identified. In the same decade, Brum-Zorrila & Cazenave (1974) applied 3:1 methanol:acetic acid as a fixative solution and Giemsa solution as a stain.

Matsumoto (1977) pioneered the observation of chromosomes in spider embryos. Embryos are a valuable source of mitotic metaphase cells due to the high rate of cellular division that occurs during embryonic development. There are a number of tissues that can be used in cytogenetic studies of spiders, such as gonads (testes and ovaries), cerebral ganglion, and cultured blood cells, as described by Wang & Yan (2001).

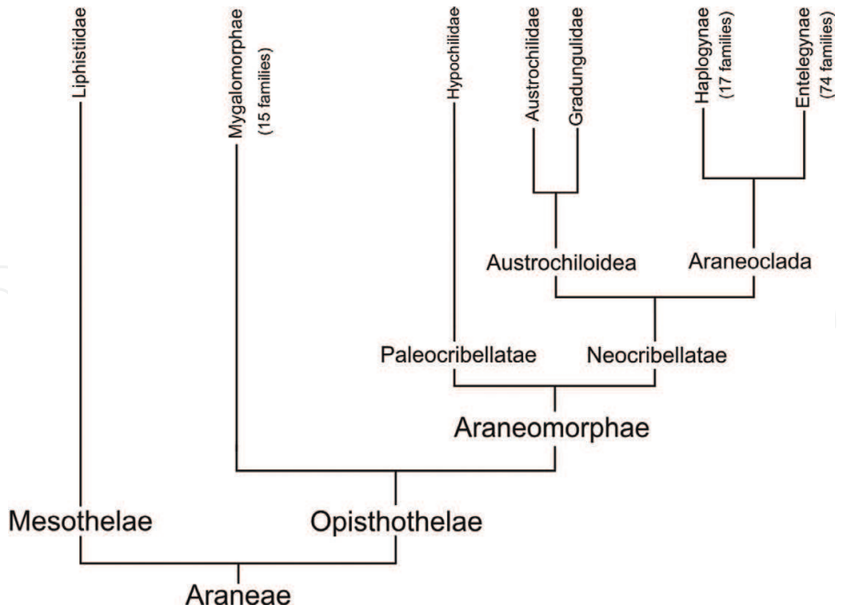

Fig. 1. Phylogenetic relationships within major clades of spiders according to Coddington & Levi (1991). The number of families was determined according to Platnick (2011).

The gonads, especially the testes, have been found to be more suitable than other tissues for karyotype analysis in the vast majority of cytogenetic investigations. Analysis of gonads allows both mitotic and meiotic chromosomes to be studied. In addition to data regarding the diploid number, length, and morphology of chromosomes, analyses of chromosomes during meiosis have contributed to the identification of types of sex chromosome systems (SCS) in spiders. This is very important in the case of Araneae due to the diversity of simple or multiple SCS that have been recorded in representatives of this order. Furthermore, in investigations of mitotic cells, it is not possible to recognise certain types of SCS, such as X0 and X_1X_2Y, by only taking into account the difference in the diploid number observed in male and female individuals. However, analysis of meiotic cells allows investigation of the behaviour of chromosomes in relation to association, synapsis, recombination, and segregation. These features are indispensable for understanding the origin and evolution of sex chromosomes.

2. Sex chromosome systems (SCS) in spiders

Currently, there are 678 cytogenetic records in spiders (www.arthropodacytogenetics.bio.br/spiderdatabase). Of these, 456 species (67.3%) have an SCS of the X_1X_20 type; 105 species (15.5%) have an X0 system; 59 species (8.7%) have an $X_1X_2X_30$ system; 10 species (1.5%) have an SCS of the X_1X_2Y type; 5 species (0.7%) have an $X_1X_2X_3X_40$ system; 5 species (0.7%) have an XY SCS; 5 species (0.7%) have an SCS of the $X_1X_2X_3Y$ type; 1 species (0.1%) has an SCS of the $X_1X_2X_3X_4X_5Y$ type; and 1 species exhibits variations of a multiple X_nY_n SCS. In 31 species (4.6%), the SCS has not been identified (Fig. 2). The number of cytogenetic records (678) in spiders is slightly higher than the number of spider species analysed chromosomally (665) because more than one type of SCS has been registered for some species.

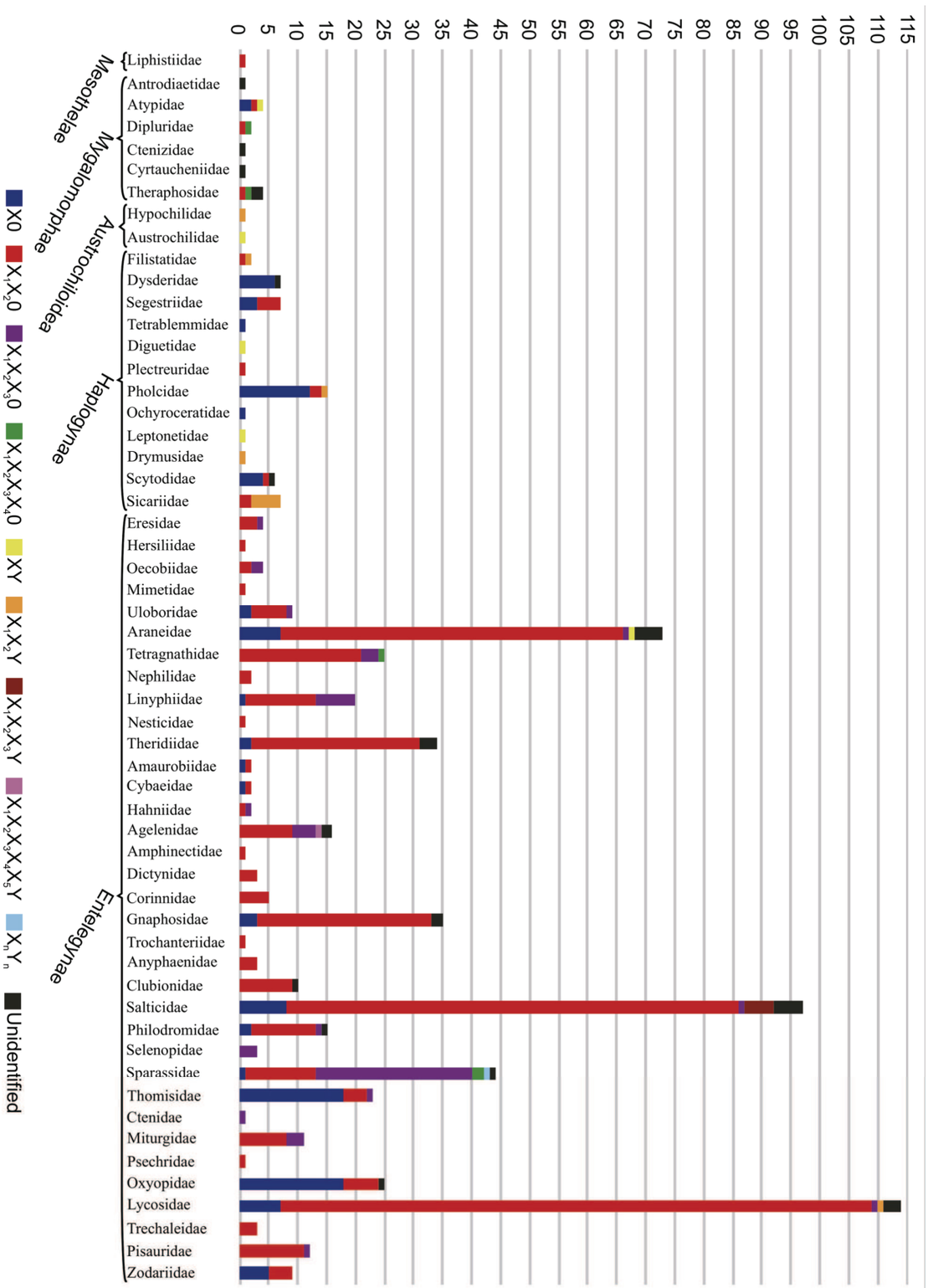

Fig. 2. Distribution of sex chromosome systems within cytogenetically characterised spider families.

2.1 Meiotic behaviour of sex chromosomes

The pioneering works describing the X_1X_20 and X0 SCS in spiders were those of Wallace (1900, 1905) and Berry (1906), respectively. These researchers identified the sex chromosomes based on the positive heteropycnotic behaviour of these elements during meiosis (Fig. 3). According to White (1940), the term heteropycnosis was introduced to describe the different levels of condensation and staining that certain chromosomes exhibit in the course of mitosis and/or meiosis. This heteropycnotic pattern can be positive or negative, and it is related to a high or low degree of chromosome condensation, respectively.

Manifestation of heteropycnosis is commonly visualised in the sex chromosomes, especially in male meiotic cells; the high level of chromosome condensation in these cells seems to prevent recombination between nonhomologous regions of heteromorphic sex chromosomes (McKee & Handel, 1993). However, the autosomes and female sex chromosomes can also exhibit chromatin differentiation in some stages of the cell cycle.

In spider spermatogenesis, a heteropycnotic pattern of the sex chromosomes has been recorded for roughly 25% of the species that have been cytogenetically examined, which belong to different suborders (Mygalomorphae and Araneomorphae) and families. Regardless of the type of SCS, 95% of these spider species showed positively heteropycnotic sex chromosomes in premeiotic interphase and prophase I nuclei (Fig. 3a-c, e-g, i-m) and, occasionally, also in metaphase II cells (Fig. 3d). In late meiotic stages, the sex chromosomes usually appeared to be isopycnotic (Fig. 3o-p). The heteropycnotic pattern of sex chromosomes can be used as an additional criterion to determine the type of SCS in spiders, as the number of positive heteropycnotic corpuscles frequently corresponds to the number of sex chromosomes.

It is of note that in some SCS that were originated through relatively recent rearrangements between autosomes and sex chromosomes, such as the $X_1X_2X_3Y$ system of *Evarcha hoyi* (under *Pellenes hoyi*) (Maddison, 1982), the X_nY_n system observed in *Delena cancerides* (Rowell, 1985), and the $X_1X_2X_3X_4X_5Y$ system found in *Malthonica ferruginea* (Král, 2007), only the ancient sex chromosomes exhibit positive heteropycnosis in the course of male meiosis.

Recently, positive heteropycnotic behaviour of one autosomal bivalent was verified during male meiosis of some spiders belonging to the families Dipluridae, Theraphosidae (Mygalomorphae), Diguetidae, and Sicariidae (basal Araneomorphae). According to Král et al. (2006, 2011), this bivalent could represent sex chromosomes in an early stage of differentiation because in addition to positive heteropycnosis, this bivalent showed a recurrent association with the sex chromosomes during the initial prophase I substages. Conclusive proof of the relationship between this homomorphic chromosome pair and sex determination has been obtained through ultrastructural chromosome analysis of the synaptonemal complex.

The modes of sex chromosome association and segregation are interesting features to investigate in meiotic cells. In spiders with an XY SCS, the sex chromosomes can present associations that vary from chiasmatic, such as those found in *Leptoneta infuscata* (Leptonetidae), to terminal pairing, such as in *Diguetia albolineata* and *Diguetia canities* (Diguetidae) (Král et al. 2006). An achiasmatic terminal association of the sex chromosomes has been recorded in some basal Araneomorphae with X_1X_2Y SCS. In representatives of the families Drymusidae, Filistatidae, Hypochilidae, Pholcidae, and Sicariidae, in which all sex

chromosomes are biarmed, the arms of the metacentric X chromosomes showed end-to-end pairing (Fig. 3n) with arms of the tiny Y chromosome (Oliveira et al. 1997, Silva et al. 2002, Král et al. 2006). In contrast, in *Pholcus phalangioides* (Pholcidae), which carries a submetacentric X_2 chromosome, only one arm of this sex chromosome was terminally paired with the Y chromosome (Král et al. 2006).

In derivative araneomorphs that possess other types of multiple SCS, such as $X_1X_2X_3Y$ and $X_1X_2X_3X_4X_5Y$, in which the sex chromosomes do not show a high degree of morphological and/or structural differentiation due to their recent origin, the association of the sex chromosomes during meiosis can be chiasmatic between some elements and achiasmatic between others. In the $X_1X_2X_3Y$ SCS of *E. hoyi*, an interstitial or terminal chiasma was present between one arm of the large submetacentric Y chromosome and the long arm of the acrocentric X_2 chromosome (Maddison, 1982). In *M. ferruginea* (Agelenidae), the X_1, X_2, and X_3 sex chromosomes appeared as univalents that were terminally associated with the X_4X_5Y trivalent; this trivalent was composed of one large-sized Y chromosome and two small-sized acrocentric X chromosomes. Although Král (2007) did not register the presence of chiasma between these sex chromosomes due to the precocious dissociation of these elements during prophase I, ultrastructural analysis revealed the occurrence of a recombination nodule in the X_4X_5Y trivalent.

From the zygotene stage to metaphase I, the X chromosomes of multiple X SCS usually present a parallel disposition (Fig. 3 e-g, j-l), without evidence of chiasmata, and proximity between each X chromosome commonly involves the centromere region (Král et al. 2011). Occasionally, in some mygalomorph species of the family Theraphosidae, the sex chromosomes of the $X_1X_2X_3X_40$ system exhibit an end-to-end association (X_1X_2Y-like pairing), and in representatives of the family Dipluridae, the sex chromosomes can appear as univalent elements that are highly condensed and separated. In addition, an X_1X_2Y-like pairing of the sex chromosomes has been observed in *Stegodyphus lineatus* (Eresidae) and *Pax islamita* (Zodariidae), which are carriers of the $X_1X_2X_30$ and X_1X_20 SCS, respectively (Král et al. 2011).

Contrary to data revealed by conventional chromosome analyses, in which the sex chromosomes of multiple X systems appeared to exhibit a simple behaviour that involved only parallel pairing, more recent cytogenetic ultrastructural studies have supplied surprising information. Benavente and Wettstein (1980) were the first to describe the presence of junctional lamina between the X_1 and X_2 sex chromosomes of *Schizocosa malitiosa* (under *Lycosa malitiosa*); this junctional lamina was structurally similar to the synaptonemal complex, formed in the early substages of prophase I, and persisted to the late substages.

Wise (1983) also encountered evidence of a junctional lamina in prophase I in two carriers of the X_1X_20 system, *Allocosa georgicola* (under *Lycosa georgicola*) and *Rabidosa rabida* (under *Lycosa rabida*). Furthermore, a terminal association between sex chromosomes and one homomorphic bivalent was observed in *S. malitiosa* and *A. georgicola*. However, the association between sex chromosomes and a homomorphic bivalent was only explained in recent ultrastructural analyses of *Pardosa morosa* (Lycosidae) and the agelenids *Malthonica campestris* and *Malthonica silvestris* performed by Král (2007) and Král et al. (2011). These studies indicated that this homomorphic bivalent is an element that belongs to the SCS; that is, the system included one pair of homomorphic sex chromosomes in addition to the morphologically differentiated X_1 and X_2 or X_1, X_2 and X_3 sex chromosomes (Fig. 3h).

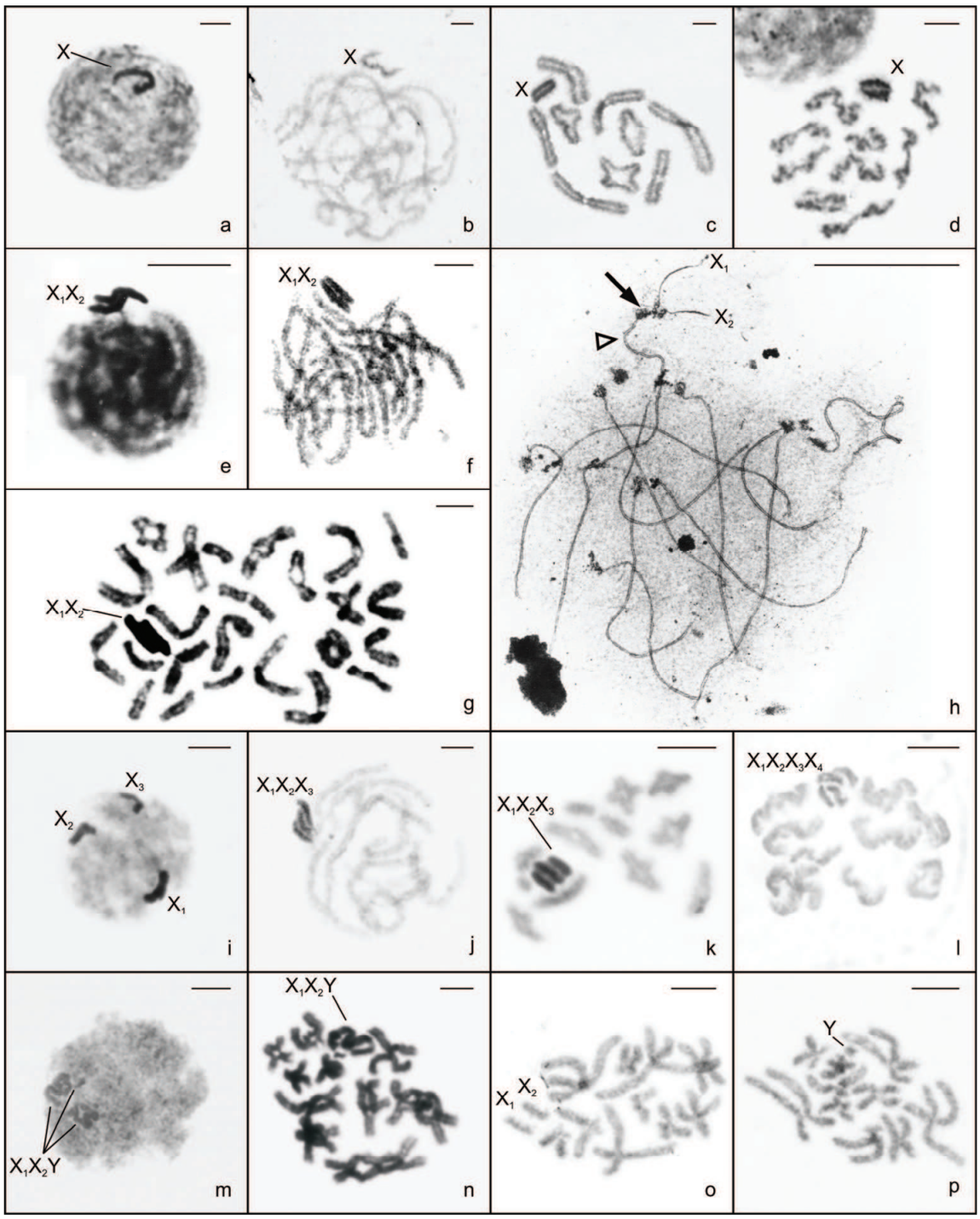

Fig. 3. Behaviour of the sex chromosomes during meiosis in male spiders. a – d. *Hogna sternalis* (X0); e. *Lycosa erythrognatha* (X_1X_20); f. *Falconina* sp. (X_1X_20); g. *Polybetes* sp. (X_1X_20); h. *Phoneutria* sp. (X_1X_20); i – k. *Trachelas* sp. ($X_1X_2X_30$); l. *Xeropigo* sp. ($X_1X_2X_3X_40$); m – p. *Loxosceles variegata* (X_1X_2Y). a, e, i, m. Premeiotic interphase nuclei. b, f, h, j. Pachytene cells. c, g, k, l, n. Diplotene cells. d, o, p. Metaphase II nuclei. In almost all cells, the sex

chromosomes can be easily recognised by their high degree of condensation and positive heteropycnosis (a-g, i-m) and/or association behaviour (e-h, j-l, n). Note the parallel pairing of the X chromosomes of the multiple sex chromosome system (e-f, j-l) and the end-to-end paring of the X_1X_2Y chromosomes (n). In h, observe the probable junctional lamina (arrow) between the X_1 and X_2 chromosomes and the terminal association of these sex chromosomes with a homomorphic bivalent (arrowhead). Scale bar=10 μm.

Although employing cytogenetic techniques to identify specific chromosomal regions has provided relevant data on spider chromosomes, only approximately 50 and 30 species were characterised with respect to the constitutive heterochromatin and nucleolar organiser regions (NORs), respectively. In these species, constitutive heterochromatin exhibited a similar distribution among autosomes and sex chromosomes, occurring mainly in pericentromeric regions. However, in at least three representatives of the basal araneomorphs with an X_1X_2Y SCS, *Pholcus phalangioides*, *Loxosceles intermedia*, and *Loxosceles laeta*, the Y chromosome was completely heterochromatic (Silva et al., 2002, Král et al. 2006). This reinforces the results obtained in analyses of the association behaviour of sex chromosomes during meiosis I; that is, the Y chromosome exhibits a high degree of differentiation and does not share homology with the X_1 and X_2 chromosomes. In mygalomorphs, basal and derived araneomorphs, the NORs are located predominantly on the terminal regions of one to three autosome pairs. Nevertheless, among basal araneomorph species with an X0 SCS, NORs can occur on autosomes and the X chromosome (Dysderidae, Pholcidae and Tetrablemmidae) or only on the X chromosome (Ochyroceratidae, Leptonetidae, and Scytodidae). Recently, Král et al. (2011) described the presence of NORs on the X_2 sex chromosome of derived araneomorph species belonging to the family Tetragnathidae. According to these authors, this unusual NOR localisation may be due to the translocation of rDNA cistrons from autosomes to sex chromosomes.

2.2 Early descriptions and discussions of nomenclature, function and origin

Carnoy (1885) presented the first, although inaccurate, chromosome numbers of some spider species. However, this study did not mention the existence of chromosomes that could be related to sex determination. Wallace (1900, 1909) was the first to describe double "accessory chromosomes" in a spider, *Agelenopsis naevia* (under *Agalena naevia*), and to associate the presence of these elements with sex determination. However, Wallace (1900, 1909) was not able to observe such chromosomes in females, thus concluding that male embryos were produced by fusion between a spermatozoon with accessory chromosomes and an egg without such elements, and female embryos were formed by fusion between a spermatozoon and an egg that both lack accessory chromosomes.

According to Wallace (1909), the accessory chromosomes corresponded to those that Wagner (1896) described as a "nucleolus". Subsequently, these chromosomes in spiders were also referred to as "heterochromosomes" (Montgomery, 1905) or "odd-chromosomes" (Berry, 1906). The nomenclature of "accessory chromosomes" was adopted by Painter (1914) and others. In a brief communication describing the X element in *Amaurobius* sp., King (1925) was the first to use the term "sex chromosome" in spiders. The designation of "accessory chromosomes" was still used by Hard (1939), but by the late 1940's, the nomenclature of "sex chromosomes" was definitively adopted in spiders.

An early explanation of the origin and evolution of sex chromosomes in spiders and other groups of organisms was elaborated by Montgomery (1905). According to this author, there

were two types of so-called "heterochromosomes"; those that occurred in pairs in spermatogonia and then associated to form bivalents in spermatocytes (paired type), and those that were unpaired, or single, in spermatogonia and continued to be unpaired in the spermatocytes during the course of meiosis. According to this study, unpaired heterochromosomes could originate from those of the paired type through subsequent modifications. Furthermore, Montgomery (1905) stated that heterochromosomes of the paired type were derived from "ordinary chromosomes", but these heterochromosomes no longer carried out the same activities as the "ordinary chromosomes" and had the tendency to disappear. Thus, excessively minute heterochromosomes could represent the last stage before total deletion of these elements, instead of the first stage in the origin of this type of chromosome. Montgomery (1905) also suggested that heterochromosomes arose from "ordinary chromosomes" concomitantly with a change in chromosomal number, most likely from a higher to a lower number. However, the relationship between heterochromosomes and sex determination was only a hypothesis at that time because there was no record of such chromosomes in oocytes.

According to Painter (1914), the fact that accessory chromosomes were consistent with respect to their number, form, and behaviour in spider species belonging to 13 families suggested that these elements must have a very important and constant function in the life cycle of these spiders, in contrast to the autosomes, which were numerically variable among different species. Painter (1914) also noted that the accessory chromosomes were related to sex determination. The point of view of Painter (1914) was contrary to the conclusion presented by Wallace (1909), i.e., male embryos were produced by the fusion of one spermatozoon without accessory chromosomes and one egg with such elements, whereas female embryos were formed by the fusion of a spermatozoon and egg that both carried accessory chromosomes. The conclusion of Painter (1914) can be considered correct for all spider species without a Y chromosome.

2.3 Origin of the X_1X_20 sex chromosome system

The X_1X_20 SCS has been considered a plesiomorphic feature in spiders because it occurs in representatives of the phylogenetically basal family Liphistiidae (Mesothelae) (Suzuki, 1954). Various hypotheses concerning the origin of this system in spiders have been put forth.

Revell (1947) was the first to suggest that the X_1X_20 SCS most likely originated from an X0 system in spiders, considering the proposition of White (1940), who suggested that duplication of the X chromosome from an X0 system gave rise to the multiple X chromosome systems (Fig. 4). This hypothesis was based on the similarity of the sizes of X chromosomes and the probable homology between the X chromosomes during prophase I in a multiple sex chromosome system. However, Revell (1947) verified the presence of multiple X chromosomes of different sizes in *Tegenaria*, and he suggested that these X chromosomes had undergone evolutionary differentiation after originating from an X0 system (Fig. 5).

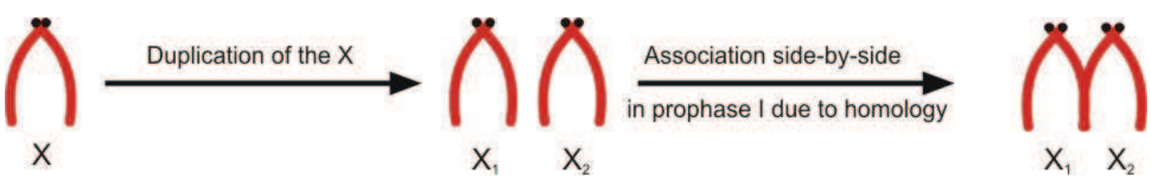

Fig. 4. Interpretive scheme of the origin of the X_1X_20 SCS based on descriptions of White (1940).

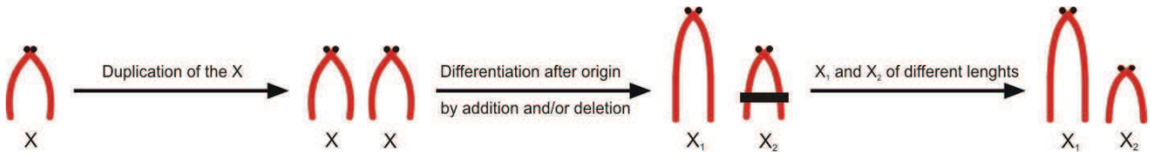

Fig. 5. Schematic representation of the origin of the X_1X_20 SCS based on descriptions of Revell (1947).

Studying the meiotic cells of *Araneus quadratus* (under *Aranea reaumuri*), Pätau (1948) suggested that there was no indication of homology between the X_1 and X_2 chromosomes; however, this author did not exclude the possibility of partial homology. Absence of homology between the X_1 and X_2 chromosomes was corroborated by Hackman (1948), Suzuki (1952) and Mittal (1964). Moreover, Pätau (1948) proposed that the X_1X_20 SCS was formed by centric fission of a large X chromosome in an X0 system.

Due to the fact that all X chromosomes of X0 systems that were registered at that time exhibited subterminal or terminal centromeres, Pätau (1948) suggested that the smaller X_1 and X_2 chromosomes had originated from the X0 system not only by simple centric fission, but through additional rearrangements such as 1) centric fragmentation and fission in the long arm terminal region followed by inversion of the long chromosome segment, resulting in a dicentric chromosome; 2) fission in the middle region of the dicentric chromosome, forming two acrocentric X_1 and X_2 chromosomes of similar size (Fig. 6).

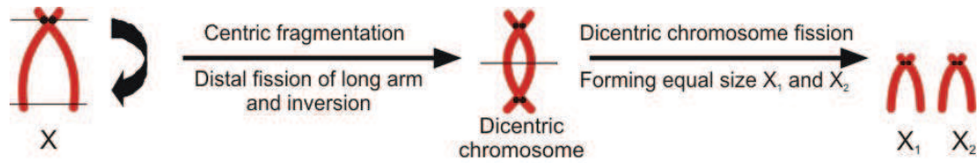

Fig. 6. Interpretive scheme of the origin of the X_1X_20 SCS based on descriptions of Pätau (1948).

Bole-Gowda (1950) asserted that the X_1X_20 SCS originated from an X0 system in the ancestor of spiders by fission in the middle of the X chromosome producing an acentric chromosome segment that then translocated to a supernumerary centric fragment. These rearrangements produced X_1 and X_2 chromosomes of similar sizes, one of which retained the original centromere of the X chromosome, while the other kept the supernumerary centromere (Fig. 7). Suzuki (1954) was in agreement with the hypothesis described by Pätau (1948) but disagreed with the assertion of Bole-Gowda (1950) regarding the origin of the X_1X_20 system in spiders because no explanation was provided for the origin of the supernumerary centric fragment involved in this hypothesis.

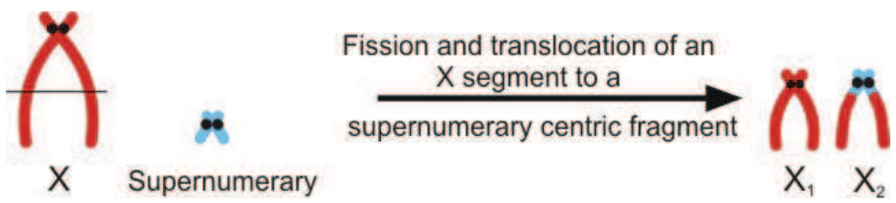

Fig. 7. Schematic representation of the origin of the X_1X_20 SCS based on the descriptions of Bole-Gowda (1950).

Considering the terminal position of the centromere and the size of the X_1 and X_2 chromosomes, Postiglioni & Brum-Zorrilla (1981) suggested that non-disjunction or duplication of a single telocentric X chromosome may have been responsible for the origin of the X_1X_20 SCS of *Lycosa* sp.3 (Fig. 8a). According to these researchers, the lack of homology between these chromosomes was most likely due to the occurrence of other rearrangements. However, the authors did not exclude the possibility that the origin of the X_1X_20 system of *Lycosa* sp.3. could have occurred by centric fission of a metacentric X chromosome (Fig. 8b).

Although previous authors reported that female X chromosomes form normal bivalents during meiosis (Hackman, 1948; Pätau, 1948; Sharma et al., 1959), Král (2007) and Král et al. (2011) found that the female X chromosomes of entelegyne and mygalomorph spiders paired during meiosis and also exhibited heterochromatinisation similar to that observed in male meiosis. This event could prevent recombination between the X chromosomes and accelerate their differentiation, a process that is consistent with the hypothesis of Postiglioni & Brum-Zorrilla (1981).

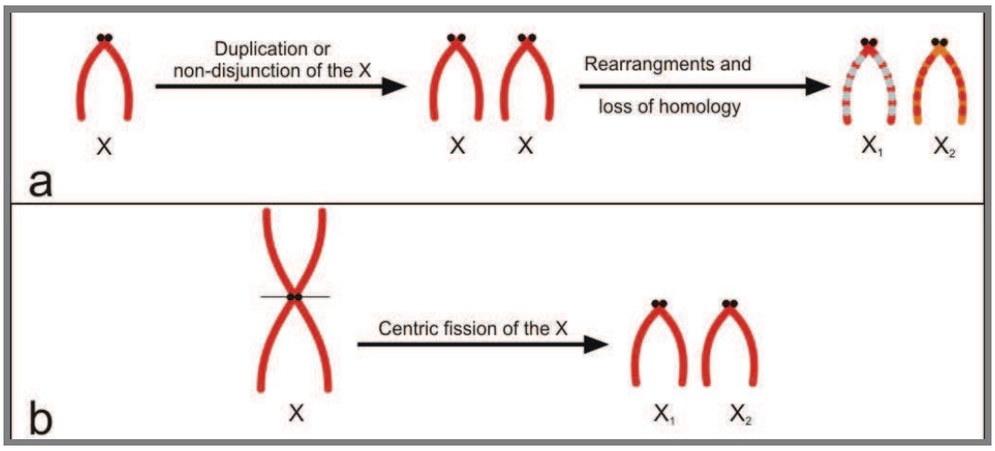

Fig. 8. Interpretive scheme of the origin of the X_1X_20 SCS based on descriptions of Postiglioni & Brum-Zorrilla (1981).

In addition to these hypotheses, some researchers have considered the X_1X_20 SCS to have originated secondarily from other multiple SCS. Oliveira et al. (2007) proposed that the X_1X_20 system could have arisen by gradual heterochromatinisation and erosion of the Y chromosome (Fig. 9). This hypothesis was based on the fact that the pholcid *Spermophora senoculata*, which exhibits an X_1X_2Y system, was considered phylogenetically basal (Bruvo-Mararic et al., 2005) in relation to *Crossopriza lyoni*, which shows an X_1X_20 SCS.

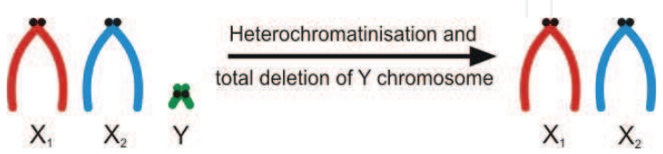

Fig. 9. Schematic representation of the origin of the X_1X_20 SCS based on the descriptions of Oliveira et al. (2007).

In some species of the genus *Malthonica* (Agelenidae), Král (2007) encountered three types of SCS, X_1X_20, $X_1X_2X_30$, and $X_1X_2X_3X_4X_5Y$, and therefore suggested that in this genus, the $X_1X_2X_30$ condition was ancestral and gave rise to the X_1X_20 system through a tandem fusion

between two X chromosomes (Fig. 10). This proposition was based on the peculiar meiotic behaviour of the X chromosomes belonging to the $X_1X_2X_30$ SCS, the great difference in sizes between the X chromosomes of the X_1X_20 SCS, and the presence of the $X_1X_2X_30$ system in *Tegenaria parietina*, which is morphologically closely related to *Malthonica*.

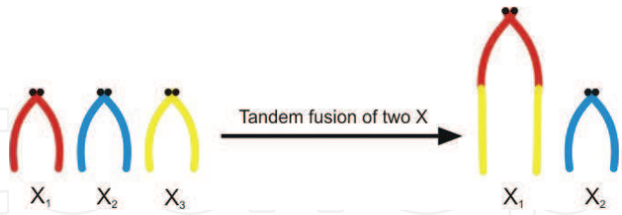

Fig. 10. Interpretive scheme of the origin of the X_1X_20 SCS based on descriptions presented by Král (2007).

2.4 Origin of the $X_1X_2X_30$ sex chromosome system

Revell (1947) found $2n♂=40+X_1X_20$ in *Tegenaria atrica* and $2n♂=40+X_1X_2X_30$ in *Tegenaria domestica*. Considering that the number of autosomes was constant (40 autosomes) in these two *Tegenaria* species, the author suggested that the X1X2X30 SCS originated from the X_1X_20 system, which was derived from an X0 system. However, this author did not state the chromosome rearrangements that were responsible for the origin of the $X_1X_2X_30$ system. The existence of X chromosomes of different lengths in species with an $X_1X_2X_30$ system was considered by Revell (1947) as evidence that the multiple X chromosomes of the $X_1X_2X_30$ system were modified after the origination of this SCS.

According to Pätau (1948), in the *Tegenaria* species studied by Revell (1947), the largest X chromosome found in *T. atrica* (X_1X_20) was equivalent to the sum of the lengths of the two smallest X chromosomes observed in *T. domestica* ($X_1X_2X_30$). In this case, an X_1X_20 SCS could give rise to an $X_1X_2X_30$ system through rearrangements similar to those proposed by Pätau (1948) for the origin of the X_1X_20 SCS (Fig. 11, 6). This explanation was supported by Suzuki (1954) and Sharma et al. (1959). However, these authors analysed *Selenops radiatus*, which showed three X chromosomes of equal size, and proposed that the similarity in the length of the sex chromosomes in some species with the $X_1X_2X_30$ system could be the result of additional rearrangements after their origin from an X_1X_20 system.

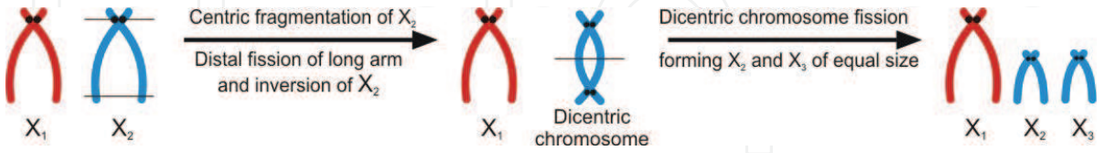

Fig. 11. Schematic representation of the origin of the $X_1X_2X_30$ SCS based on the descriptions of Pätau (1948).

Sharma et al. (1959) demonstrated that the six X chromosomes in the zygotene and pachytene stages in *Selenops radiatus* females (males were $X_1X_2X_30$) did not show any positive heteropycnosis and formed only normal bivalents but did not form multivalents; similar meiotic behaviour of chromosomes was observed in female meiotic cells of a species with four X chromosomes (males were X_1X_20) by Hackman (1948), Pätau (1948) and Suzuki (1954), reinforcing the suggestion that there was no homology between the X chromosomes of the X_1X_20 and $X_1X_2X_30$ SCS.

Bole-Gowda (1952) proposed that the $X_1X_2X_30$ system found in *Heteropoda venatoria* arose from an ancestor with an X_1X_20 system by translocation of a segment of one X chromosome of the X_1X_20 system and one supernumerary centric fragment (Fig. 12). This is similar to this author's hypothesis for the origin of the X_1X_20 system from the X0 system.

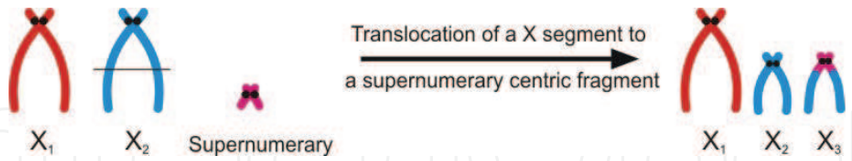

Fig. 12. Interpretive scheme of the origin of the $X_1X_2X_30$ SCS based on descriptions of Bole-Gowda (1952).

To explain the origin of the $X_1X_2X_30$ SCS found in *Lycosa* sp. (*thorelli* group), Postiglioni & Brum-Zorrilla (1981) hypothesised that non-disjunction of one X chromosome of the X_1X_20 system, followed by loss of homology between the X chromosomes had occurred (Fig. 13). To corroborate the hypothesis of non-disjunction, the authors cited the observation of a particular behaviour involving early condensation and isolation of one X chromosome at the pachytene stage. Taking into account that the X_1X_20 system could be ancestral in spiders, Postiglioni & Brum-Zorrilla (1981) suggested that each sex chromosome would undergo independent mutations during the course of evolution; however, if one of the X chromosomes had suffered a recent non-disjunction, these last two elements would present similar behaviour during meiotic prophase I, and the X chromosome not involved in the event would conserve its individuality and would appear condensed in early stages.

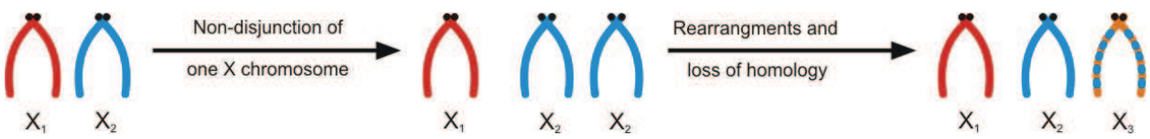

Fig. 13. Schematic representation of the origin of the $X_1X_2X_30$ SCS based on descriptions presented by Postiglioni & Brum-Zorrilla (1981).

Parida & Sharma (1986) observed that in some spider species with an $X_1X_2X_30$ SCS, two X chromosomes were small and one was large, suggesting that this system was derived from a small fragment of the X_1 or X_2 chromosome of an X_1X_20 system by deletion of most of its chromatin and a subsequent increase in length by duplications (Fig. 14).

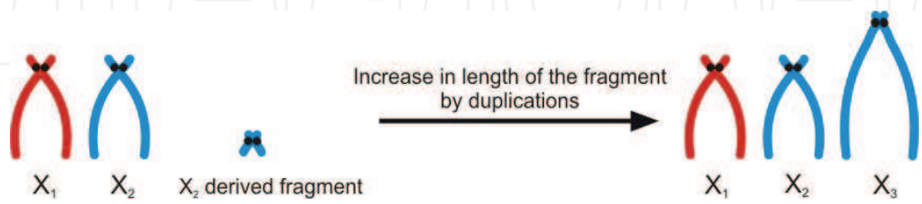

Fig. 14. Interpretive scheme of the origin of the $X_1X_2X_30$ SCS based on descriptions of Parida & Sharma (1986).

2.5 Origin of the $X_1X_2X_3X_40$ sex chromosome system

Data & Chatterjee (1983, 1988) were the first to record an $X_1X_2X_3X_40$ SCS in spiders. This SCS was found in *Metellina segmentata* (*Meta segmentata*) (Tetragnathidae) and *Bhutaniella*

sikkimensis (*Heteropoda sikkimensis*) (Sparassidae). In 1988, these researchers presented a proposal for the origin of the $X_1X_2X_3X_40$ system: duplication or non-disjunction of one X chromosome of the $X_1X_2X_30$ SCS, with subsequent loss of homology (Fig. 15). This proposition was similar to that formulated by Postiglioni & Brum-Zorrilla (1981) to explain the origin of the X_1X_20 and $X_1X_2X_30$ systems.

Fig. 15. Interpretive scheme of the origin of the $X_1X_2X_3X_40$ SCS based on descriptions of Datta & Chatterjee (1988).

In *Diplura* species, which employ an $X_1X_2X_3X_40$ system, Král et al. (2011) found that one heteropycnotic and one isopycnotic portion could be distinguished in the X_1 and X_2 chromosomes, most likely corresponding to the original X_1 and X_2 chromosomes and the original autosomes, respectively, indicating that the X_1 and X_2 sex chromosomes originated by sex chromosome/autosome translocation. Additionally, Král et al. (2011), suggested that this system probably originated by duplication of the X_1X_20 system via non-disjunctions or polyploidisation (Fig. 16) based on the chromomere pattern and size of the sex chromosomes observed in the $X_1X_2X_3X_40$ *Diplura*.

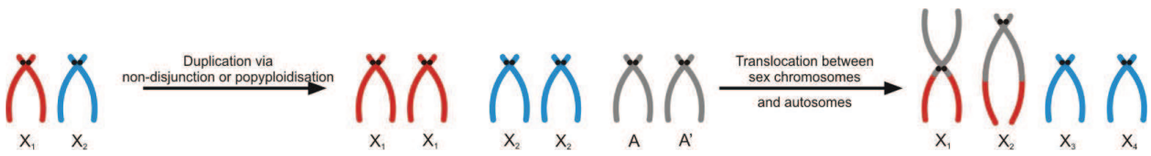

Fig. 16. Schematic representation of the origin of the $X_1X_2X_3X_40$ SCS based on the descriptions of Král et al. (2011).

2.6 Origin of the X0 sex chromosome system

Hackman (1948) found the supposed first case of a metacentric X chromosome in spiders in *Oxyopes ramosus* and noted that the X0 SCS verified in *Oxyopes* (metacentric), *Myrmarachne*, *Misumena*, and *Xysticus* (acrocentric) had most likely been derived from the X_1X_20 system in two ways:

1. The metacentric X of the X0 system could have been derived by centric fusion between X_1 and X_2 chromosomes (Fig. 17). This mechanism was also employed by several authors (Bole-Gowda, 1952; Suzuki, 1954; Postiglioni & Brum-Zorrilla, 1981; Řezáč et al., 2006; Král et al., 2011; Stávale et al. 2011) to explain the origin of the X0 SCS, which involves a metacentric X, in many spider groups.
2. The acrocentric X of the X0 system could have originated through gradual elimination of one X chromosome of the X_1X_20 SCS, as suggested by Suzuki (1952, 1954). This author put forth this proposition based on the fact that some thomisid species with an X_1X_20 system presented gradual differences between the lengths of X_1 and X_2 chromosomes (with both showing the same, slightly different or markedly different sizes). Furthermore, some species even exhibited an X0 system, suggesting that elimination of one X of the X_1X_20 system had taken place in the course of evolution (Fig. 18).

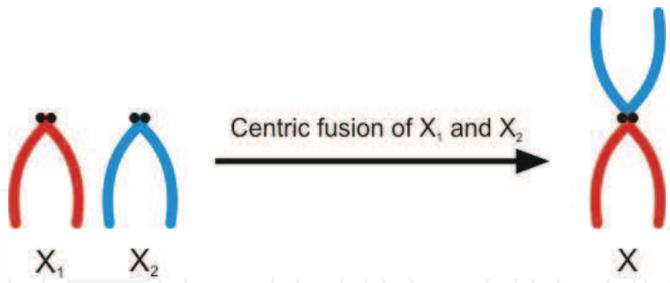

Fig. 17. Schematic representation of the origin of the X0 SCS based on descriptions presented by Hackman (1948).

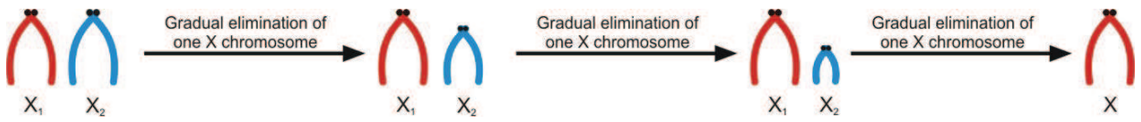

Fig. 18. Interpretive scheme of the origin of the X0 SCS based on descriptions of Hackman (1948).

Bole-Gowda (1950) proposed that the X0 system found in several spider species could have evolved by reciprocal translocation between the X_1 and X_2 chromosomes, preceded by distal fission in one sex chromosome and proximal fission in the other X, giving rise to a large acrocentric X chromosome, as found in *Oxyopes hindostanicus*; the centric fragment produced in this process was lost (Fig. 19).

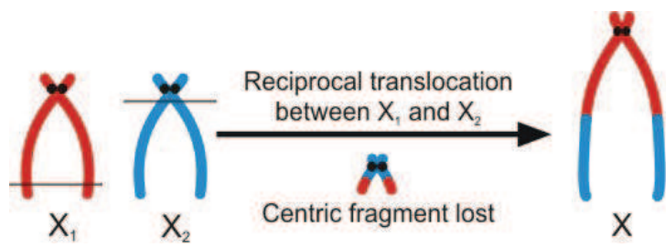

Fig. 19. Schematic representation of the origin of the X0 SCS based on descriptions presented by Bole-Gowda (1950).

Datta & Chatterjee (1989, 1992) proposed that the X0 system found in lycosid and uloborid spiders originated from the X_1X_20 SCS by centric fusion of the X_1 and X_2 chromosomes, followed by pericentric inversion (Fig. 20a) or partial deletion (Fig. 20b) in one of the X chromosome arms, giving rise to an acrocentric element. Alternatively, the acrocentric X chromosome could have originated from tandem fusion between the X_1 and X_2 chromosomes (Fig. 20c).

Tandem fusion was postulated as the mechanism involved in the derivation of the acrocentric X chromosome (X0 system) of *Zodarion* from the acrocentric X_1 and X_2 chromosomes (X_1X_20 system) present in species of the same genus (Pekár & Král, 2001). Pekár et al. (2005) proposed that two positive heteropycnotic bodies observed in the premeiotic interphase nuclei of two *Zodarion* species with the X0 SCS were segments of the X chromosome that corresponded to the original X_1 and X_2.

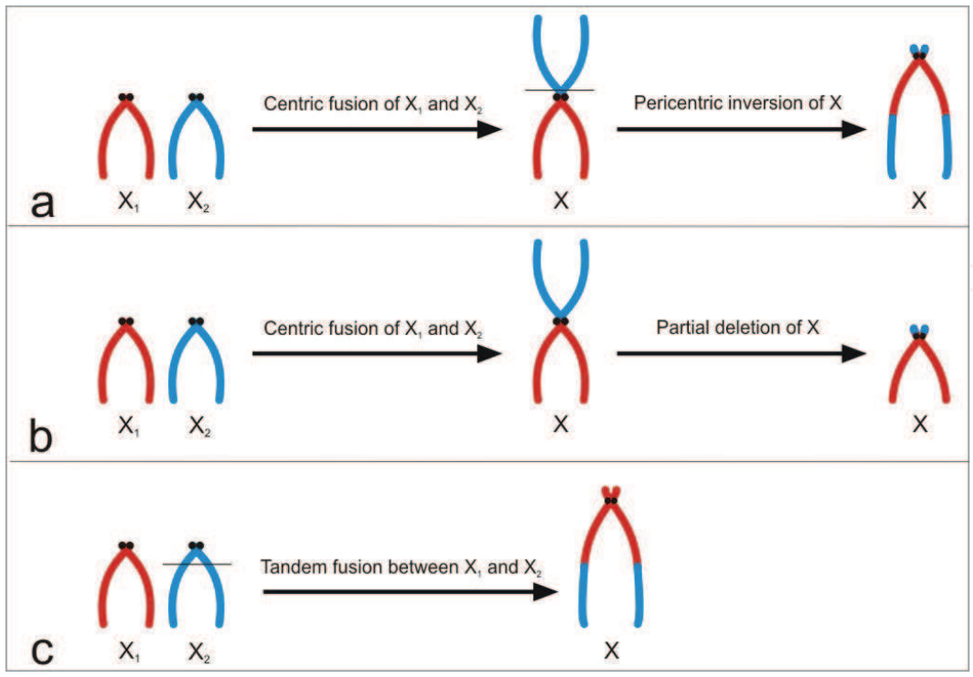

Fig. 20. Interpretive scheme of the origin of the X0 SCS based on descriptions of Datta & Chatterjee (1989, 1992).

According to Král et al. (2006), the XY SCS, which was originated from the X_1X_2Y system, gave rise to an X0 SCS through loss of the Y chromosome (Fig. 21). The SCS of the X0 type was found in many pholcids and Scytodes (Scytodidae).The evidence for this degeneration and complete elimination of the Y chromosome was the high level of constitutive heterochromatin detected in this chromosome in *Pholcus phalangioides*.

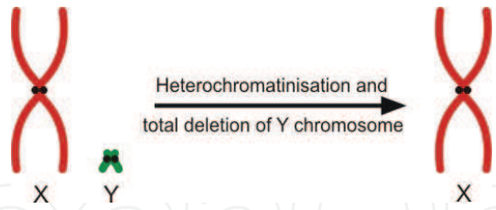

Fig. 21. Schematic representation of the origin of the X0 SCS based on descriptions of Král et al. (2006).

2.7 Origin of the XY sex chromosome system

Řezáč et al. (2006) described the first XY SCS in a spider of the genus *Atypus* (Mygalomorphae). According to these authors, this neo-XY system was formed from an X0 system, which was recorded in other species of this genus and involved rearrangements between the X chromosome and autosomes.

Král et al. (2006) studied the evolution of the chromosomes in several basal araneomorphs and formulated some hypotheses about SCS evolution. These authors discovered that SCS that include a Y chromosome are more common in spiders than previously believed, at least in basal araneomorphs. Several species with XY and X_1X_2Y SCS were described in many families,

and the authors highlighted the fact that in some species previously described as carriers of the X_1X_20 system, the tiny Y chromosome could have been neglected. Based on the diversity of SCS in basal araneomorphs, specifically in pholcids, Král et al. (2006) proposed that the X_1X_2Y SCS involving metacentric chromosomes in this group of spiders was similar to that found in Filistatidae and *Loxosceles* and was converted into an XY SCS. First, by pericentric inversion transforming one of the metacentric X chromosomes into a subtelo- or acrocentric form, the X_1X_2Y became similar to that described in *Pholcus phalangioides* (Pholcidae). Subsequently, the other X chromosome of the X_1X_2Y system was also pericentrically inverted, forming a hypothetical configuration in which both X chromosomes of the X_1X_2Y system exhibit acrocentric morphology. In the next step, centric fusion between the acrocentric X chromosomes of the hypothetical X_1X_2Y SCS occurred, generating an XY system, as found in *Smeringopus pallidus* (Pholcidae) and *Diguetia* (Diguetidae). In *Diguetia albolineata*, which exhibits an XY SCS, both arms of the metacentric Y chromosome paired with only one arm of the metacentric X during meiosis. In *Diguetia canities*, the metacentric X chromosome was supposedly pericentrically inverted, resulting an acrocentric element (Fig. 22).

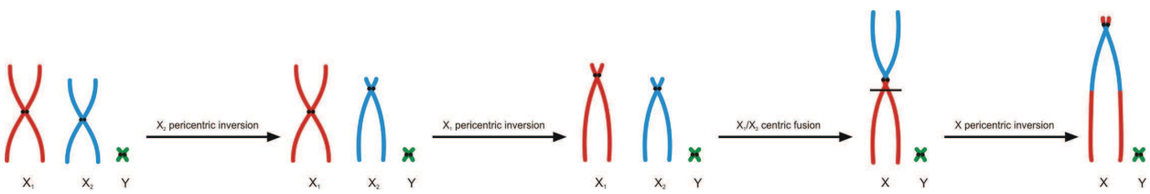

Fig. 22. Interpretive scheme of the origin of the XY SCS of Pholcidae and Diguetidae based on the descriptions of Král et al. (2006).

The proposed origin of the XY SCS observed in *Leptoneta* (Leptonetidae) was quite different. The XY system was believed to have originated from the X0 system, not from the X_1X_2Y system, in a mechanism involving translocation between the X and one autosome constituting the neo X chromosome; the homolog of the autosome involved in the rearrangement formed the Y chromosome (Fig. 23). This hypothesis put forth by Král et al. (2006) was based on the fact that the distal part of the X chromosome in *Leptoneta*, which has an XY SCS (probably corresponding to the translocated autosome), presented a different pattern of condensation during meiosis I. This last characteristic was not detected in the sex chromosomes of *Diguetia* species.

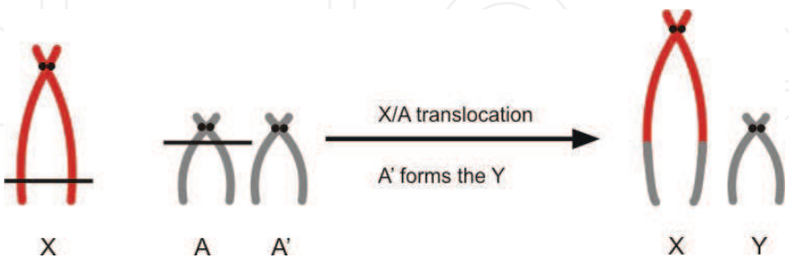

Fig. 23. Schematic representation of the origin of the XY SCS of Leptonetidae based on the descriptions of Král et al. (2006).

2.8 Origin of the X_1X_2Y sex chromosome system

Silva (1988) was the first to record an X_1X_2Y SCS in spiders. Although the author noted the possibility that the small acrocentric chromosome found in *Loxosceles laeta* was a

supernumerary chromosome, she concluded that this element could correspond to the Y chromosome of the X_1X_2Y SCS. A very general citation of many types of rearrangements that could be involved in the origin of the X_1X_2Y system was presented, though without explaining the sequence of steps involved in the evolution of this SCS in spiders. Subsequently, Silva et al. (2002) proposed that the X_1X_2Y system found in *Loxosceles* (Sicariidae) was derived from an X_1X_20 SCS through a mechanism involving translocations between X chromosomes and autosomes; however, they did not provide details associated with this process.

2.9 Origin of the $X_1X_2X_3Y$ sex chromosome system

Maddison (1982) described an SCS of the $X_1X_2X_3Y$ type in five species of Salticidae and, surprisingly, verified that in *Evarcha hoyi* (under *Pellenes hoyi*), some individuals presented the $X_1X_2X_3Y$ system, whereas others showed the X_1X_20 system.

According to Maddison (1982), during the process of arising from the X_1X_20 system, the X_1 chromosome of the $X_1X_2X_3Y$ system remained unaltered, while the X_2 chromosome became tandemly fused (or centrically fused followed by pericentric inversion) with an autosome that then constituted the distal portion of the neo X_2 long arm. The homolog of this autosome involved in the autosome/X_2 fusion became centrically fused with other autosome, forming the Y chromosome (short and long arms, respectively); the homolog of this last autosome (the Y long arm) became the X_3 chromosome without undergoing modifications (Fig. 24). This hypothesis was based on the difference in diploid number detected in salticid species (i.e., individuals with the X_1X_20 system had two additional autosomal pairs when compared with individuals with the $X_1X_2X_3Y$ system). These two autosomal pairs could be the pairs involved in fusions with the original X_1X_20 system. Furthermore, the meiotic features of the sex chromosomes, such as pycnosis, achiasmatic and chiasmatic pairing, and segregation, were considered to represent additional supporting evidence of this mode of origin of the $X_1X_2X_3Y$ SCS.

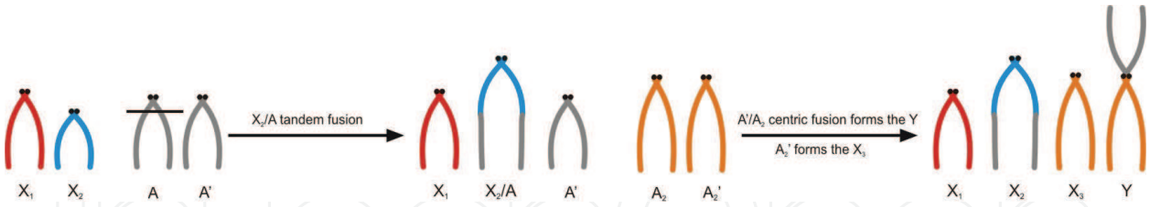

Fig. 24. Interpretive scheme of the origin of the $X_1X_2X_3Y$ SCS based on descriptions of Maddison (1982).

2.10 Origin of the $X_1X_2X_3X_4X_5Y$ sex chromosome system

The $X_1X_2X_3X_4X_5Y$ SCS verified in *Malthonica ferruginea* by Král (2007) formed a multivalent association in the pachytene stage, which was constituted by three univalents ($X_1X_2X_3$) and one trivalent (X_4X_5Y). In the trivalent, a synaptonemal complex was observed between the metacentric Y and the X_4X_5 chromosomes. Pairing between the univalents and the trivalent occurred end-to-end and involved only the X chromosomes. This mode of pairing was not visualised at the end of the diplotene stage. Observation of end-to-end pairing between the X chromosomes and a specific bivalent during meiosis of related species (Král, 2007), as well as in other spider groups (Benavente & Wettstein, 1977; Wise, 1983), compelled Král (2007) to hypothesise that the $X_1X_2X_3X_4X_5Y$ SCS originated from the $X_1X_2X_30$ system. First, the three

univalents ($X_1X_2X_3$) paired with a proto-X proto-Y bivalent or homomorphic sex chromosome pair (a bivalent that did not present morphological peculiarities but probably exhibited molecular differentiation into new sex chromosomes). Subsequently, the proto-Y chromosome underwent centric fusion with an autosomal element, forming a neo Y (metacentric) that maintained the pairing with the protoX (newly denominated X_4). The homolog of the autosome element involved in centric fusion with the protoY was designated the X_5 chromosome, which paired with its homologous arm in the neo Y (Fig. 25). According to Král (2007), these proto-X and proto-Y chromosomes probably represented ancestral chromosomes involved in the origin of the multiple X chromosomes by nondisjunction.

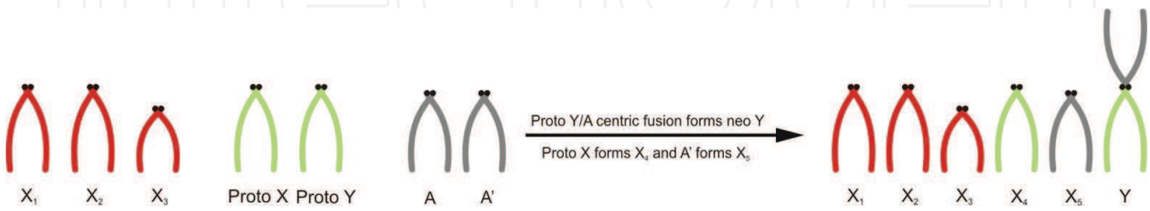

Fig. 25. Schematic representation of the origin of the $X_1X_2X_3X_4X_5Y$ SCS based on the descriptions of Král (2007).

2.11 Origin of multiple X_nY_n sex chromosome systems

Rowell (1985, 1988, 1990, 1991), Hancock & Rowell (1995), and Sharp & Rowell (2007) described a range of multiple X_nY_n SCS in populations of the social spider *Delena cancerides* (Sparassidae). Considering that some populations of this species presented an $X_1X_2X_30$ SCS, the authors provided an explanation for the origin of the multiple X and multiple Y chromosomes from the $X_1X_2X_30$ SCS, which is a system also found in other sparassid species. The first step in this process was centric fusion between two X chromosomes of the original $X_1X_2X_30$ SCS, giving rise to one metacentric X chromosome, while one X chromosome was unchanged. Subsequently, the telocentric X underwent centric fusion with one telocentric autosome, and the homolog of this autosome became part of the SCS. Subsequently, a series of centric fusions between the newly formed sex chromosome and telocentric autosomes gave rise to populations with $X_1X_2X_3Y$, $X_1X_2X_3X_4Y_1Y_2$ (Fig. 26), and multiple X and Y chromosome systems. In all of these populations, the metacentric X formed by the fusion of two original X chromosomes was a univalent, and the neoX and neoY chromosomes, which had originated through centric fusions between autosomes, formed chromosomal chains with different numbers of elements involved (from 3 to 19 elements) during meiosis.

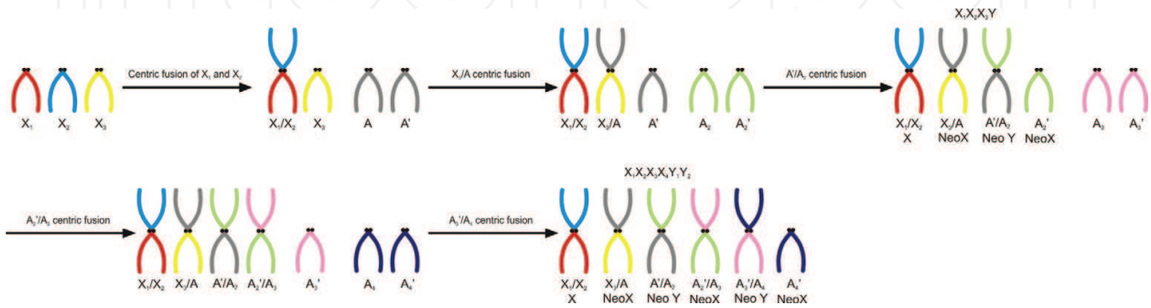

Fig. 26. Interpretive scheme of the origin of the X_nY_n SCS based on descriptions of Rowell (1985, 1988, 1990, 1991), Hancock & Rowell (1995), and Sharp & Rowell (2007).

3. Conclusion

Despite the fact that spider meiosis analyses have been carried out for more than 100 years, relatively little has been learned about sex chromosome origin and evolution in this group. The vast majority of studies on this topic have been based solely on assumptions or on basic chromosomal characteristics (chromosome length, number, meiotic condensation, and meiotic segregation). Recent advances in spider cytogenetics, such as ultrastructural analysis of cells during meiosis and examination of female meiosis, have added new insights into SCS evolution. However, only 665 (~1.6%) of the 42,423 known spider species (110 families) have been chromosomally characterised. Fifty-four families have not been studied cytogenetically, resulting in several gaps in the existing hypotheses on sex chromosome evolution.

To provide a broader knowledge base leading to better inferences regarding the origin and evolution of sex chromosomes, further efforts involving spider meiosis analysis should include a broader range of species and use conventional, ultrastructural (synaptonemal complex), and molecular (rDNA and telomere FISH and chromosome painting) cytogenetic techniques.

4. Acknowledgments

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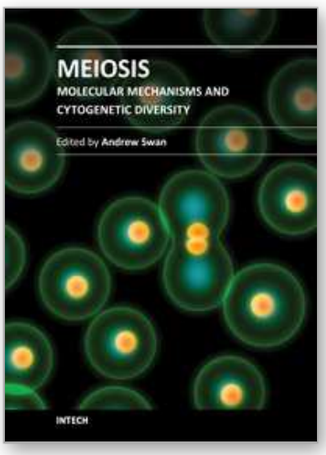

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Meiosis, the process of forming gametes in preparation for sexual reproduction, has long been a focus of intense study. Meiosis has been studied at the cytological, genetic, molecular and cellular levels. Studies in model systems have revealed common underlying mechanisms while in parallel, studies in diverse organisms have revealed the incredible variation in meiotic mechanisms. This book brings together many of the diverse strands of investigation into this fascinating and challenging field of biology.

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