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Chromosomes and sex determination in 13 araneid spiders of North-Eastern India

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Abstract

The diploid chromosome number of 13 species belonging to the family Araneidae (Araneae) ranges between 16 and 25. The ♂ sex-determining mechanism seems to be $X_1X_2X_3X_4O$ in one species; $X_1X_2X_3O$ in three species and X_1X_2O in the remaining 9 species. The $X_1X_2X_3X_4O$, ♂ sex-determining mechanism is reported for the first time in spiders. All the chromosomes are with terminal centromeres. C-band preparations in 5 species suggest procentric localization of constitutive heterochromatin in all the chromosomes, though distally located C-band positive blocks are also visible in a few chromosomes.

It is suggested that chromosomal evolution in this family has taken place by gradual reduction in diploid number through tandem/centric fusion followed by pericentric inversion in autosomes and nondisjunction/duplication of one X, with subsequent loss of homology in sex chromosomes.

Introduction

The spiders are world wide in distribution. Review of literature reveals that though there exist about 30000 described spider species, only 330 species have been chromosomally studied which include about 45 species belonging to the largest spider family Araneidae (Berry, 1906; Hackman, 1948; Patau, 1948; Suzuki, 1951, 1954; Bole-Gowda, 1953, 1958; Sharma *et al.*, 1959, 1960; Mittal, 1960, 1961, 1966; Sokolov, 1960; Diaz & Saez, 1966; and Matsumoto, 1977).

We have undertaken in our laboratory a cytogenetic survey of the spider fauna of North-Eastern India and the present communication incorporates the diploid number, chromosome morphology and sex-determining mechanism of 13 species of araneid spiders and probable karyotypic inter-relationship amongst the members of the cytogenetically known spider species belonging to the family Araneidae.

Materials and methods

The materials for the present study were collected from different parts of North-Eastern India, viz. Dibrugarh (94°55′E, 27°23′N), Gingia Tea Garden (93°55′E, 26°50′N), Tezpur (92°56′E, 26°40′N), Gauhati (91°40′E, 26°10′N), Shillong (91°53′E, 25°34′N) and Jowai (92°8′E, 25°20′N). The number of individuals collected with time and locality of collections are given in Table 1.

The gonads were fixed in a freshly prepared 1:3 (by volume) mixture of glacial acetic acid and ethanol and the squashed preparations were stained either in Heidenhain's Haematoxylin or in Giemsa. C-band preparations were made following Sumner (1972) with suitable modifications.

The spiders were identified by Dr. B. Tikader and Dr. B. Biswas of the Zoological Survey of India and the voucher specimens have been submitted to the museum of the Department of Zoology, North-Eastern Hill University, India.

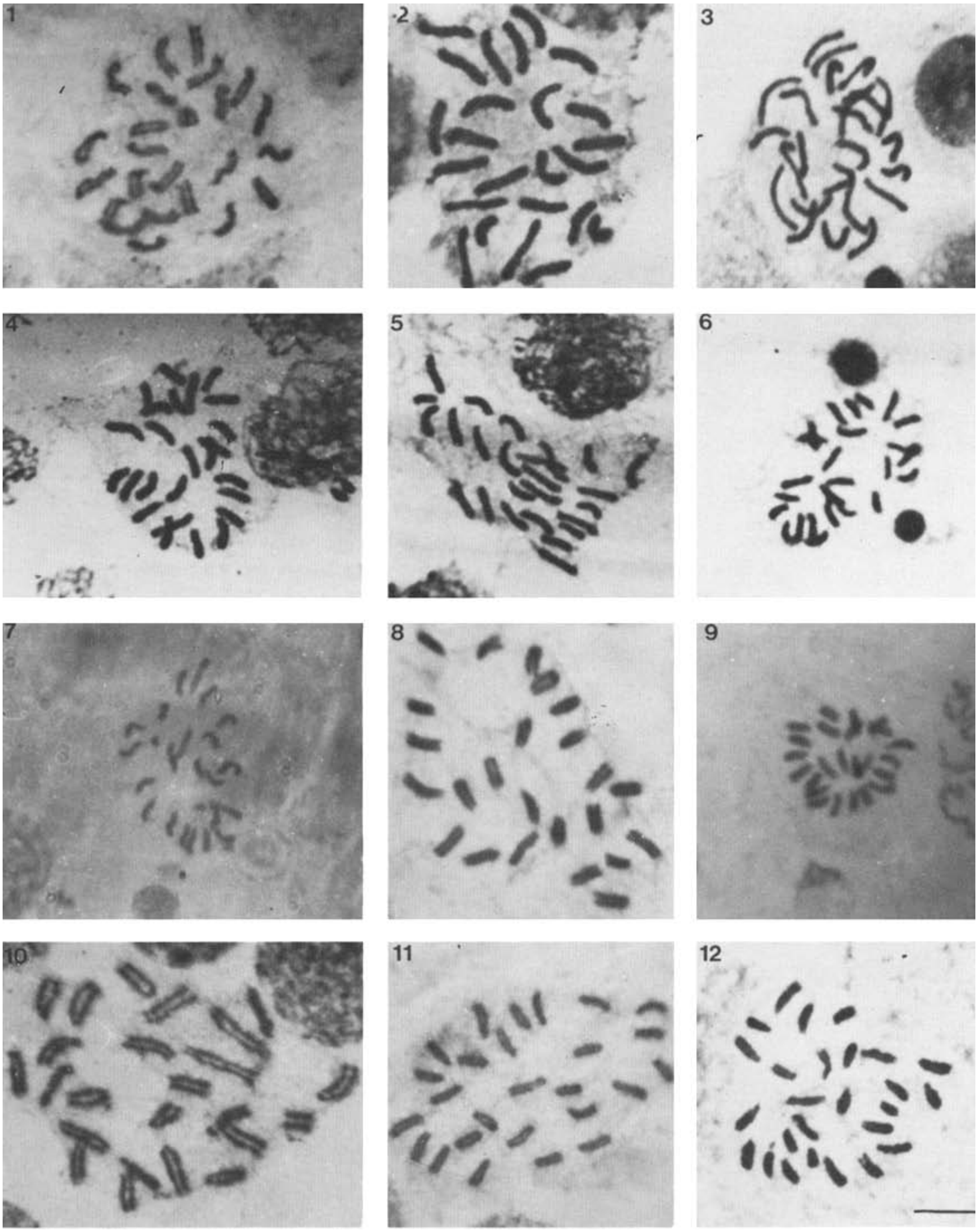
Table 1. Name, sex, numbers of individuals studied, chromosome number, sex-determining mechanisms, month and locality of collection of 13 studied araneid species.

Species	Sex	Nos. of individuals studied	2n	n	Sex determination	Month of collection	Locality
Argiope shillongensis Sinha	♂	20	24	11, 13	X_1X_2O	Jan ’80	Tezpur
						Feb ’81	Gingia Tea Garden, Tezpur
Argiope shillongensis Sinha	♀	5	26	-	$X_1X_1X_2X_2$	Nov. ’81	Dibrugarh
						Dec ’81	Shillong
Cyrtophora citricola (Forskal)	♀	9	26	-	$X_1X_1X_2X_2$	Feb ’81	Tezpur
Cyclosa bifida (Dol.)	♂	15	24	11, 13	X_1X_2O	May, June ’79, ’80, ’81	Shillong
C. spirifera (Simon)	♂	15	24	11, 13	X_1X_2O	Mar, Apr ’79, ’80	Shillong Gauhati
Gasteracantha hasseltii Koch	♂	4	16	7, 9	X_1X_2O	Jan ’81	Dibrugarh
						Feb ’82, ’83	Tezpur
Gasteracantha hasseltii Koch	♀	3	18	-	$X_1X_1X_2X_2$	Sep ’80, ’81	Shillong
G. leucomelaena (Dol.)	♂	6	16	7, 9	X_1X_2O	Feb ‘81, ’83	Tezpur
G. leucomelaena (Dol.)	♀	5	18	-	$X_1X_1X_2X_2$	Jan ’81	Dibrugarh
						Sep ’80, ’81	Shillong
Leucauge celebesiana (Walckenaer)	♂	15	25	11, 14	$X_1X_2X_3O$	Aug. Sep, Oct ’79, ’80, ’81	Shillong
						Mar ’80	Jowai
						Jan ’81	Tezpur
L. decorata (Blackwall)	♂	8	25	11, 14	$X_1X_2X_3O$	Sep, Oct ’80, ’81	Shillong
L. tessellata (Thorell)	♂	12	25	11, 14	$X_1X_2X_3O$	Aug ’80	Shillong
Meta segmentata (Clerck)	♂	3	24	10, 14	$X_1X_2X_3X_4O$	Jan ’81	Shillong
Neoscona achine (Simon)	♂	20	24	11, 13	$X_1X_2X_3O$	Apr, May ’81	Shillong
N. poonaensis Tikader & Bal	♂	5	24	11, 13	X_1X_2O	Feb ’81, ’82	Tezpur
Nephila clavata Koch	♂	17	24	11, 13	X_1X_2O	Aug, Sep ’80, ’81	Shillong

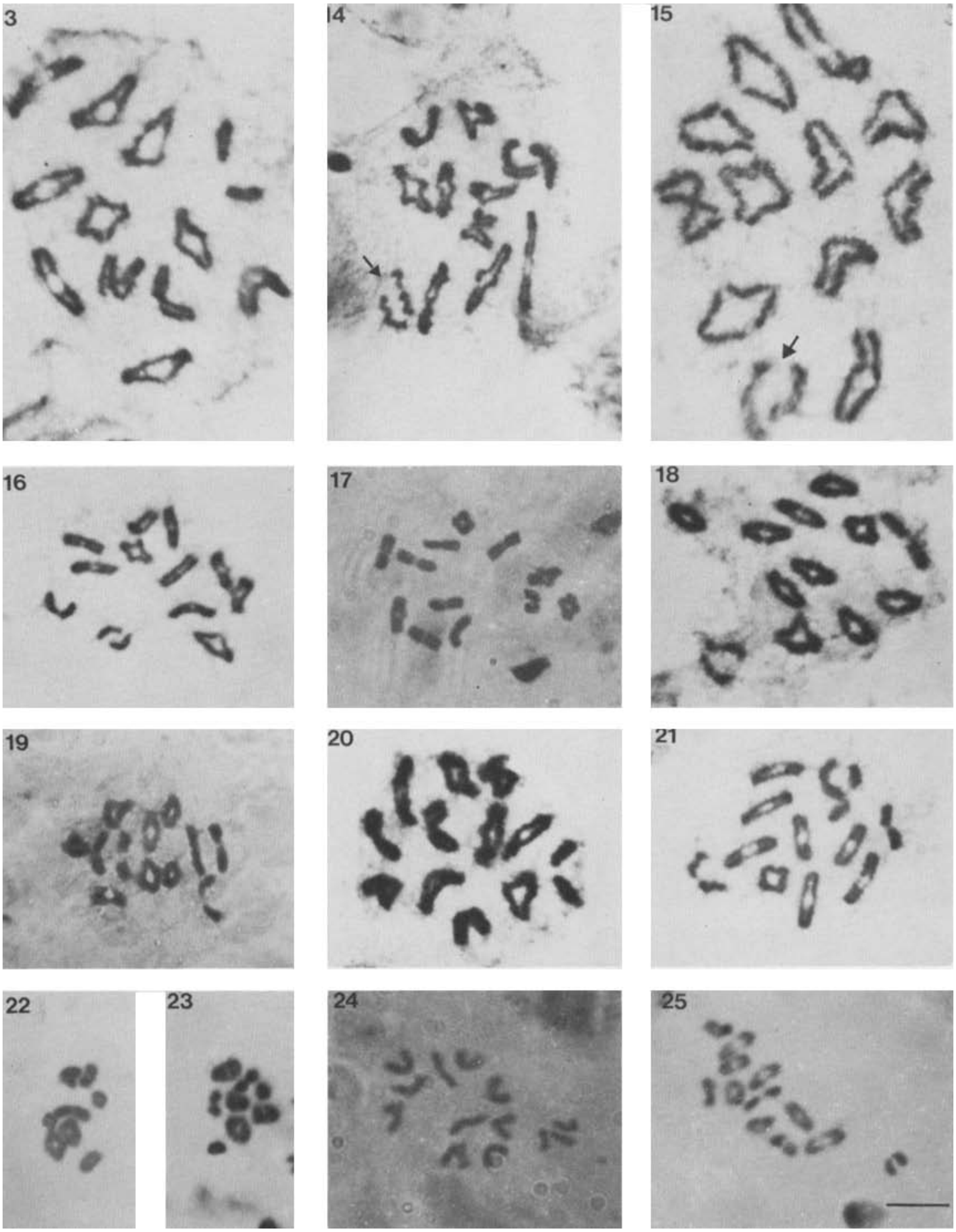
Results

The chromosome number and sex-determining mechanism have been briefly outlined in Table 1. The spermatogonial metaphase count from many well-spread nuclei discerns the diploid number as 16 in two species of the genus *Gasteracantha*, 25 in the three species of the genus *Leucauge* and 24 in the rest (Figs. 1–10). The oogonial metaphase count reveals the female diploid complement to be 18 in the two species of the genus *Gasteracantha* and 26 in *A. shillongensis* and *C. citricola* (Figs. 11 and 12). The chromosomes in the gonial stages appear to be small and rod-shaped, with terminally located centromeres as revealed by C-banding. None of the species offers any appreciable size variations except for the presence of two very small chromosomes in *M. segmentata*. Secondary constrictions are readily visible in a pair of chromosomes of *C. bifida* (Fig. 2). Most of the species show a single procentric C-band (Figs. 36–39) in all the chromosomes. In a few species an additional C-band was found at the distal end of some chromosomes. There are two such chromosomes in *A. shillongensis* and *C. spirifera* (Figs. 36 and 37). *N. achine*, *N. poonaensis* and *N. clavata* have three, four and five chromosomes, respectively, showing a distally located C-band (Figs. 38 and 39) in addition to the procentric one. No species was found to possess an intercalary C-band.

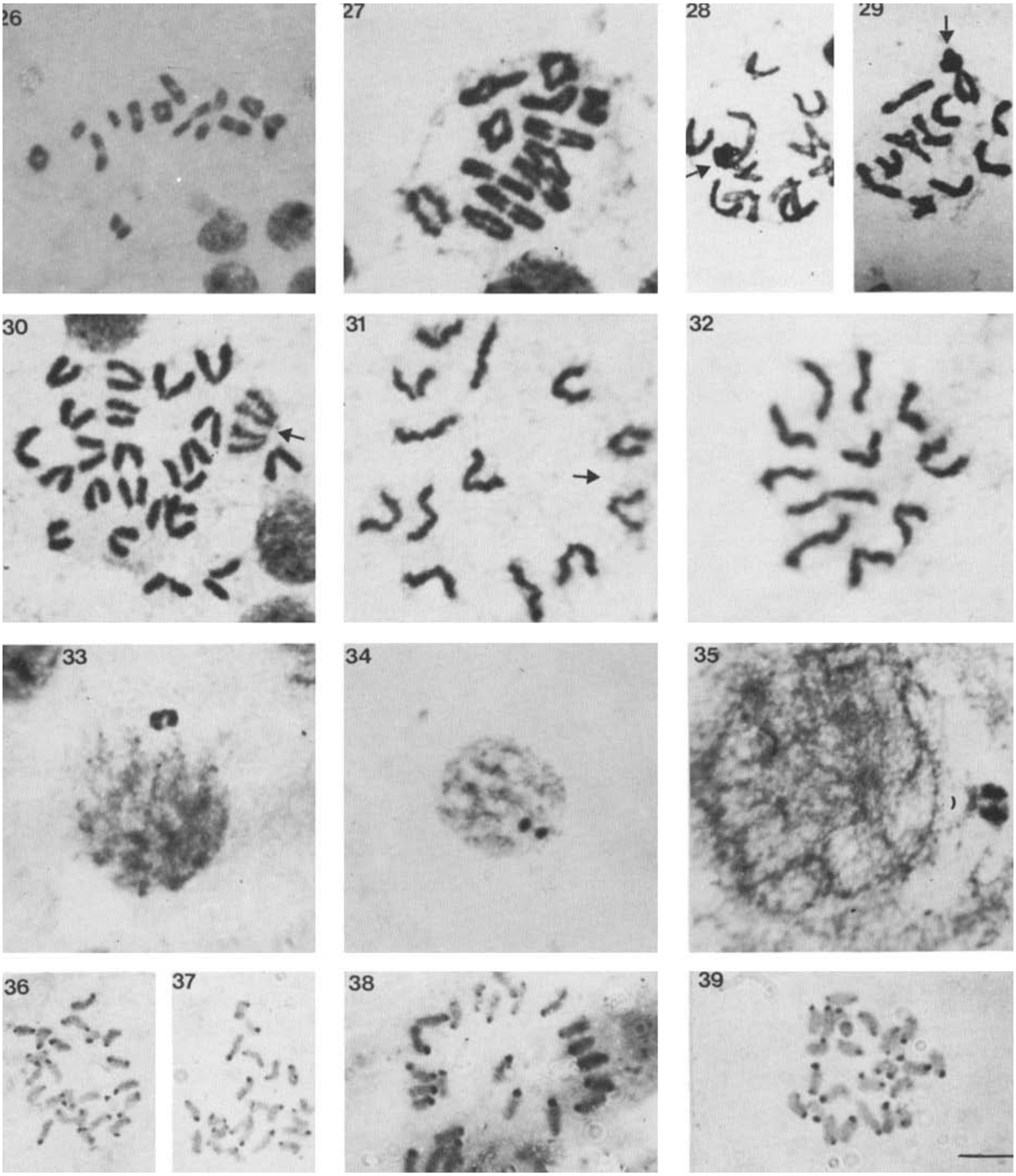
The premeiotic interphase nuclei reveal highly condensed heteropycnotic elements (Figs. 33–35), the number of which usually corresponds to the number of univalent sex chromosomes during diplotene, diakinesis and metaphase 1 (Figs. 13–27). However, it may be stated that the diplotene nuclei of all the *Leucauge* species show a mass of positively



Figs. 1–12. Spermatogonial (1–10) and oogonial (11–12) metaphases: (1, 11) *Argiope shillongensis*; - (2) *Cyclosa bifida*; - (3) *C. spirifera*; - (4) *Leucauge celebesiana*; - (5) *L. decorata*; - (6) *L. tessellata*; - (7) *Meta segmentata*; - (8) *Neoscona achine*; - (9) *N. poonaensis*; - (10) *Nephila clavata*; - (12) *Cyrtophora citricola*. Bar. 10 μm.



Figs. 13–25. Diplotene (13–15), Diakinesis (16–18) and Metaphase I (19–25): (13, 20) *Cyclosa bifida*; - (14, 21) *C. spirifera*; - (15, 18) *Nephila clavata*; - (16, 25) *Neoscona achine*; - (17) *N. poonaensis*; - (19) *Argiope shillongensis*; (22) *Gasteracantha hasseltii*; - (23) *G. leucomelaena*; - (24) *Meta segmentata*. Arrows, despiralized X_1 and X_2. Bar, 10 μm.



Figs. 26–39. Spermatogonial metaphases (C-banding) (36–39), premeiotic interphase (33–35), early (28) and late diplotene (29), metaphase I (26–27), early anaphase I (30) and metaphase II (31, with 13 elements, and 32, with 11 elements): (26, 39) *Neoscona poonaensis*; - (27, 30, 31, 32, 35) *N. clavata*; - (28) *Leucauge celebesiana*; - (29) *L. tessellata*; (33, 37) *Cyclosa spirifera*; - (34, 38) *N. achine*; - (36) *Argiope shillongensis*. Bar, 10 μm. Arrows, heteropycnotic X chromosomes or bodies formed by them.

heteropycnotic bodies (Figs. 28 and 29) which take individual forms during diakinesis. During metaphase I the sex chromosomes in all the species do not differ in staining affinity from that of the autosomal bivalents. The sex chromosomes are usually not identifiable in anaphase I or metaphase II by pycnosis. However, in *N. clavata* two chromosomes in anaphase I and metaphase II exhibit negative heteropycnosis (Figs. 30 and 31). Since these two chromosomes are lacking in the opposite group at anaphase I or in those metaphase II nuclei which have two chromosomes less than the other type, they can be designated as sex chromosomes. It may be stated that in *C. spirifera* and *N. clavata* the sex chromosomes appear to be in a comparatively despiralised state (Figs. 14 and 15). As stated earlier, it has not been possible to characterise the X chromosome with any special C-band.

The univalents during diplotene, diakinesis and metaphase I and the occurrence of two different types of metaphase II plates in the males account for the existence of three types of sex determination systems, viz. $X_1X_2X_3O$ - $X_1X_1X_2X_2X_3X_3$ in the three species of the genus *Leucauge*; $X_1X_2X_3X_4O$ - $X_1X_1X_2X_2X_3X_3X_4X_4$ in *M. segmentata*; and X_1X_2O - $X_1X_1X_2X_2$ in the rest.

Discussion

The family Araneidae is also known as Epeiridae (Bole-Gowda, 1953, 1958) or Argiopidae (= Argyopidae) (Pocock, 1900; Dyal, 1935; Comstock, 1948; Suzuki, 1951, 1954; Sokolov, 1960). However, Rower (1942), Mittal (1960, 1961, 1966) and Tikader (1982) used the term Araneidae for this family. The genus *Leucauge* has been included in this family following Tikader (1982), though Suzuki (1954), Bole-Gowda (1958) and Sharma *et al.* (1959) included this genus in the family Tetragnathidae.

Chromosomal information on the family Araneidae is available for about 55 species only, including the 13 species presently studied (Tables 1 and 2). The 2n number in this family ranges from 14 to 46. The family's modal number may be regarded as 13 ($11A + X_1X_2$; $2n = 24$) as shown by 45 species out of the 55 studied. All the chromosomes are with terminal centromeres. However, only two species, viz. *A. dumetorum* (Hackman, 1948) and *A. scylla* (Suzuki, 1954), have 10 biarmed autosomes with a diploid number of 14. This reduction in 2n in these two species may be interpreted as the result of centric fusion involving 10 pairs of autosomes from the species with the modal number since they maintain an equity in the number of arms (24).

The prevalent sex determination system in males seems to be of the X_1X_2O type. It is also interesting to note that a decrease in the diploid chromosome number does not affect the balance between X_1X_2 and the autosomes, as shown in *A. ventricosus* ($2n = 46$) and *A. scylla* ($2n = 14$). A single species, viz. *A. sericata* (Berry, 1906), has been reported to be of the XO type (Table 2). The present study has also revealed the presence of $X_1X_2X_3O$ (in 3 species) and $X_1X_2X_3X_4O$ (in 1 species), in addition to the X_1X_2O system. Bole-Gowda (1958) reported the sex-determining mechanism of *L. decorata* to be X_1X_2O. However, Sharma *et. al.* (1959) reported the sex-determining mechanism of this species as of the $X_1X_2X_3O$ type, which corresponds with the present study. The X_1X_2O system is predominant in most of the families of spiders and is presumed to have given rise to the XO and $X_1X_2X_3O$ systems. The former might have originated by tandem or centric fusion of the two Xs, followed by pericentric inversion.

Though it may be presumed that in the $X_1X_2X_3O$ system, the third X originated either from X_1 or X_2, its exact mode of origin is not clear. According to Suzuki (1954), while one of the three Xs in $X_1X_2X_3$ spiders may represent one of the Xs in the X_1X_2 species, the other X originated from the remaining one by a complicated process of misdivisions of the centromere, followed by inversion, resulting in a dicentric X chromosome that subsequently underwent breakage, forming two X chromosomes. It may be inferred from this hypothesis that in an $X_1X_2X_3O$ male spider one of the Xs will always be of a larger size than the other two. However, on the other hand, a large number of spider species with the two Xs of approximately equal size, accompanied by a comparatively smaller X, have been observed. This probably prompted White (1973, p. 671) to advocate the origin of X_3 from a small supplementary fragment derived from X_1 or X_2 by deletion. However, he

Table 2. Chromosome number and sex-determining mechanism of 45 species belonging to the family Araneidae (excluding the presently studied species).

Species	Sex	2n	n	Sex determination	References
Acusilas coccineus	♂	24	11, 13	X_1X_2O	Matsumoto, 1977
Acusilas coccineus	♀	26	-	-	Matsumoto, 1977
Aranea angulata	♂	-	11, 13	X_1X_2O	Hackman, 1948
A. cucurbitina	♂	-	11, 13	X_1X_2O	Hackman, 1948
A. diademata (*Araneus diadema*)	♂	-	11, 13	X_1X_2O	Hackman, 1948
A. diademata (*Araneus diadema*)	♀	-	13	-	Hackman, 1948
A. diademata (*Araneus diadema*)	♂	-	11, 13	X_1X_2O	Sokolov, 1960
A. diademata (*Araneus diadema*)	♂	24	11,13	X_1X_2O	Mittal, 1960, 1966
A dumetorum	♂	14	6, 8	X_1X_2O	Hackman, 1948
A. dumetorum	♀	-	8?	-	Hackman, 1948
A feae	♂	24	11, 13	X_1X_2O	Bole-Gowda, 1953, 1958
A. foliata	♂	24	11, 13	X_1X_2O	Hackman, 1948
A. fuscocoloratus	♂	-	11, 13	X_1X_2O	Suzuki, 1954
A. japonicus	♂	-	11, 13	X_1X_2O	Suzuki, 1951
A. mitificus	♂	-	11, 13	X_1X_2O	Suzuki, 1951
A. opima	♂	24	11, 13	X_1X_2O	Suzuki, 1951
A. reaumuri	♂	24	11, 13	X_1X_2O	Patau, 1948
A. reaumuri	♀	26	13	-	Patau, 1948
A. saganus	♀	26	-	-	Suzuki, 1954
A. scylla	♂	14	6, 8	X_1X_2O	Suzuki, 1951
A. sericata (= *Epeira sclopetaria*)	♂	23	11, 12 (probably)	XO	Berry, 1906
A. sexpunctata	♂	-	11, 13	X_1X_2O	Hackman, 1948
A. ventricosus	♂	46	22, 24	X_1X_2O	Suzuki, 1951
A. sp.	♂	24	11, 13	X_1X_2O	Suzuki, 1951
Araneus pavidus	♂	24	11, 13	X_1X_2O	Mittal, 1960
A. umbratica	♂	24	11, 13	X_1X_2O	Mittal, 1960, 1966
A. sp.	♂	24	11, 13	X_1X_2O	Mittal, 1960
Argiope amoena	♂	24	11, 13	X_1X_2O	Suzuki, 1951
A. pulchella	♂	-	11, 13	X_1X_2O	Bole-Gowda, 1958
Cyclosa atrata	♂	-	11, 13	X_1X_2O	Suzuki, 1951
C. confraga	♂	24	11, 13	X_1X_2O	Mittal, 1960, 1966
C. conica	♂	24	11, 13	X_1X_2O	Mittal, 1960, 1966
C. octotuberculata	♂	24	11, 13	X_1X_2O	Suzuki, 1951
C. octotuberculata	♀	26	-	-	Suzuki, 1951
C. sedeculata	♂	-	11, 13	X_1X_2O	Suzuki, 1954
C. walckenaerii	♂	24	11, 13	X_1X_2O	Mittal, 1960, 1966
C. sp.	♂	24	11, 13	X_1X_2O	Mittal, 1960
Cyrtophora citricola	♂	24	11, 13	X_1X_2O	Mittal, 1960, 1966
Eustela sp.	♂	24	11, 13	X_1X_2O	Mittal, 1961
Larinia directa	♂	24	11, 13	X_1X_2O	Mittal, 1960, 1966
L. punctifera	♂	24	11, 13	X_1X_2O	Suzuki, 1954
L. sp.	♂	24	11, 13	X_1X_2O	Sharma *et al.*, 1960
L. sp.	♂	24	11, 13	X_1X_2O	Mittal, 1960, 1966
Leucauge blanda	♂	24	11, 13	X_1X_2O	Suzuki, 1954
L. decorata	♂	24	11, 13	X_1X_2O	Bole-Gowda, 1958
L. decorata	♂	25	11, 14	$X_1X_2X_3O$	Sharma *et al.*, 1959
Meta reticulata	♂	-	11, 13	X_1X_2O	Hackman, 1948
M. segmentata ssp. *mengei*	♂	-	11, 13	X_1X_2O	Sokolov, 1960
M. yunohamensis	♂	24	11, 13	X_1X_2O	Suzuki, 1954
Metepeira lathyrina	♂	24	11, 13	X_1X_2O	Diaz & Saez, 1966
Neoscona arabesca	♂	24	11, 13	X_1X_2O	Mittal, 1960
Nephila clavata	♂	-	11, 13	X_1X_2O	Suzuki, 1951
Zilla stroemi	♂	-	11, 13	X_1X_2O	Hackman, 1948

did not explain the mode of acquisition of the centromere by this fragment. In the absence of sufficient information including data on chromosome measurement, we are inclined to accept the view put forward by Postiglioni and Brum-Zorrilla (1981) that the X_3 originated either by duplication or nondisjunction of one X with subsequent loss of homology. The X_4 of the $X_1X_2X_3X_4O$ system, encountered for the first time during the course of the present investigation, probably originated in a similar way.

Suzuki (1954) classified the spiders into three types according to chromosome numbers. Spiders with extremely high chromosome numbers have been regarded as primitive, while those with chromosome numbers between 18 to 24 comprise the intermediate type; and the modern type includes those with less than 15 chromosomes. Thus, there seems to be a general trend in reduction of chromosome number in spiders and it is highly significant that in only a few species the karyotype has some or all the chromosomes metacentric. According to White (1973), a major barrier for the establishment of centric fusions (and thus metacentric chromosomes) exists in the spiders due to strong proximal chiasma localization in the male leading to improper disjunction in interchange heterozygotes. He therefore presumes that centric fusions led to the formation of metacentrics, which were later converted to acrocentrics by pericentric inversions. He holds this mode to be more plausible than tandem fusions of the chromosomes as suggested by Suzuki (1954). However, interstitial and terminal localization of chiasmata has been observed in a large number of spider species (Brum-Zorrilla & Cazenave, 1974; Maddison, 1982), including the presently studied araneids. Tandem fusion of two autosomes will result in a large single-armed chromosome and a minute element containing a centromere flanked on either side by very small chromatin materials. The latter will be inert and subsequently lost. With the limited data on chromosome measurements, we prefer at present to consider fusions (*i.e.* tandem and centric fusion), followed by pericentric inversion to be the favoured pathways in karyotypic evolution in spiders.

Thus, *A. ventricosus* representing 2n = 46 (Suzuki, 1954) (Table 2) may be considered as the most primitive within the cytogenetically known araneids.

It may be argued that the family's modal number 13 (11A + X_1X_2; 2n = 24) has originated from species with a diploid number of 46 by tandem/centric fusion of 22 pairs of autosomes followed by pericentric inversion. Other araneids with different karyotypes may have evolved in a similar way from those with diploid number of 24. The probable hypothetical karyotypic interrelationship amongst the 55 studied species of the family Araneidae is given in Figure 40, which indicates occurrence of distinct karyotypic orthoselection in this family.

Heteropycnosis of sex chromosomes in meiosis and normal behaviour in mitosis indicate their facultative heterochromatinised nature, a fact substantiated by the failure of the C-banding technique to impart any distinctive characteristic feature to them.

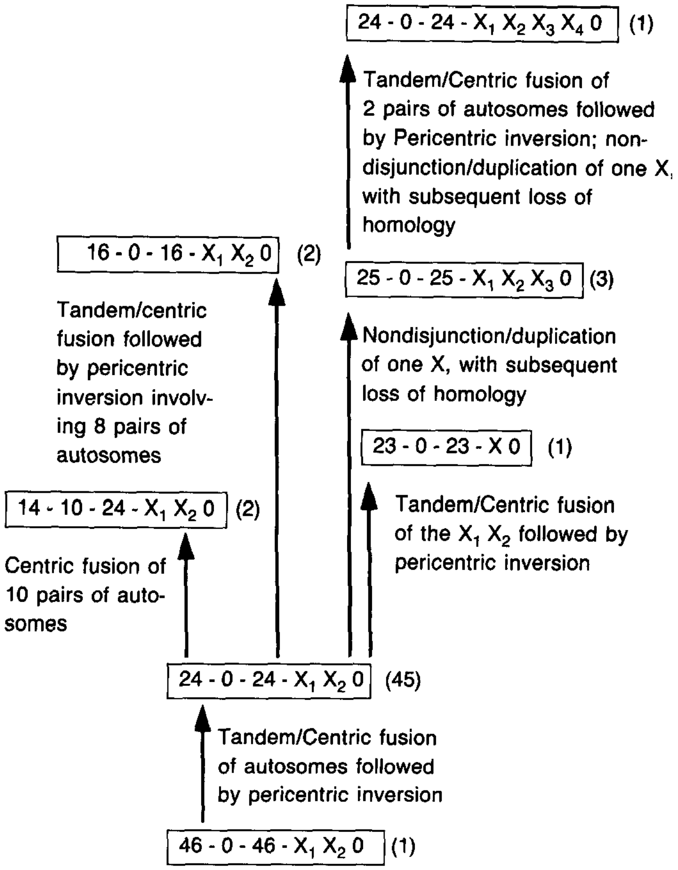


Fig. 40. Hypothetic karyotypic relationships among the members of the family Araneidae. Each box contains: male diploid chromosome number, number of biarmed chromosomes, FN, sex determining mechanism. In parentheses outside box, number of species cytologically known.

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