

Cytological Studies in Spiders
II. Chromosomal Investigation in the Twenty Two
Species of Spiders Belonging to the Four Families,
Clubionidae, Sparassidae, Thomisidae and
Oxyopidae, which Constitute Clubionoidea,
with Special Reference to
Sex Chromosomes

By
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(With 2 Tables and 21 Figures)

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* A part of the expence of this study has been defrayed by the Scientific Research Expenditure of the Department of Education.

INTRODUCTION

The aim of the study of this series and the general aspects of the chromosome investigation were fully given in the previous paper (SUZUKI 1951). In the present description the chromosomes of twenty two Japanese species of spiders belonging to the four families, Clubionidae, Sparassidae, Thomisidae and Oxyopidae, which constitute Clubionoidea, will be dealt with.

As is well known the X_1X_2O type of sex determination is characteristic for a large majority of the modern spiders belonging to many different families, but some different types such as XO and $X_1X_2X_3O$ type have been found recently in several limited families (REVELL 1947, HACKMAN 1948, SUZUKI 1950a, SUZUKI and OKADA 1950, GOWDA 1950). Such sex determining mechanisms, particularly XO mechanism, have never been so completely investigated as to make clear how widely both types occur in spiders. Studying such aberrations seems to be very useful for interpreting the evolution of sex chromosomes. In respect to this point, the above described Sparassidae, Thomisidae and Oxyopidae deserve careful study, for in these families a large number of aberrations are expected to occur. Thus in the following pages special attention will be paid for the analysis of the morphological feature and behaviour of sex chromosomes.

MATERIAL AND METHODS

The material used in the present study is twenty two Japanese species of spiders belonging to the four families, Clubionidae, Sparassidae, Thomisidae and Oxyopidae, which constitute the Clubionoidea Group of the suborder Arachnomorphae (=Araneomorphae) in the BRISTOWE's arrangement of spiders' families. All the material is shown in the Table I. The

TABLE I. MATERIAL

Species	Sex	Number of individ.	Stage	Month	Locality
Fam. Clubionidae					
Subfam. Clubioninae					
<i>Chiracanthium japonicum</i> EÖS. & STR.	♂	3	juv.	Apr.	Mitaki
" "	♂	5	subad.	"	"
" "	♂	8	"	May	Mitaki, Fukuoji
" "	♂	2	ad.	"	Mitaki
" "	♂	4	ad.	June	"
" <i>kompiricola</i> DÖN. & STR.	♂	8	subad.	May	Mitaki, Fukuoji
" "	♂	2	ad.	"	Mitaki
" "	♂	3	"	June	"
" <i>unicum</i> EÖS. & STR.	♂	4	subad.	May	Iwakuni
<i>Clubiona japonicola</i> EÖS. & STR.	♂	3	subad.	Apr.	Mitaki

<i>Clubiona japonicola</i> EÖS. & STR.	♂	5	subad.	May	Mitaki
"	♂	3	subad. & ad.	June	"
"	♂	1	subad.	Sept.	"
"	♂	3	subad. & ad.	Oct.	"
" <i>lera</i> EÖS. & STR.	♂	1	subad.	Mar.	"
"	♂	2	subad. & ad.	May	Iwakuni, Fukuoji
Subfam. Micariinae					
<i>Micaria unifascigera</i> EÖS. & STR.	♂	3	subad. & ad.	Mar.	Mitaki
"	♂	1	subad.	Apr.	"
"	♂	1	ad.	June	"
Subfam. Corinninae					
<i>Trachelas japonicus</i> BÖS. & STR.	♂	3	ad.	Apr.	Iwakuni
Fam. Sparassidae					
Subfam. Heteropodinae					
<i>Heteropoda forcipata</i> (KARSCH)	♂	1	subad.	May	"
Subfam. Sparianthidinae					
<i>Thellicopsis seneca</i> (L. KOCH)	♂	3	subad.	"	Mitaki, Iwakuni
"	♂	1	"	June	Iwakuni
"	♂	2	"	July	"
Fam. Thomisidae					
Subfam. Misumeninae					
<i>Misumenina tricuspidata</i> (FABRICIUS)	♂	1	juv.	Feb.	Hirosima Univ.
"	♂	1	"	Mar.	"
"	♂	29	juv. & subad.	Apr.	"
"	♂	10	subad. & ad.	May	"
<i>Xysticus insulicola</i> B.S. & STR.	♂	4	subad.	Apr.	Mitaki, Showa-Village, Hiroshima Univ.
"	♂	1	subad.	Mar.	Hiroshima Univ.
"	♂	4	"	Apr.	Mitaki
"	♂	6	subad. & ad.	May	"
<i>Coriarachne fuscipes</i> (KARSCH)	♂	2	subad.	Mar.	Showa Village
<i>Oxyptila decorata</i> KARSCH	♂	1	subad.	May	Iwakuni
"	♂	2	ad.	June	Iwakuni, Mitaki
<i>Oxytate setosa</i> KARSCH	♂	2	subad.	Mar.	Iwakuni
"	♂	7	"	Apr.	Iwakuni, Mitaki, Showa Village
"	♀	4	juv. & subad.	"	Iwakuni, Showa Village
"	♂	2	"	May	"
"	♂	1	juv.	Aug.	Iwakuni
"	♀	2	"	"	"
<i>Diaea subadulta</i> BÖS. & STR.	♂	1	subad.	May	Showa Village
Subfam. Philodrominae					
<i>Philodromus roseus</i> KISHIDA	♂	3	juv.	Mar.	Hiroshima Univ.
"	♂	19	juv. & subad.	Apr.	"
"	♂	11	subad. & ad.	May	"
" <i>nigrostriatus</i> BÖS. & STR.	♂	1	subad.	Apr.	Iwakuni
"	♂	1	"	May	"
" <i>auricolus japonicola</i> BÖS. & STR.	♂	1	"	Apr.	Iwakuni
"	♂	2	"	May	Iwakuni, Mitaki
"	♂	1	"	"	Iwakuni
<i>Tibellus tenellus</i> (L. KOCH)	♂	1	"	"	"
Fam. Oxyopidae					
<i>Oxyopes serialatus</i> L. KOCH	♂	10	juv.	Mar.	Hiroshima Univ.
"	♀	13	"	"	"
"	♂	6	juv. & subad.	Apr.	"
"	♀	2	juv.	May	"
"	♂	12	subad. & ad.	"	"
"	♂	4	subad. & ad.	June	Fukuoji, Mitaki
<i>Nishina generosa</i> KISHIDA	♂	1	subad.	Apr.	Hiroshima Univ. Miiri Village

species name, sex, date of fixation, number of individuals and locality of the material are given in the table.

The chromosome study of all the material was carried out based on the permanent preparations of the male and the female gonads. In fixation the testes and ovaries alone were dissected out in 0.7 % sodium chloride solution and immediately put into the fixatives; in some cases when the specimens were too small, however, the gonads were preserved with small piece of visceral mass. As fixatives NAVASHIN's solution, modified NAVASHIN's solution, ALLEN-BOUIN's solution, CAROTHER's solution, FLEMMING's weak solution, FLEMMING's strong solution, modified FLEMMING's weak solution and CHAMPY's solution were employed. In respect to the dehydration, section and staining, the same methods described in the previous paper (SUZUKI 1951) were used.

The drawings were made at table level with the aid of an objective 120, ocular 20 and ARBE's camera lucida.

OBSERVATION

I. Family Clubionidae

In this family the chromosomes of *Clubiona* and *Micaria* have so far been investigated by HACKMAN (1948). In the present study three species of *Chiracanthium*, two species of *Clubiona* (subfamily Clubioninae), one species of *Micaria* (subfam. Micariinae) and one species of *Trachelas* (subfam. Corinninae) have been observed, of which *Chiracanthium* and *Trachelas* are quite new material for cytological survey.

The chromosome number of the four species studied by HACKMAN was uniformly 12 in haploid, but that of the present seven material varies between 12 and 14. Despite the variation of the chromosome number, the sex determining mechanism in all the studied species is alike and X_1X_2O type.

1. *Chiracanthium japonicum* BÖSENBERG et STRAND

(Figure 1 A-I)

This spider is comparatively large in body size and is usually met with in the field. The male gonads from a large number of individuals collected between April and June provided the present material. The fixatives employed were NAVASHIN's solution, modified NAVASHIN's solution, CAROTHER's solution and modified FLEMMING's weak solution, all of which gave pretty good results.

The testes of juvenile individuals fixed in April contain numerous spermatogonial metaphase plates and those of subadults fixed in May are favourable for observing the meiotic divisions. The spider matures in

the last part of May and June.

The spermatogonial chromosomes in this family are generally large and favourable for observation. On the other hand, it is difficult to obtain the good preparations of the meiotic divisions in which exact count of chromosome number can be made, for in these divisions, especially in the first division, the chromosomes are packed closely together and they are thickly condensed. For this reason HACKMAN (1948) has been unable to obtain excellent metaphase plate of the first division except a single species.

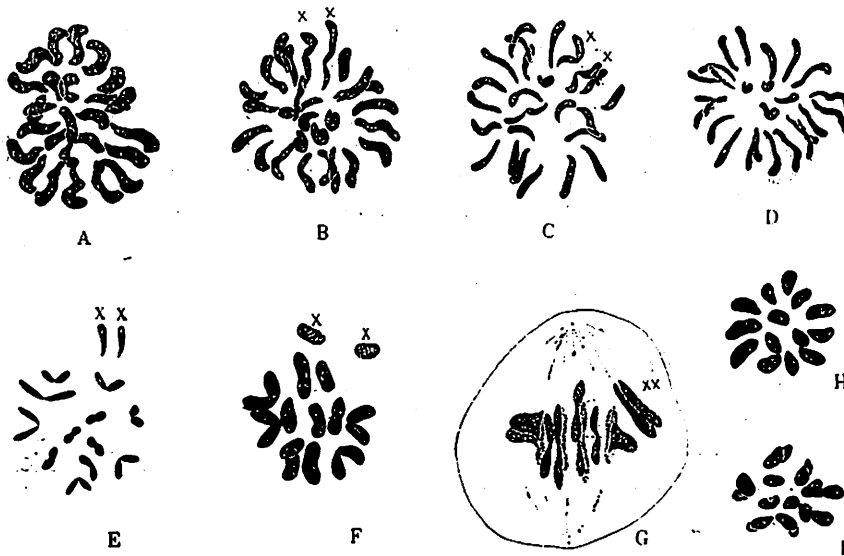


Figure 1. *Chiracanthium japonicum*. All drawings at a magnification of $3000\times$ (reduced from $4000\times$). A-D, spermatogonial metaphases, showing 26 chromosomes. E-F, primary spermatocyte metaphases, showing 12 bivalents and 2 univalent X's. G, lateral aspect of the first division metaphase. H, secondary spermatocyte metaphase, showing 14 chromosomes. I, the same, with 12 chromosomes.

In the present material a large number of spermatogonial metaphase plates were obtained. Every plate shows the diploid chromosome number 26 (Fig. 1 A-D). All the chromosomes are acrocentrics, which are of terminal or subterminal spindle attachment. The general appearance of the metaphase plates varies in the different plates. In some cases the chromosomes are highly condensed and deeply stained with hematoxylin, most of them are stout rods and with irregularly curved, bizarre contours and some assume scale-like form (Fig. 1 A). In others, particularly, when the sections were differentiated excessively, the chromosomes show a quite different feature from that mentioned just above and exhibiting a typical rod shape, in which precise morphological analysis is possible (Fig. 1 B-D). The two chromosomes situated in the twelve o'clock directing of

the dial in Fig. 1 B, are distinguished from others due to the largest size and the presence of a transverse constriction in a certain locus of the proximal half, and each element appears as if consisting of two chromosome segments. The similar feature is seen in 1-2 o'clock in Fig. 1 C too. Careful observation shows that almost all the spermatogonial spindles contain two such special chromosome elements. The even number of the diploid set suggests the existence of two sex chromosomes and the above described two are regarded as two complex sex chromosomes.

Such a characteristic structure of some spermatogonial chromosomes makes us recall the X_a -chromosome in *Heteropoda venatoria* (SUZUKI and OKADA 1950), and the X_1X_2 -elements in some argiopid spiders (SUZUKI 1951). As it will be mentioned later, the similar feature of the X-elements has been observed in many species belonging to Sparassidae, Thomisidae and Oxyopidae studied in the present paper.

As already mentioned, it is considerably difficult to obtain good preparations of the first meiotic division, but in numerous preparations only a few excellent metaphase plates were found. At first metaphase exist fourteen chromosomes without exceptions, twelve of which are bivalent autosomes and the remaining two are univalent X-elements (Fig. 1 E, F). As in the spermatogonial metaphase two types were found regarding the configuration of chromosome elements. In some plates the chromosomes are stout (Fig. 1 F) and in others comparatively fine elements (Fig. 1 E). The autosome bivalents are mostly V- or dumb-bell shaped, in which the chiasma is interstitial. The two X's are always clearly distinguishable at the first metaphase. When viewed from lateral they assume two elongated rods of nearly equal length, which are the largest in the set and arranged closely together on the peripheral region of the spindle and directing their proximal end towards the same pole (Fig. 1 G), but no chiasmata are formed between them. As is shown in Fig. 1 E, F, the X_1 and X_2 situate sometimes completely apart with some considerable distance between them. Each X possesses a single spindle attachment in the proximal end and at first anaphase goes undividedly to the same pole, thus in respect to the sex chromosomes, two sorts of the secondary spermatocytes are expected to produce. Fig. 1 H, I, show the metaphase spindles of the secondary spermatocytes, the former contains fourteen monads ($12 A + 2 X$) and the latter twelve ones ($12 A$). The chromosomes of the metaphase II are globular or short rods with slightly pointed proximal end. Two elements situated in the eight and nine o'clock in the Fig. 1 H, are larger than others and likely to represent 2 X's.

2. *Chiracanthium kompiricola* DÖNITZ et STRAND (Figure 2 A-F)

The present material very much resembles the previous species in the

morphological characters and habitat. Numerous pairs of testes from subadult and adult individuals captured between May and June were preserved in the modified NAVASHIN's solution and FLEMMING's weak solution.

The general features of chromosomes, namely, the number, morphology, behaviour and sex determining mechanism in the present material resemble those of the preceding species.

In the spermatogonial metaphase twenty six chromosomes of acrocentric type are clearly counted, and as in the former case the chromosomes are very stout, curved irregularly and some of them assume scale-like form (Fig. 2 A, B). On the other hand, in some spindles (Fig. 2 C, D) the chromosome elements are not so stout, but slender and short rods with gradual size difference. In this species, also, the largest pair is considered to be the sex chromosomes, but they could not be distinguished so clearly.

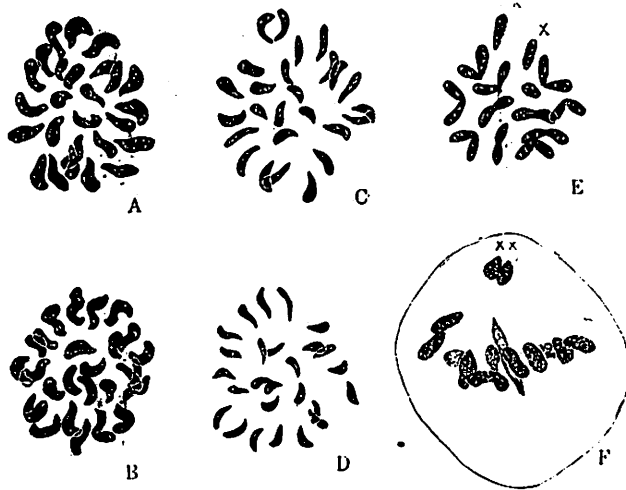


Figure 2. *Chiracanthium kompricola*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A-D, spermatogonial metaphases, showing 26 chromosomes. E, primary spermatocyte metaphase, showing 12 bivalents and 2 univalent X's. F, side view of the first division metaphase.

The chromosomes of the first metaphase are pictured in Fig. 2 E. At metaphase I exist fourteen chromosomes, two of which are typical univalent rods and representing the X-elements, the remaining twelve are autosome bivalents which are of typical V- or dumb-bell shape. In the profile the chromosomes are highly condensed and the 2 X's assume stout rods of more or less pointed end (Fig. 2 F). At metaphase I the 2 X's lie only rarely on the equatorial plate, usually standing on the intermediate region between the equatorial plate and one of the poles and at anaphase

they finish the movement towards the pole, when autosomes begin to separate.

As in the previous species, there are two kinds of metaphase plates in the second division: in some 12 autosomes alone and in others 12 autosomes plus 2 X's are present.

3. *Chiracanthium unicum* BÖSENBERG et STRAND

(Figure 3 A-G)

The present material is considerably small in size and the body is greenish yellow. Numerous specimens are met with in the field in early summer. The testes from subadult individuals secured in May were employed for the present material. The fixative used was modified NAVASHIN's solution. A large number of dividing figures and all phases of spermatogenesis were observed in the preparations.

In respect to the general feature of chromosomes marked similarities can be found between the present material and the above mentioned two forms.

The spermatogonial metaphase shows the diploid chromosome number 26 invariably (Fig. 3 A-C). In some figures the chromosomes are of slightly curved rod shape, with smooth outline (Fig. 3 B, C), in others they are irregularly curved and showing more or less bizarre contours (Fig. 3 A).

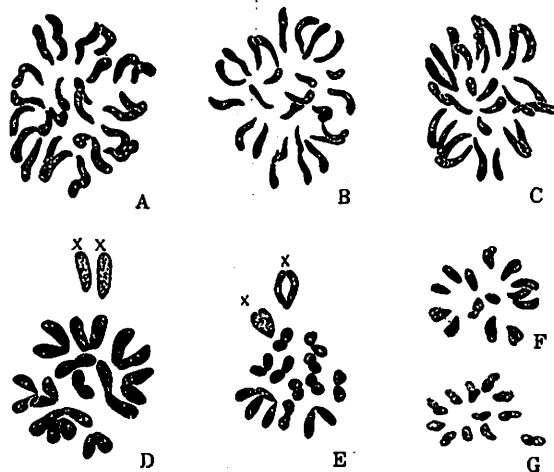


Figure. 3. *Chiracanthium unicum*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A-C, spermatogonial metaphases, showing 26 chromosomes. D, E, Primary spermatocyte metaphases, showing 12 bivalents and 2 univalent X's. F, secondary spermatocyte metaphase, showing 14 chromosomes. G, the same, with 12 chromosomes.

The two chromosomes situating in twelve o'clock in Fig. 3 A, are distinguished from others because of the particular form. They are clearly constricted in the interstitial region and in that locus they are bent, so that each of them looks as if it is consisted of two chromosome segments. These two elements seem to be homologous with those of *Chiracanthium japonicum* and regarded as sex chromosomes.

The primary spermatocyte spindles are very large and in which twelve autosome bivalents and two univalent X-elements are present (Fig. 3 D, E). At this stage the 2 X's are standing usually as two isolated rods on the peripheral circle of the spindle, sometimes a clear longitudinal split is visible in them and each X assumes a typical V-shape. The individual X seems to be of nearly equal size. But sometimes a minute difference alone was noticed. As in many others, at first anaphase, the 2 X-elements pass one pole and divide equationally in the second division. The chromosomes of the second metaphase are pictured in Fig. 1 F, G. The former contains 14 chromosomes (12 A+2 X) and the latter 12 ones (12 A).

4. *Clubiona japonicola* BÖSENBERG et STRAND (Figure 4 A-F)

This is one of the most common *Clubiona*-species in Japan and throughout the whole year except winter, the material of different stages is met with. In the present study the testes of numerous individuals captured between April and October were fixed in the NAVASHIN's solution, modified NAVASHIN's solution, CAROTHER's solution and ALLEN-BOUIN's solution etc., all of which were found to be not so favourable for the fixation of dividing chromosomes, for at metaphase, especially in the first division, the chromosomes are packed closely and some are fused, so that it is difficult to count chromosomes exactly. Thus the present material is not favourable for chromosomal study. But fortunately I have been able to obtain some good preparations in which important phases of spermatogenesis have been observed.

The chromosome number of three Finnish species of *Clubiona* has been reported as 12 in haploid by HACKMAN (1948), but it was determined at diakinesis or second division and not in the first metaphase.

In the testes of the subadult individuals many spermatogonial spindles were found, but since the chromosomes are small and some are often overlapped, the accurate chromosome number is difficult to count. The number of chromosomes was reported briefly by me (1950a) as 21 in diploid and 9 in haploid, but the later reinvestigation reveals 22 in diploid and 12 in haploid. As shown in Fig. 4 A, favourable metaphase shows the diploid chromosome number 22, in which the elements are small rods and without any characteristic structure. So it is difficult to distinguish sex

chromosomes, at diakinesis, however, two compact globular X-elements are clearly observed, which are highly condensed and deeply stained and lying side by side near the nuclear membrane (Fig. 4 B).

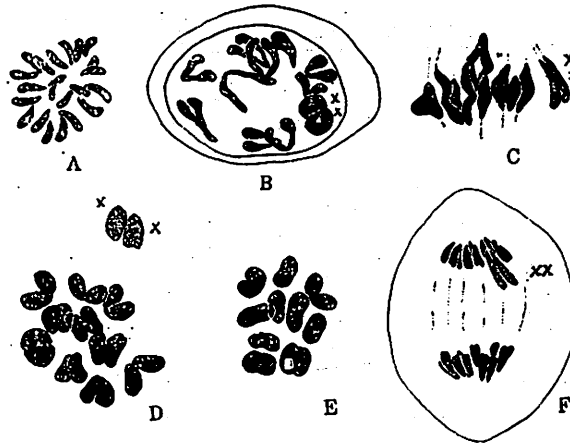


Figure 4. *Clubiona japonicola*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A, spermatogonial metaphase, showing 22 chromosomes. B, diakinesis. C, lateral view of the first division metaphase. D, primary spermatocyte metaphase, showing 10 bivalents and 2 univalent X's. E, the same, with 10 bivalents. F, side view of the first division telophase.

As already mentioned, to obtain good sections of the first division is very hard. Among a large number of preparations, only a few favourable metaphase plates have been found, in which the chromosomes and plates are considerably large and the chromosome number has been counted accurately (Fig. 4 D, E). In the plate ten autosomal bivalents and two X's are existed. In the profile of the first metaphase two X's are elongated rods of approximate length and they stand on the peripheral region of the equatorial plate, each of which is of a single spindle attachment and directing its proximal end towards the same pole (Fig. 4 C). Judging from the size in the first division, the two X-elements are regarded as the largest pair in the complement. Sometimes they show a longitudinal split at metaphase I. Here also, at anaphase they remove towards one pole undividedly and in the ensuing division they separate themselves equationally.

5. *Clubiona lena* BÖSENBERG et STRAND (Figure 5 A-G)

The material for this study consists of the testes from two subadult and one adult individuals which were collected in March and May and were fixed in modified NAVASHIN's fluid.

In the testes from one subadult fixed in March existed a large number of division figures and other phases of spermatogenesis. In the systematic viewpoint, the present specimen is closely related to the just above mentioned species, *C. japonicola*. The chromosome number of this species is 24 in diploid and 13 in haploid, and differs clearly from that of *C. japonicola* and three Finnish *Clubiona*-species. Except the chromosome number, however, the general feature of chromosomes are similar to that of *C. japonicola*.

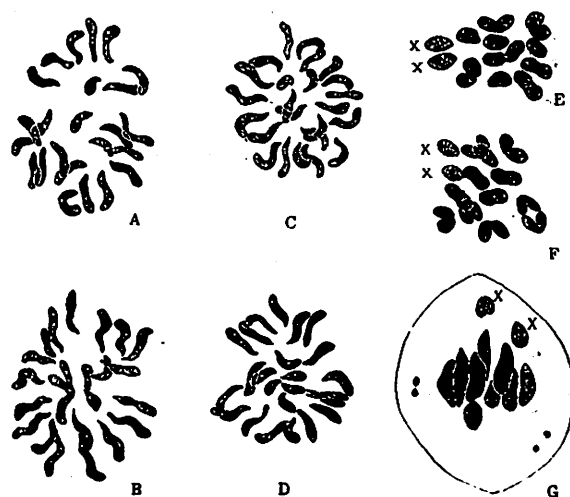


Figure 5. *Clubiona lena*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A-D, spermatogonial metaphases, showing 24 chromosomes. E, F, primary spermatocyte metaphases, showing 11 bivalent and 2 univalent X's. G, side view of the first division metaphase, showing 2 X's and 2 pairs of chromatic bodies.

The chromosomes of the spermatogonial spindles are comparatively large and in excellent figures, they are lying well apart each other, so that the material is favourable for chromosomal observation. A careful examination of spermatogonial dividing figures reveals the diploid chromosome number 24 without exceptions (Fig. 5 A-D). All the chromosomes are acrocentric type and rod shaped, as in Fig. 5 A, they are typical rods of slight size difference and are of smooth outlines. In Fig. 5 B, the elements are bent somewhat distinctly and shows irregular contours. Judging from the meiotic division, two multiple X's should be included in the spermatogonial chromosomes, though it is difficult to identify them in this plate.

The polar views of metaphase I are pictured in Fig. 5 E, F. In every plate eleven bivalents and two univalent X's can be found. The chromosomes are highly condensed and the bivalents are of dumb-bell shape, some of which are globular or short rods. In respect to the morphological character and behaviour of the sex chromosomes, similar feature can be

found between the present species and *C. japonicola*.

At first metaphase minute chromatic bodies which are stained faintly with hematoxylin are often observed in the nuclear cavity. In one figure they show a paired arrangement on the equatorial plate and look as if two pairs of them are in the course of division as autosome bivalents (Fig. 5 G). They show marked similarities to the planosomes described by PAINTER (1914) in many spiders, but their origin and fate could not be clearly traced.

Subfamily Micariinae

6. *Micaria unifascigera* BÖSENBERG et STRAND

(Figure 6 A-E)

The testes from two subadult and three adult specimens were preserved in CAROTHER'S solution and modified NAYASHIN'S solution during the time between March and June, which served as the material for the present study.

The chromosomes of *Micaria* have already been observed by HACKMAN (1948). He reported that *M. decorata* shows that the haploid chromosome number is 12 and the nucleus and chromosomes are larger than those of other *Clubiona*-species. In the present species the chromosomes and nucleus are not so large, compared with those of the related forms of *Clubiona* and *Chiracanthium*, but rather smaller, and in many cases they are packed together and found to be not favourable for cytological study. Despite the bad fixation of chromosomes, the X-elements are always distinguishable at the first metaphase, as is shown in Fig. 6 B-D,

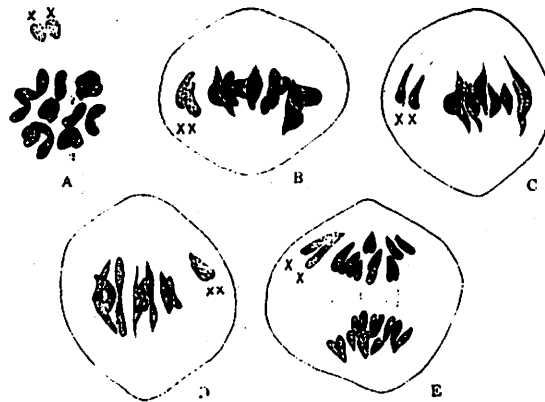


Figure 6. *Micaria unifascigera*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A, primary spermatocyte metaphase, showing 10 bivalents and 2 univalent X's. B-D, side views of the first division metaphases, showing various arrangement of 2 X's. E, early telophase of the first division, side view.

the two X's are of rod shape of nearly equal size and standing on the eccentric position of the spindle, directing their proximal end towards the same pole. Judging from the observation of the first division, the X_1X_2 -elements are regarded as the largest one pair in the set. The 2 X's are prereductional in this case also. The determination of the autosome number at metaphase I is rather difficult due to the lack of favourable preparations, but in some relatively good division figures (Fig. 6 A) ten autosome bivalents were counted as in the *M. decorata*. The autosome bivalents are V-shaped or of dumb-bell shaped.

Subfamily Corinninae

7. *Trachelas japonicus* BÖSENBERG et STRAND

(Figure 7 A-C)

The members of this subfamily have never been studied cytologically. The testes from three adult individuals collected in April and fixed in modified NAVASHIN's solution constitute the material for this study. Owing to the lack of the material the meiotic chromosomes alone have been observed. The testes of mature spiders were filled with sperms and spermatids, and only a few dividing figures of the primary spermatocytes have been found within several cysts. As in the foregoing species, *Micaria unifascigera* the chromosomes and nucleus are considerably small and

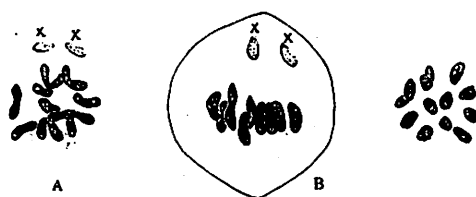


Figure 7. *Trachelas japonicus*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A. primary spermatocyte metaphase, showing 10 bivalents and 2 univalent X's. B. side view of the first division. C. secondary spermatocyte metaphase with 12 chromosomes.

they defy careful observation. In some of the first metaphase plates ten autosome bivalents and two separated univalent X's were counted. The chromosome feature shown in Fig. 7 A, resembles that of *Micaria unifascigera* (Fig. 6 A). At metaphase I the 2 X's lie on the spindle completely apart and both elements are of almost equal length (Fig. 7 B). At first anaphase, they remove precociously to one pole as in the related species. An excellent, second metaphase plate was obtained, in which 12 globular chromosomes were clearly observed (Fig. 7 C).

II. Family Sparassidae

The chromosomes of this family have been investigated quite recently by HACKMAN (1948) in *Microrommata viridissima* and by SUZUKI and OKADA (1950) in *Heteropoda venatoria*. Further observations have been done in the two Japanese species, *Heteropoda forcipata* and *Thelcticopis severa*. According to the above mentioned authors high chromosome number and $X_1X_2X_3O$ type of sex determination are characteristic for the two species. The similar condition has been demonstrated in the present material, too.

Subfamily Heteropodinae

8. *Heteropoda forcipata* (KARSCH)

(Figure 8 A-H)

The present material is closely related to *Heteropoda venatoria* studied by SUZUKI and OKADA (1950), in the taxonomic standpoint.

The testes from a single subadult individual captured in May was employed for the material of the present study. As a fixative modified NAVASHIN's solution was used, which gave the favourable results. The testes of the present material is so large that many preparations were made, in which numerous number of clear division figures and all phases of spermatogenesis have been investigated. The present material is very favourable for chromosome study because of their larger size of chromosomes.

In respect to the number, morphological characters and behaviour of chromosomes striking similarities can be found between the present species and the related form, *H. venatoria*, in accordance with taxonomic relation. As shown in Fig. 8 A, B, the diploid number of chromosomes is 41. All the chromosomes are acrocentric type, which are of terminal or subterminal spindle attachment. They assume typical rods of varying size, some are slightly and others distinctly curved. The chromosomes are stained deeply with hematoxylin and showing smooth outline, so that even if some are overlapped, the chromosome number can be counted definitely. In the excellent spermatogonia one chromosome is distinguished from others due to the larger size and particular shape. As is shown in Fig. 8 A, B, the element labelled as X is slender, elongated rod and bent acutely in the interstitial region, it is somewhat larger than any others. In some slides it has a distinct constriction in the interstitial region and shows a clear bipartite structure (Fig. 8 C). When the presumed homologous chromosome pairs are picked out, the chromosome in the question is found to have no mate, thus it is regarded as sex chromosome. The characteristic feature of this element is quite similar to the X_3 -element of *Heteropoda venatoria*

studied by the author and OKADA (1950). Except this unpaired X no such particular chromosomes are recognized.

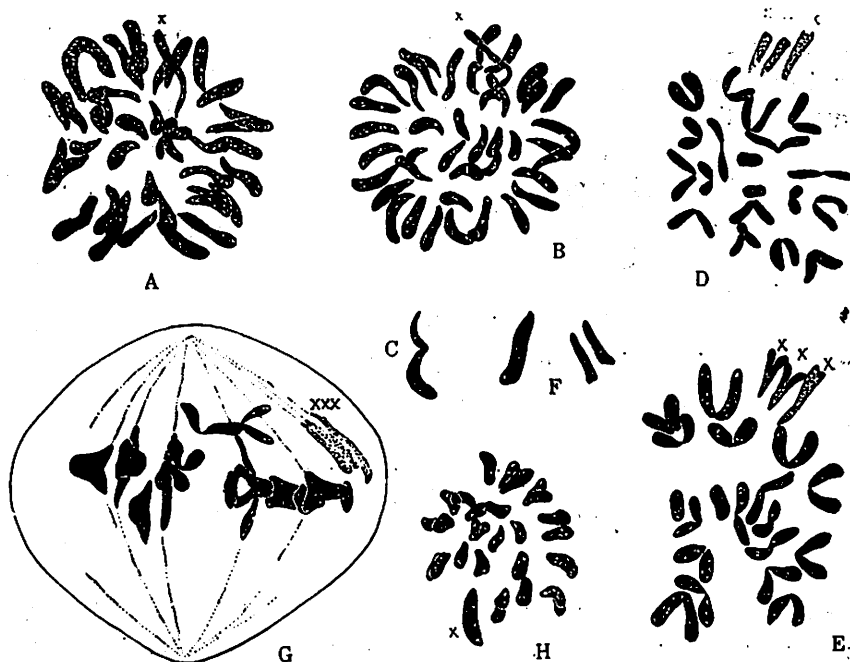


Figure 8. *Heteropoda forcipata*. All drawings at a magnification of 5000 \times (reduced from 4000 \times). A, B, spermatogonial metaphase, showing 41 chromosomes. C, one X-element from spermatogonial metaphase, showing bipartite structure. D, E, primary spermatocyte metaphases, showing 19 bivalents and 3 X's. F, 3 X's from the first division metaphase, polar aspect, showing larger X separated from 2 smaller X's. G, profile view of the first division metaphase, showing 3 X's. H, secondary spermatocyte metaphase, showing 21 chromosomes.

The nuclear plate of the primary spermatocyte is remarkably large and in this nuclear cavity many distinct chromosome elements are evenly distributed. As is seen in Fig. 8 D, E, every metaphase plate contains nineteen autosome bivalents and three univalent X-elements, which are situated always on the peripheral region of the spindle, isolated from the autosome group. The autosome tetrads are mostly V-shaped, which look as if two chromosome segments were attached at their proximal end, and some are of transverse suture at apex. Some are dumb-bell forms or short rods. At metaphase I the 3 X's stand on the eccentric position of the spindle, lying parallel with each other and directing their longitudinal axes vertical to the equatorial plate. They are elongated V forms. Of these three X's two are always of approximately similar length, but the remaining one is distinctly larger. The latter is longer by about one fourth of itself than the former. The largest X-element shown in Fig. 8 G seems to be slightly constricted in the proximal region and in this constricted locus the chromo-

some is slightly curved. The structure of this X-element resembles strikingly that in the spermatogonium. In respect to the arrangement of the 3 X's at metaphase I, some variations are observed. Usually they stand parallel quite apart with an equal distance, but sometimes one larger X is separated with a considerable distance from the two smaller elements (Fig. 8 F). At any rate, these 3 X-elements possess a single spindle attachment on the proximal end and at the first anaphase they go undividedly towards one pole. In the ensuing division they separate into equal halves. Thus in respect to the chromosome number, two sorts of secondary spermatocytes are produced, one with nineteen autosome dyads plus three X-elements and another with nineteen autosome dyads alone. Fig. 8 H shows the X-class of the secondary spermatocyte, in which the chromosomes are short rods of somewhat pointed inner end, one elongated rod seems to represent the largest X-element.

Subfamily Sparianthidinae

9. *Thellicopsis severa* (L. KOCH)

(Figure 9 A-D)

The present subfamily has never been studied cytologically. This species distributes in the south-western parts of Japan, but it occurs comparatively rarely, so that the material is not so easily obtainable. Its body and testes are considerably large and favourable for dissection. As the material for the present study the testes from six subadult spiders which were captured between May and July were employed. The fixatives used were modified NAVASHIN's solution, CAROTHER's solution and FLEMING's weak solution.

The testes fixed in May and June are filled with resting nucleus and dividing figures of spermatogonia. And those preserved in early July contain largely the cell plates of early meiotic prophase and partly spermatogonial cells. Very probably the meiotic divisions may take place in mid summer. Unfortunately owing to the lack of material, I have not been able to obtain favourable preparations of the meiotic divisions, accordingly the following description is limited to the spermatogonial division alone.

A large number of spermatogonial metaphase plates were obtained. The chromosomes and cell plates are strikingly large, probably those of the present species are one of the largest among over eighty species studied by me. A careful examination reveals that the diploid chromosome number is forty three (Fig. 9 A-D). All the chromosomes are of rod shape which are of acrocentric type and most of them are remarkably large in size. Many larger chromosomes consist the outer circle, in the central region of this circle exist about 6-7 pairs of more or less small ones, many of which are of globular distal segment. In somewhat deeply stained sections the chromo-

some elements are stout and large, some of which straight and others

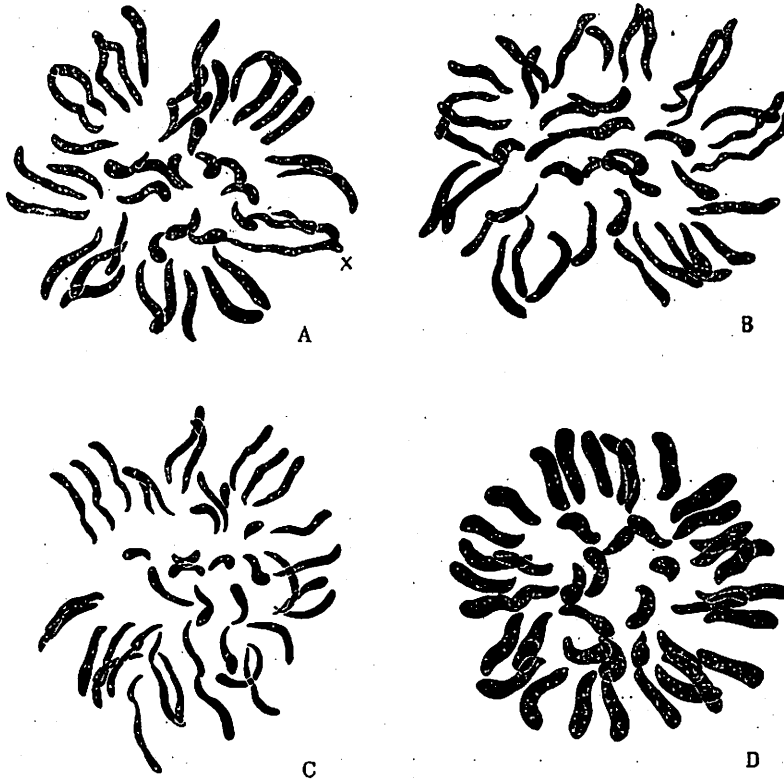


Figure 9. *Thellicopsis severa*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A-D, spermatogonial metaphases, showing 43 chromosomes.

more or less curved rods (Fig. 9 D). When the section is differentiated favourably, they show clear morphological characters, namely, many of them are much elongated rods which have long tapering proximal end and are bent irregularly. Among the chromosomes constituting the outer circle of the plate, there is only a slight size difference except some elements. In every plate some chromosomes are exceedingly large in size. In Fig. 9 A, one element which situates in four o'clock is distinguished by the notably larger size, which is the largest in the complement and has no mate. When compared it with the largest X-element of *Heteropoda*, marked similarity can be found between them. In Fig. 9 C, too, one distinctly larger chromosome is observed in seven o'clock, in which a proximal constriction is present. Even in Fig. 9 D, one element lying in 3 o'clock is obviously the largest in the set. Such largest one element is always unpaired and is considered to be homogeneous with the one X-element in *Heteropoda*. In Fig. 9 B, four particular shaped elements, two of which are existed in two o'clock and another two in three o'clock, are distinguishable.

ble in the set. These four elements, particularly three of which, are extremely elongated and near the middle or in the interstitial region with a distinct constriction, by which each element is divided into both proximal and distal segments, of which proximal segment is markedly thin and is bent distinctly or somewhat spirally, and as a result, the chromosome itself assuming a very characteristic form. Some of them may probably represent sex chromosomes, but in this respect no definite conclusions can be reached owing to the lack of the observation of the meiotic division.

Quite recently I have heard from MCINTOSH that two forms males of *Delena* and *Olios* belonging to the same family as the present species show the diploid chromosome number 43 and 3 X's mechanism, so that very probably the present species males also contain three X-elements.

III. Family Thomisidae

This family is divided into two subfamilies, Misumeninae and Philodrominae. Some authors regard these two subfamilies as separate families. In the Misumeninae the chromosomes have so far been studied in one species of *Misumena* and two species of *Xysticus* (PAINTER 1914, HACKMAN 1948). In the Philodromine four species of *Philodromus*, one species of *Thanatus* and one species of *Tibellus* have been investigated cytologically by HACKMAN (1948).

In the present report the following twelve species of eight genera belonging to the both subfamilies have been dealt with. Subfamily Misumeninae: *Misumena tricuspidata*; *Xysticus insulicola*; *X. ephippiatus*; *Coriarachne fulvipes*; *Oxyptila decorata*; *Oxytate setosa*; *Diaea subadulta*. Subfamily Philodrominae: *Philodromus roseus*; *P. nigrostriatipes*; *P. aureolus japonicola*; *Tibellus tenellus*.

Subfamily Misumeninae

10. *Misumena tricuspidata* (FABRICIUS) (Figure 10 A-O)

The present species is one of the most common spiders in gardens and fields in Japan. Numerous specimens from the juvenile to the adult individuals captured during the time between February and May were used for the present material. The male gonads were fixed in CAROTHER'S solution, NAVASHIN'S solution, modified NAVASHIN'S solution and CHAMPY'S solution, all of which gave favourable results. The testes of the juvenile individuals fixed in March and early April contained many spermatogonial division figures, and those obtained in the middle of April and May were favourable for the observation of meiotic divisions.

The closely related species, *Misumena vatia* has been studied cyto-

logically by HACKMAN (1.c.). By him the species possesses 12 chromosomes in haploid and the single XO type of sex determination. Regarding the chromosome number and sex chromosome the present material gave the same result as *M. vatia* in the present study, however, more accurate observations have been done through all phases of spermatogenesis than in *M. vatia*. HACKMAN failed to observe spermatogonial spindles, but a large number of excellent division figures were obtained in this species. As is shown in Fig. 10 A-D, every plate contains twenty three chromosomes of short rods which are of a slight size difference. Usually all the chromosomes seem to be packed closely in the nucleus. When the homologous pairs are picked out according to shape and size, one is found to have no mate, which is seemingly the largest one and is regarded as X-element. A careful examination reveals more characteristic structure of X-element. It seems to be the largest in the complement and in some

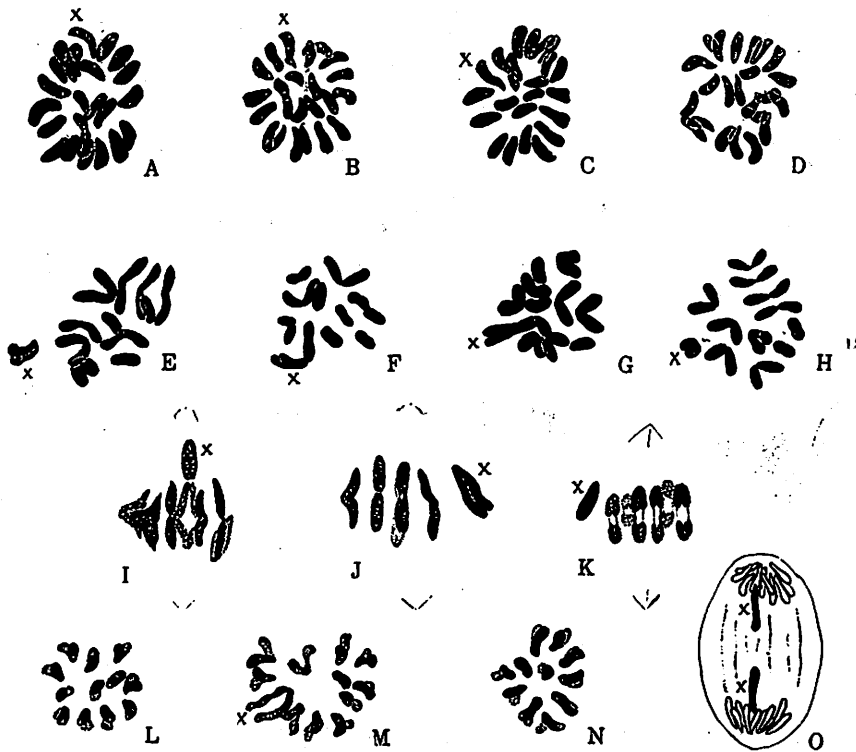


Figure 10. *Misumena tricuspidata*. All drawings at a magnification of 2400 \times (reduced from 3000 \times). A-D, spermatogonial metaphases, showing 23 chromosomes. E-H, primary spermatocyte metaphases, showing 11 bivalents and a single univalent X. I-K, side views of the first division metaphases, showing a single X. L, M, secondary spermatocyte metaphases, showing 12 chromosomes, 11 chromosomes, N, the same, with 11 chromosomes. O, side view of telophase of the second division, showing X-element.

sections it curves distinctly in one side and often with a slight but clear proximal constriction (Fig. 10 B). And in some plates it is slender and more or less faintly stained than any others (Fig. 10 A). These morphological characters of the X-element are observed often in some of the present subfamily as will be described later.

At first metaphase eleven autosome bivalents and a single X-element are clearly recognized (Fig. 10 E-H). HACKMAN (1. c.) reported that the meiotic chromosomes of *M. vatia* are larger than those of *Xysticus*-species, but in this respect no different conditions could be found between the *Misumena* and *Xysticus* I studied. The autosome tetrads are V shaped, dumb-bell shape or short rod with a slight median constriction. As in the usual X_1X_2 -elements, at metaphase I the single X-element situates on the peripheral position of the equatorial plate, directing its longitudinal axis parallel with the spindle fibre. In the lateral aspect the X assumes rod shape and it often reveals V-shape in a longitudinally split X (Fig. 10 I-K).

As in many others, at anaphase of the first division the single X goes undividedly to one pole. Thus here also, regarding the sex chromosome, two kinds of secondary spermatocytes are produced, one half contains eleven autosomes and a single X-element and another half with eleven autosomes alone (Fig. 10 L-N). The chromosomes in the second metaphase are small rods or of globular form. In one plate which includes 12 elements one elongated dyad which is stained faintly and of irregular outline, was observed. It forms a striking contrast with others and is regarded as X-element (Fig. 10 M). At second anaphase all the chromosome elements including the single X separate equatorially. At second telophase when daughter chromosomes reached each pole, one large chromosome was found lagging behind others in both poles, which is the largest and seems to be X-element (Fig. 10 O).

In the present species thus single X-element is fairly distinguished through all the stages of spermatogenesis.

11. *Xysticus insulicola* BÖSENBERG et STRAND

(Figure 11 A-K)

The material used in the present study is the male gonads from four subadult individuals which were collected in early April and preserved in modified NAVASHIN's solution. In the testes a large number of spermatogonial division figures and all the phases of spermatogenesis were contained.

Three species of this genus, *X. triguttatus*, *X. viaticus* and *X. ulmi* have been studied cytologically by PAINTER (1914) and HACKMAN (1. c.). PAINTER reported the existence of X_1X_2O -system in *X. triguttatus* males,

on the contrary, HACKMAN observed XO-system in *X. viaticus* and *X. ulmi*. Despite the difference of X-element, the autosome number is alike in three studied species. The chromosome number and X-chromosome mechanism of the present species accord with the result reported by HACKMAN.

I have been able to obtain favourable preparations of spermatogonial metaphase plates. As is shown in Fig. 11 A-C, twenty three distinct chromosomes are existed in every plate. The chromosomes are stout rods which are of slight size difference except a single element. Some of the autosomes show a longitudinal split. As is well distinguished in Fig. 11 A-C, a single element is extremely longer than others and regarded as a single X. When the section is stained deeply, no marked structure is noticed, but if differentiated favourably, notable feature appeared in the X. Namely, in the excellent sections, the X stains more or less faintly than others without distinct outline and in many cases it is bent sharply and near the proximal end it has a transverse constriction. Thus in the present material males have a single X-element, and which is plainly

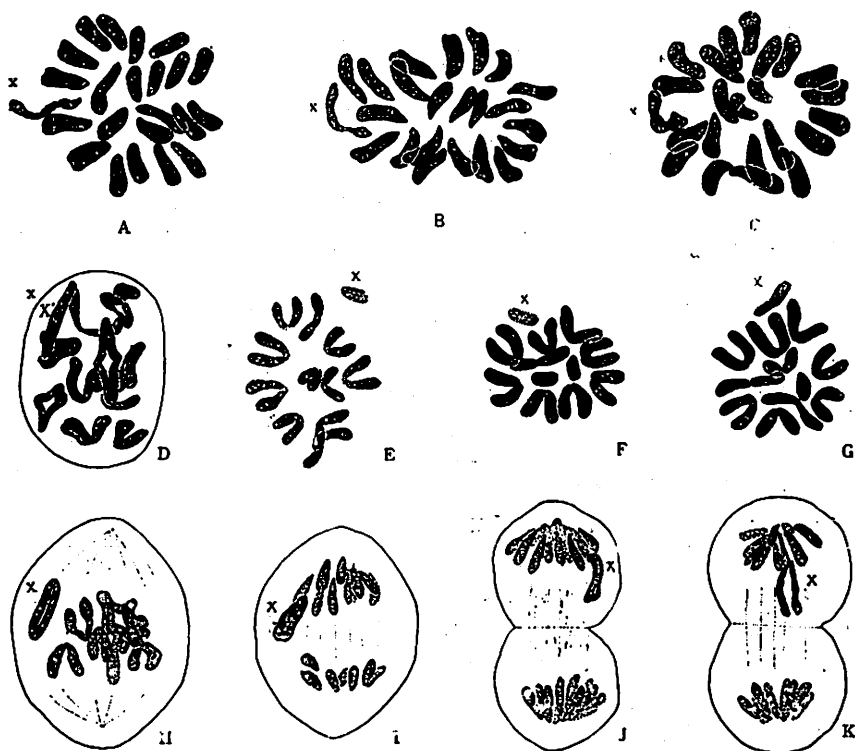


Figure 11. *Xysticus insulicola*. (A-C 3200 \times , D-K 2400 \times). A-C, spermatogonial metaphases, showing 23 chromosomes. D, prometaphase of the primary spermatocyte, showing a single X. E-G, first division metaphase, showing 11 bivalents and a single X. H, side view of the first division metaphase. I, side view of late anaphase of the first division, showing X-element. J, K, the same of the first telophase.

distinguished from others by its magnitude, abnormal structure and staining capacity.

As in the preceding species, *Misumena*, at metaphase I eleven autosome tetrads are mostly of typical V shape, only a few are of dumb-bell or short rod shape. In this case also, X-element takes its position on the outer circle of the autosomes and in the polar aspect it assumes short rod shape, but it reveals real structure of slightly curved rod by changing the focus. When viewed from lateral the X-element is an elongated rod, sometimes it shows a longitudinal split (Fig. 11 H). The split appears in comparatively early stage of the metaphase and as is shown in Fig. 11 D, it is visible even at prometaphase. The X-element migrates to the one pole in the first division as in many other forms studied. In the present material it was found that the X-element lags behind autosomes at early and late telophase (Fig. 11 I-K). The behaviour is nearly equal to that observed in *Trochosa ruricola*, *Philodromus emarginatus* and *P. aureolus* by HACKMAN (1. c.). Furthermore as shown in Fig. 11 J, K, at late telophase interzonal fibres are fairly observed between the two daughter cells, the similar feature has already been reported in *Agelena naevia* by WALLACE (1919) and in *Trochosa ruricola* by HACKMAN (1. c.).

12. *Xysticus ephippiatus* SIMON

(Figure 12 A-L)

The present species is allied to the just above described form, from the taxonomic point of view, and the two species show similar habitats. Eleven male specimens, six of which are subadults and the rest five are adults, were captured between March and May and their testes were fixed in ALLEN-BOUIN's solution, NAVASHIN's solution, modified NAVASHIN's solution and FLEMMING's strong solution. In this species too, all phases of spermatogenesis, namely, spermatogonial division and two meiotic divisions were plainly observed.

General feature of the chromosomes of the present species bears similarity with that of the preceding species, *X. insulicola* in accordance with the taxonomic relation. Namely, here too, the chromosome number is twenty three in diploid and twelve in haploid and a single XO-mechanism existed. The shape and arrangement of the spermatogonial chromosomes are nearly alike those of *X. insulicola* (Fig. 12 A-C). The unpaired X-element is distinguished from others on account of its magnitude, which is the largest in the complement and in good preparations it is constricted in the interstitial region.

At metaphase I the chromosomes are condensed more thickly than in the previous species, *X. insulicola* and assume mostly short rods of a slight median constriction, V-shaped ones are rarely found (Fig. 12 E-G).

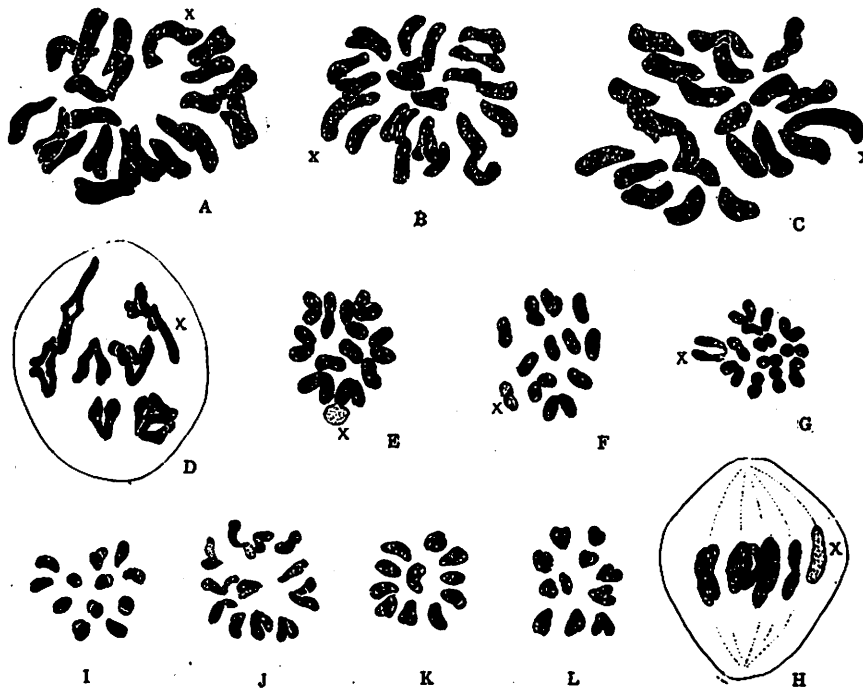


Figure 12. *Xysticus ephippiatus*. (A-C 3200 \times , E-L 2400 \times). A-C, spermatogonial metaphases, showing 23 chromosomes. D, prometaphase of the primary spermatocyte, showing a single X. E, F, metaphase I, showing 11 bivalents and a single X. G, early anaphase of the first division. H, profile view of the first division. I, J, secondary spermatocyte metaphases with 12 chromosomes. K, L, the same, with 11 chromosomes.

When differentiated excessively clear gap is visible in the median region of the autosome bivalents. At this stage the single X assumes a typical rod (Fig. 12 H), however, it shows often a longitudinal split, and as a result, bipartite or V formed structure is observed.

A large number of the good secondary spermatocyte division figures were found. All the chromosomes are distributed distinctly apart with nearly equal distance and the chromosome count was made easily (Fig. 12 I-L). One half of the secondary spermatocyte includes twelve chromosomes and another half contains eleven ones. The chromosomes are of small rod or globular shape, with somewhat pointed inner end. The X-element in this case is not clearly distinguishable.

13. *Coriarachne fulvipes* (KARSCH)

(Figure 13 A-B)

This species is very small and the body is remarkably flat and the dissection of testes is difficult.

The material employed in the present study consists of the testes

from two subadult individuals collected in March and fixed in CAROTHER's solution. In the testes many spermatogonial spindles were found, but the meiotic division figures were found only in some limited cysts.

The spermatogonial dividing figure is shown in Fig. 13 A. The chromosome elements are arranged on the equatorial plate distinctly apart each other and twenty three chromosomes are counted. The chromosomes are short rods of only a slight size difference and which are of somewhat pointed proximal end. The largest chromosome is distinguished in the complement, which has no mate and regarded as X-element. Thus the single X-element is fairly larger than the next largest pair, and is curved in one side. This character is considered to accord with that of *Misumena* and *Xysticus* mentioned above.

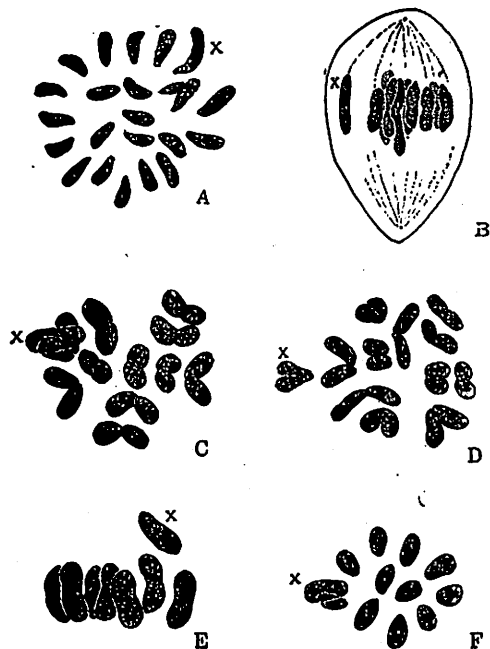


Figure 13. A-B, *Coriarachne fulvipes*. C-F, *Oxyptila decorata*. A, spermatogonial metaphase, showing 23 chromosomes (3000 \times). B, side view of the primary spermatocyte metaphase, showing a single X (2200 \times). C, D, polar views of the primary spermatocyte metaphase, showing 11 bivalents and a single X (3000 \times). E, side view of the first division metaphase (3000 \times). F, secondary spermatocyte metaphase, showing 12 chromosomes (3000 \times).

At first metaphase one rod shaped X is identified because of its peripheral situation on the spindle (Fig. 13 B). Owing to the lack of favourable material the haploid chromosome number could not be determined. Judging from the diploid number, however, twelve may be the real haploid number. Of course, the X-element passes to one pole at first anaphase. Thus in the present species also an XO-mechanism is demonstrated instead of the usual X_1X_2O -mechanism.

14. *Oxyptila decorata* KARSCH (Figure 13 C-F)

The following observations were based on the male gonads of one

subadult and two adult specimens secured in May and June. The testes were preserved in modified NAVASHIN's solution. In the present material the meiotic chromosomes alone were observed.

The chromosomes of the primary and the secondary spermatocytes are considerably large. In respect to this point, this species is probably the largest of all the studied species belonging to the subfamily I am investigating, therefore the species is very favourable for cytological investigation. The first metaphase shows eleven distinct autosome bivalents and a single univalent X without exceptions (Fig.13 C, D). The autosome bivalents are gross and mostly are dumb-bell shaped, some of which are V shaped. The X-element takes its position on the eccentric region in the spindle at first metaphase as in many others examined. In every plate it appears as single body, which assumes a stout rod, however, it shows often a longitudinal split and exhibiting a V shape. It seems to be the largest one in the primary spermatocyte chromosomes. Here too, at first anaphase the single X goes undividedly to one pole, so regarding the X, two sorts of the secondary spermatocytes are produced. The secondary spermatocyte chromosomes are of distinct globular or oval shape (Fig.13 F). In one plate which contains 12 chromosomes, one extremely larger monad was distinguished, probably it would be the representative of the X-element. Although the spermatogonial chromosomes could not be observed, it is clear that the present species males possess eleven pairs of autosomes and a single X-element.

15. *Oxytate setosa* KARSCH

(Figure 14 A-Q)

This species is a beautiful greenish thomisid spider, living on young leaves. The material for the present study consist of the male and female gonads from a large number of individuals (juvenile, subadult and adult) captured between March and August. The material was preserved largely in modified NAVASHIN's solution and partly in FLEMMING's weak solution. The two fixatives gave excellent results.

¶ The testes from the juveniles and subadults which were secured between March and May contain a large number of meiotic division figures but no spermatogonial metaphase. It seems that the spermatogonial division in the present material may take place during the relatively short period in the juvenile spider. On the contrary, many oogonial metaphase spindles have been found in the ovaries from the subadult specimen fixed in early April.

The present material is, in fact, a member of subfamily Misumeninae, but in respect to the sex chromosomes, it shows entirely different result from other forms of the same subfamily studied by HACKMAN (1. c.)

and by me. As fully described in the foregoing pages, all the studied species males of the subfamily have been found to possess a single XO-mechanism instead of usual X_1X_2O -mechanism, but in the present species males an usual X_1X_2O -mechanism has been proved to occur again.

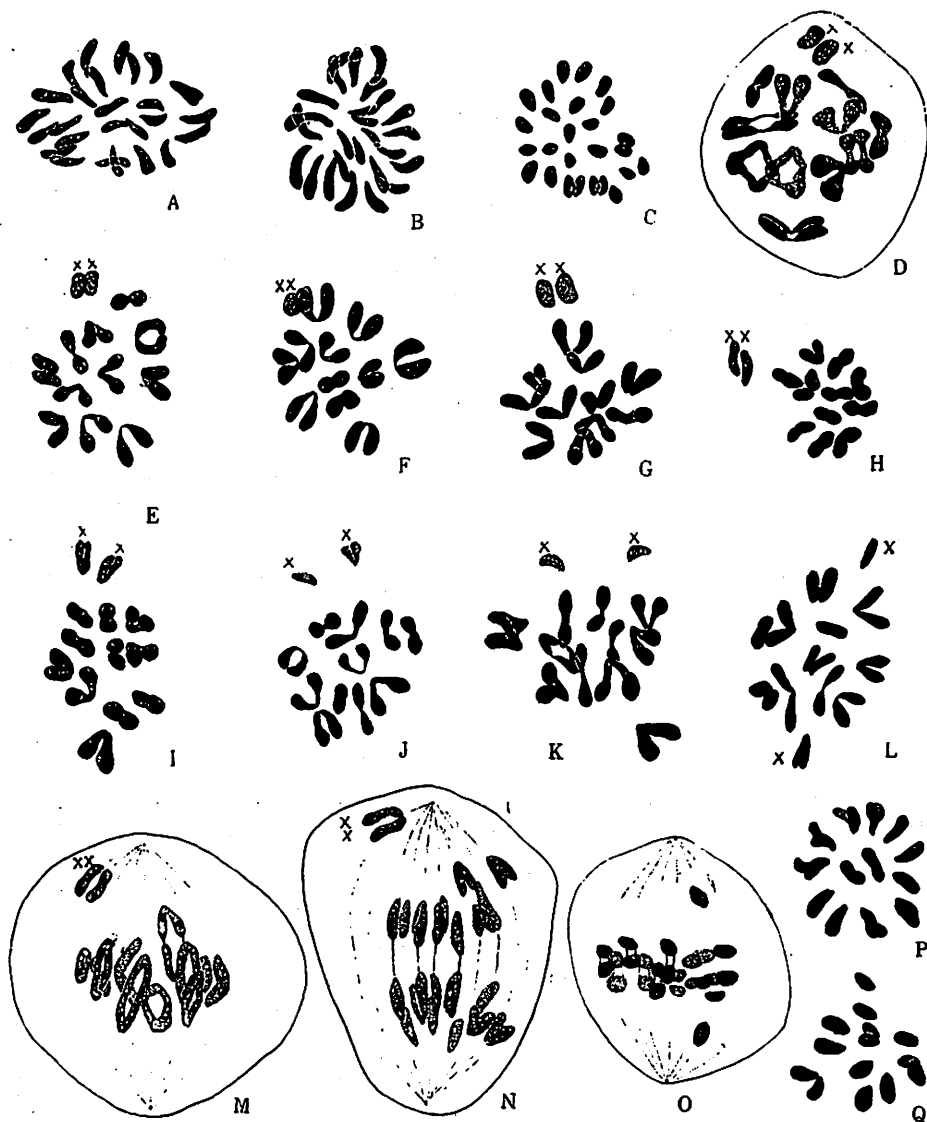


Figure 14. *Oxytate setosa*. All drawings at a magnification of $3000\times$ (reduced from $4000\times$). A-C, oögonial metaphases, showing 26 chromosomes. D-L, prometaphase and metaphases of the primary spermatocyte, showing 11 bivalents and 2 X's. M, side view of the primary spermatocyte metaphase, showing 2 X's. N, anaphase of the first division, profile view. O, profile view of the second division, showing abnormal separation of one cyad. P, secondary spermatocyte metaphase with 13 chromosomes. Q, the same with 11 ones.

As mentioned above, in spite of the lack of spermatogonial division figures, many oogonial metaphase spindles were observed, some of which are shown in Fig.14 A-C. There are twenty six chromosomes in every plate. All the chromosomes are acrocentric type, but as regards the shape and size of chromosomes several variations can be found in the different oogonia. In Fig.14 A, all the elements are relatively short rods of slight size difference, and all the chromosomes shown in Fig.14 C are highly condensed and each assumes globular rod with a slightly pointed proximal end. This kind of variation of oogonial chromosomes has already been observed in *Aranea Reaumuri* (PATAU 1948) and *Cyclosa octotuberculata* (SUZUKI 1951). In spite of the careful examination particular chromosomes suggesting the sex chromosomes were indistinguishable. Nevertheless, as will be stated below, an X_1X_2O -mechanism is demonstrated in the meiotic division of males, so that double set of X_1X_2 -elements ought to be contained in the female diploid set, namely, 4 out of 26 oogonial chromosomes are regarded as double set of X_1X_2 -elements.

Contrary to the spermatogonia, the dividing figures of the primary spermatocytes were observed distinctly. The chromosome and plate of the first metaphase are large and very favourable for precise study. The autosome bivalents of the primary spermatocyte is eleven, which is alike to that of the already studied species of the same subfamily. On the other hand, the sex chromosomes appear as two compound X's without exception (Fig.14 D-L). They are fairly distinguished in the all stages of meiotic division. At metaphase they always appear as two completely separated elements. In respect to arrangement and behaviour of the 2 X's, striking similarities are found between the present species and many others which are of usual X_1X_2O -mechanism. The individual X-element is of rod shape and nearly equal in length. They often show a longitudinal split and assuming V shape. As regards the arrangement, they show remarkable variation. In some plates both elements situate on the peripheral position of the spindle closely together (Fig.14 E, F), in others the X_1 and X_2 lie distinctly apart on the spindle with a certain distance each other (Fig.14 I-K). The distance between the two X's is variable in the different spindles. In the extreme cases as shown in Fig.14 L, one X stands on one side of the spindle and another X lies on the opposite side to the both poles and between these two X's present the autosome bivalents. Thus it is fairly true that an X_1X_2O -mechanism exists in the present species males.

The shape of the autosome bivalents is variable in the different metaphase plates. Some are V or horse-shoe shape and others are of dumb-bell shape or rod form. V or horse-shoe shaped bivalents look as if two rod chromosome segments are connected at their tapering proximal end. As is shown in Fig.14 D, at prometaphase the bivalents are particularly gross

and assume somewhat deformed appearance, at full metaphase the chromosomes are thickly condensed and they become to show clear configuration.

Here also, at anaphase the two X's go undividedly towards one pole (Fig. 14 M, N) and in the ensuing division they separate equally, so that in the secondary spermatocytes two kinds of cells are formed (Fig. 14 P, Q). One contains thirteen chromosomes ($11 A + X_1 X_2$) and the other, eleven ones (11 A). The chromosomes of the secondary spermatocyte are comparatively large, which are of globular or short rod shape with a pointed end. At metaphase II the X-elements are morphologically undistinguishable from others. At an early anaphase of the second division an abnormal separation of chromosome was observed. As is shown in Fig. 14 O, one of the dyads separates precociously and each monad goes ahead independently towards opposite pole.

Based on the above observations it is very true that the present species males have eleven pairs of autosomes and an $X_1 X_2 O$ -system. It must be noted that the occurrence of such an abnormal condition may be meaningful in considering the evolution of sex chromosomes.

16. *Diaea subadulta* BÖSENBERG et STRAND
(Figure 15 A-D)

The present genus too, belongs to the subfamily Misumeninae and no members of this genus have so far been studied cytologically. The testes from one subadult individual secured in May were fixed in modified NAVASHIN's solution.

In the sections some spermatogonial metaphase spindles were obtained, but which were not so favourable that the chromosome number could not be counted accurately. In one plate the chromosomes were counted up to twenty six. Here also, the chromosomes are of acrocentric and rod shape.

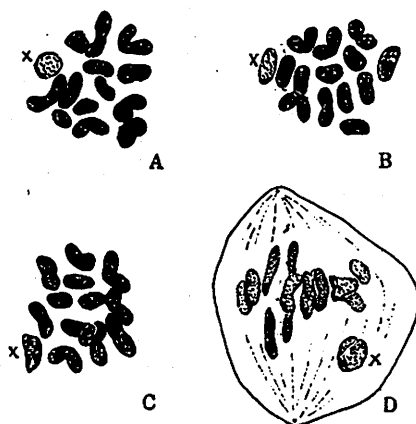


Figure 15. *Diaea subadulta*. All drawings at a magnification of $3000\times$ (reduced from $4000\times$). A-C, primary spermatocyte metaphases, showing 13 bivalents and a single X. D, side view of the first division, showing a single X.

In the primary spermatocyte the chromosomes are condensed and comparatively small in size. The bivalents are of dumb-bell shape or short rods, and V formed ones are rarely found (Fig.15 A-C). Every metaphase plate contains thirteen autosome bivalents and a single X-univalent invariably. It is thus worthwhile to notice that the autosome number of the present species differs evidently from that of all the closely related species of the same subfamily studied. Despite the different autosome number, the X-element is alike to related species. Namely, in the first division the X-element is always clearly recognized on the eccentric position of the spindle (Fig.15 D). The X assumes usually a compact rod or somewhat globular form, in which often a longitudinal split is visible.

Subfamily Philodrominae

17. *Philodromus roseus* KISHIDA

(Figure 16 A-N)

This species is common in gardens and fields in Japan, so that many fresh specimens are obtainable without difficulties. The present study was based on the observations of the testes from a number of juvenile, subadult and adult individuals which were captured during the time between March and May. The fixatives employed were NAVASHIN's solution, ALLEN-BOUIN's solution and modified FLEMMING's solution. The testes from juvenile spiders fixed in March and April contain many spermatogonial division figures and those from the subadult individuals secured in the middle of May are favourable for the observation of meiotic division.

The chromosomes of this genus have been studied by HACKMAN (1. c.) in the four species, *P. lavipes*, *P. emarginatus*, *P. aureolus* and *P. histrio*. These species males have known to have equal chromosome number 15 in haploid and two X-elements of different size. The result obtained in the present species is generally in accord with to the HACKMAN's report.

In *Philodromus* no spermatogonial metaphases have been observed by HACKMAN, in the present material, however, a large number of spermatogonial spindles have been obtained, which show the diploid chromosome number 28 beyond doubt (Fig.16. A-D). All the chromosomes are acrocentrics and are of subterminal or terminal spindle attachment. In many plates the chromosomes assume short, stout rods and mostly are curved in one side, so that at a glance they look like scale form. Such chromosomes show striking similarities with those of *Chiracanthium*-species mentioned in the foregoing pages. In some sections, however, the chromosomes are less stout and assume typical short rods. Regarding the size of chromosomes, a gradual diminution is noticed in the chromosome set, but a careful examination of the plate reveals that a single chromosome situated on the outer circle of the spindle is almost always distinguishable.

ble because of its larger size. In many cases it curves sharply and forming a striking contrast with others in the complement. It is regarded as one of the two compound X's which are possible to be identified in the first meiotic division and that it might correspond to the larger one. Another one, i. e. the smaller X is impossible to pick out in the spermatogonium because of the lack of distinct structure.

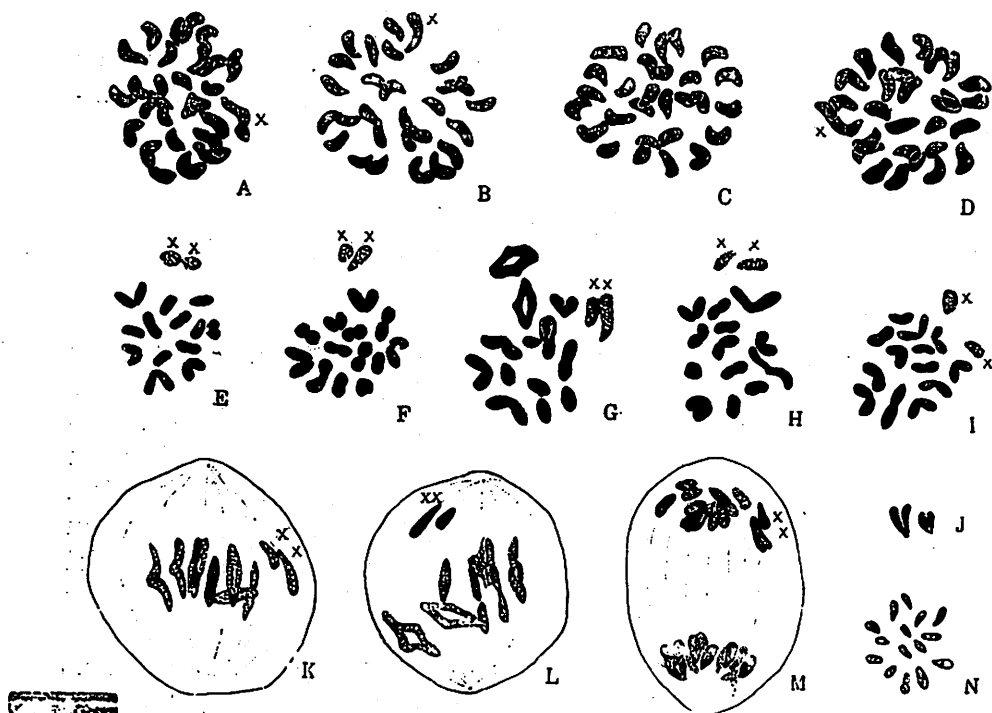


Figure 16. *Philodromus rosceus*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A-D, spermatogonial metaphases, showing 28 chromosomes. E-I, primary spermatocyte metaphases, showing 13 bivalents and 2 univalent X's. J, 2 X's from metaphase I, polar view. K, L, side views of metaphase I, showing 2 X's of different length. M, profile view of telophase of the first division. N, metaphase II, showing 15 chromosomes.

As shown in Fig.16 E-I, there are thirteen autosome bivalents and two univalent X's at first metaphase. The bivalents are V or dumb-bell shaped, and situate on the equatorial plate distinctly apart with an equal distance each other. The 2 X's are always recognizable as two isolated elements and as in many other spiders they stay on the peripheral region of the plate. The distance between the two X's is variable in the different figures. When viewed from lateral they assume rods (Fig.16 K, L), sometimes an equational split is visible in them and in such cases they show typical V shape (Fig.16 J). Individual X differs invariably in length, namely, one X is always longer than another X. In lateral aspect the ratio of the length is 3:2, which is equal to the four Finnish *Philo-*

dromus-species studied by HACKMAN (1. c.).

Here too, the X-elements are prereducational, so that two kinds of the secondary spermatocytes are produced. One half possesses fifteen chromosomes ($13 A + X_1 X_2$) and the other half contains thirteen ones (13A). The chromosomes of the second metaphase are small rods (Fig. 16 N). It was often observed that at first telophase the 2 X's lag behind others (Fig. 16 M).

18. *Philodromus nigrostriatipes* BÖSENBERG et STRAND
(Figure 17 A-H)

Two subadult males were captured in April and May, and their testes were preserved in modified NAVASHIN's solution.

The present species is closely related to the preceding species in the systematic standpoint, and in respect to the general feature of chromosomes striking similarities were found between the two materials. The chromosomes and nuclei of the former, however, are larger than those of the latter.

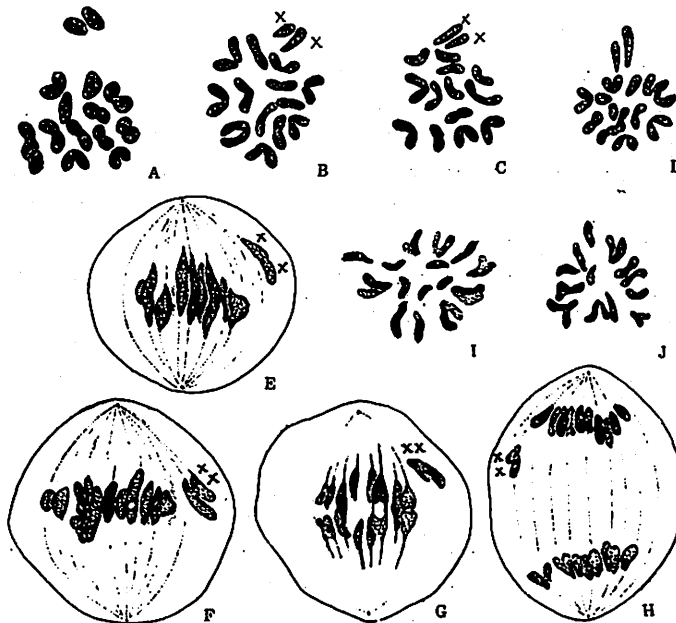


Figure 17. *Philodromus nigrostriatipes*. All drawings at a magnification of $3000\times$ (reduced from $4000\times$). A-D, primary spermatocyte metaphases, showing 13 bivalents and 2 X's. E, F, profile views of the first division metaphases. G, early anaphase of the first division. H, early telophase of the first division. I, secondary spermatocyte metaphase with 15 chromosomes. J, the same with 13 chromosomes.

The spermatogonial chromosomes are rod shaped, the number has

not been determined because of the lack of good dividing figures. On the other hand, numerous meiotic division figures were obtained. As in the previous species, the primary spermatocyte contains thirteen autosome bivalents and two univalent sex chromosomes (Fig.17 A-D). The X_1 and X_2 are distinguished as separate elements on the eccentric region of the spindle and here also, clear size difference is observed between them (Fig. 17 E-G). The ratio of the length is equal to the previous case. At first telophase such figures were found that the 2 X's lagging behind the autosomes (Fig.17 H).

Two sorts of the secondary spermatocytes were observed, one of which reveals 15 chromosomes and the other, 13 ones (Fig.17 I, J). The secondary spermatocytic chromosomes are relatively slender. The X-element can not be recognized morphologically in the second division.

19. *Philodromus aureolus japonicola* BÖSENBERG et STRAND
(Figure 18 A-O)

The material employed in the present study is the testes from three subadult individuals collected in April and May. The fixative was modified NAVASHIN's fluid.

The Finnish *P. aureolus*, the ground form of the present material has already been studied cytologically by HACKMAN (l. c.). According to HACKMAN the *P. aureolus* males show 15 haploid chromosome number and X_1X_2O -mechanism as in the allied forms of the same genus studied. In the present subspecies males, however, single XO-mechanism has been proved, though an equal autosome number is present.

In the spermatogonial division the odd chromosome number of 27 is clearly counted (Fig.18 A). This suggests the occurrence of a single X-element in the male. The chromosomes are relatively short rods, which are of slight size difference. Most of them are curved in one side and with tapering proximal end. The appearance of this metaphase plate resembles that of the above described *P. roseus* (compare Fig.18 A with Fig.16 B). As is well known in Fig. 18 A, the presumed homologous chromosomes arrange parallel on the metaphase plate and a single one situated in six o'clock position is found to have no mate, which is somewhat but distinctly larger than any others and is considered to represent an X-element. Except the size difference no particular morphological characters were recognized. The existence of a single X-element is well demonstrated again in the meiotic division.

Fig. 18. B, C show the prometaphases of the first division, in which an X-element is distinguishable from others because of its peripheral position, characteristic rod form and more or less different staining capacity. In the Finnish *P. aureolus* HACKMAN found two closely situated X-elements

of distinct size difference at prometaphase (HACKMAN's Figs. 220-221). In the present case, however, no such figures were observed, though numerous slides were examined. At full metaphase the single X takes its eccentric position on the spindle as in many others and is clearly identified. Namely, in the profile view of the first division it assumes always a single rod, here also, a longitudinal split is often visible (Fig. 18 G-I).

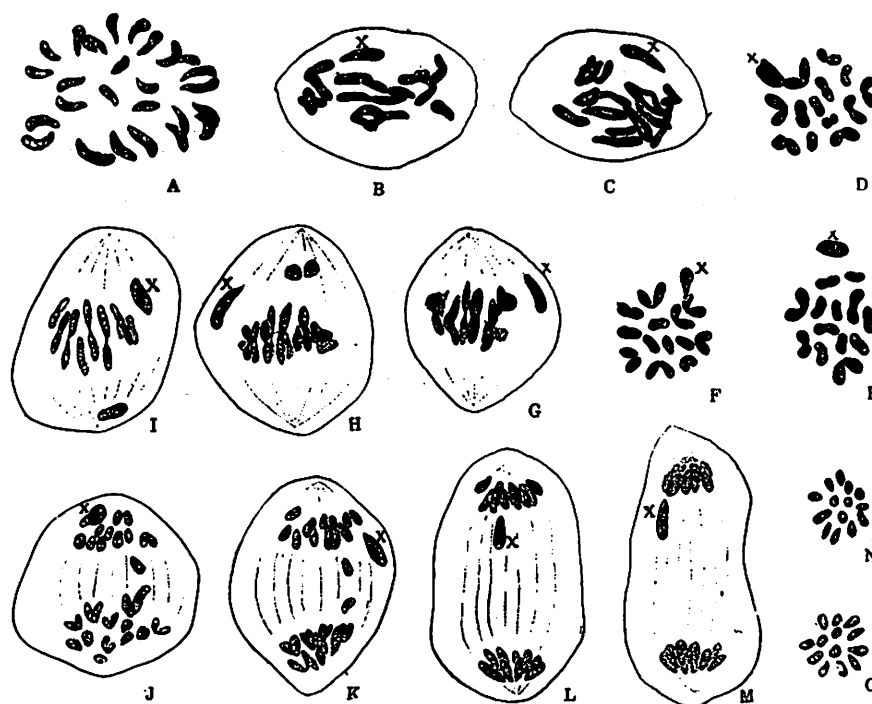


Figure 18. *Philodromus aurcolus japonicola*. Except A (3000 \times) all drawings at a magnification of 2200 \times (reduced from 2400 \times). A, spermatogonial metaphase, showing 27 chromosomes. B, C, primary spermatocyte prometaphases, showing a single X-element. D-F, primary spermatocyte metaphases, showing 13 bivalents and a single univalent X. G-I, profile views of the first division meta-anaphases, showing a single X and abnormal separation of autosome bivalents. J, K, late anaphases of the first division, lateral aspects, showing the abnormality in the separation of one autosome bivalent. L, M, lateral aspects of the first division telophases. N, secondary spermatocyte anaphase with 14 chromosomes. O, the same with 13 chromosomes.

At metaphase I thirteen autosome bivalents are present without exception. The bivalents are condensed and are of dumb-bell shape or V shape (Fig. 18 D-F). The general configuration of the bivalents is remarkably similar to that of the Finnish *P. aureolus* (HACKMAN's Fig. 212).

At telophase of the first division it has been found that a single X-element lags behind autosomes (Fig. 18 K-M) as in *P. rosaeus* and *P. nigrostriatipes* described above.

In the secondary spermatocyte the chromosomes were clearly counted,

where some are of thirteen and others fifteen elements. The chromosomes are short rods and at anaphase they assume distinct globular or small rod shape (Fig. 18 N, O).

Based on the above observation, it is fairly true that the present material males possess thirteen pairs of autosomes and a single X-element.

In the first division some abnormalities were found in the separation of autosomes as is shown in Fig. 18 H-K.

20. *Tibellus tenellus* (L. KOCH)

(Figure 19 A-I)

The male gonad from a single subadult specimen collected in May was fixed in modified NAVASHIN's fluid. In the present genus, one Finnish member, *Tibellus oblongus* has already been investigated cytologically in the HACKMAN's paper (1948). By HACKMAN the species males have eleven autosomes in haploid and X_1X_2 elements. Although the same X-elements were demonstrated in the present species, the autosome number was thirteen, which is different from the Finnish species. The spermatogonial chromosomes and all phases of the spermatogenesis were observed in the same testis.

The spermatogonial chromosomes were counted in a single metaphase plate, in which the diploid chromosome number showed 28 (Fig. 19 A).

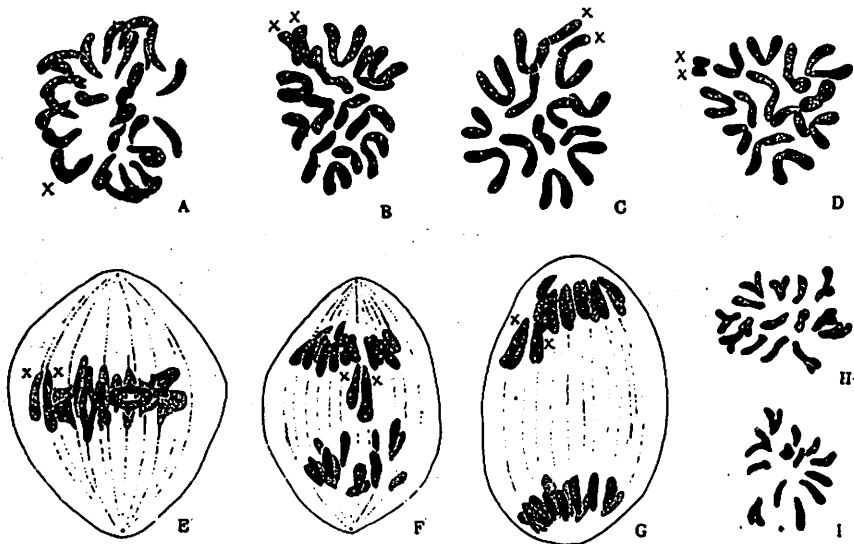


Figure 19. *Tibellus tenellus*. Except A (3000 \times) all drawings at a magnification of 2200 \times (reduced from 2400 \times). A, spermatogonial metaphase, showing 28 chromosomes. B-D, primary spermatocyte metaphases, showing 13 bivalents and 2 univalent X's. E, side view of the first division metaphase. F, G, late anaphase and early telophase of the first division respectively. H, secondary spermatocyte metaphase, showing 15 chromosomes. I, the same with 13 chromosomes.

The chromosomes are curved rod shape as in the related species of the same subfamily. In this case, however, the chromosome length is slightly but distinctly larger than that in others. In Fig.19 A, one situated in seven o'clock position is distinguished due to the largest size and proximal constriction. The similar feature has already been found in *Philodromus roseus* etc. and such chromosome is regarded as an X-element of the two multiple sex chromosomes.

In the first division a large number of beautiful metaphase spindles were obtained. At this stage the chromosomes are large and distinct and very favourable for observation. As is shown in Fig.19 B-D thirteen autosome bivalents and two X-elements are plainly counted. The bivalents are mostly large typical V shape, in which a chiasma is considered to be located in the proximal region. The general feature of the bivalents differs strikingly from that of *T. oblongus* pictured by HACKMAN (HACKMAN's Fig. 216).

The two X-elements are found clearly on the outer circle of the spindle, which are pointing their proximal end to one pole (Fig.19 E). Clear size difference can be observed between the X_1 and X_2 . In the present case the ratio is approximately 4:3, which is equal to that of *T. oblongus* studied by HACKMAN (1. c.). Thus it is known that the relative length of the smaller X to the larger one in this species is larger than that in *Philodromus roseus* and *P. nigrostriatipes*. The variation of the relative length of the 2 X's seems to be worthwhile to notice in explaining the evolution of the sex chromosomes in spiders.

At early and late telophase of the first division the X-elements usually lag behind autosomes (Fig.19 F, G). The secondary spermatocytic metaphase resembles generally to that of *Philodromus nigrostriatipes* mentioned above and here too, in respect to the X-elements, two sorts of cells are observed (Fig.19 H, I).

IV. Family Oxyopidae

In the present family the following four species belonging to two different genera have already been studied cytologically: *Oxyopes salticus* by PAINTER (1914), *O. ramosus* by HACKMAN (1. c.), *O. hindustanicus*, and *Peucetia viridana* by GOWDA(1950), all these spiders except the last one, are known to show similarities in the general feature of the chromosomes, i. e. they have equal chromosome number of eleven in haploid and single XO type of sex determination.

In the present study two Japanese species, *Oxyopes sertatus* and *Nishina generosa* were dealt with. The results obtained are similar to those of so far reported *Oxyopes*-species. Furthermore, in *Oxyopes* the occurrence of single X-element has been demonstrated by the direct observation of

the female chromosomes also.

21. *Oxyopes sertatus* L. KOCH

(Figure 20 A-O)

The present species is one of the most common spiders in Japan and a large number of specimens captured during the time between March and June, were employed for the study. The male and female gonads were preserved in CAROTHER's solution, NAVASHIN's solution and modified NAVASHIN's solution.

The testes of the juvenile spiders fixed in early spring are very favourable for the observation of the spermatogonial division. The oogonial division figures too, have been obtained in the ovaries from the juvenile females secured in the same season. On the other hand, the maturation division has been observed based on the testes from the subadult individuals fixed in April and May.

In the present material the nucleus and chromosomes are comparatively large and the chromosome number is small, so that it is favourable for chromosome study. In the spermatogonia exist twenty one distinct chromosomes as in *O. ramosus* and *O. hindustanicus*. All the chromosomes are acrocentric and usually stout rod shaped, some of which are slightly curved in one side (Fig. 20 A-C). When the section is stained lightly the chromosomes show true outline, in which the chromosomes are typical rods and with a tapering inner end, some are of distal globular segment. In many plates a single element is distinguished from others by the larger magnitude and particular shape. It has no mate in the complement and is distinctly the largest of all, and sometimes it curves sharply in the interstitial region. In some cases a clear constriction is found in that locus. When constricted strongly as in Fig. 20 C, the chromosome shows a clear bipartite structure, nevertheless, it is never true metacentric but acrocentric and regarded as a single X-element. It is very interesting that in respect to the morphological character of the single X, marked similarity is found between the present material and many species belonging to the subfamily Misumeninae.

The X-element of *Oxyopes ramosus* reported by HACKMAN (1. c.) is the largest one in the set and it is provided with a non-staining transverse suture and in that region it is divided into two arms of different length, and he regarded it as metacentric. The X-element pictured in his plate (Hackman's Figs. 91 and 269) is markedly similar with that pictured in Fig. 20 A (labelled as X). The X-element of Indian *Oxyopes hindustanicus* studied by GOWDA (1950) is also the largest one in the set and is straight rod shaped.

In the oogonial metaphase twenty two chromosomes are clearly count-

ed (Fig. 20 D). The configuration of the chromosomes is like that of the spermatogonium. Here the chromosome number is even and no unpaired chromosome is found. The largest one pair is clearly distinguished from others in the set and is considered to be the double X-elements. Thus the single X-element existed in the male is found as a couple in the female.

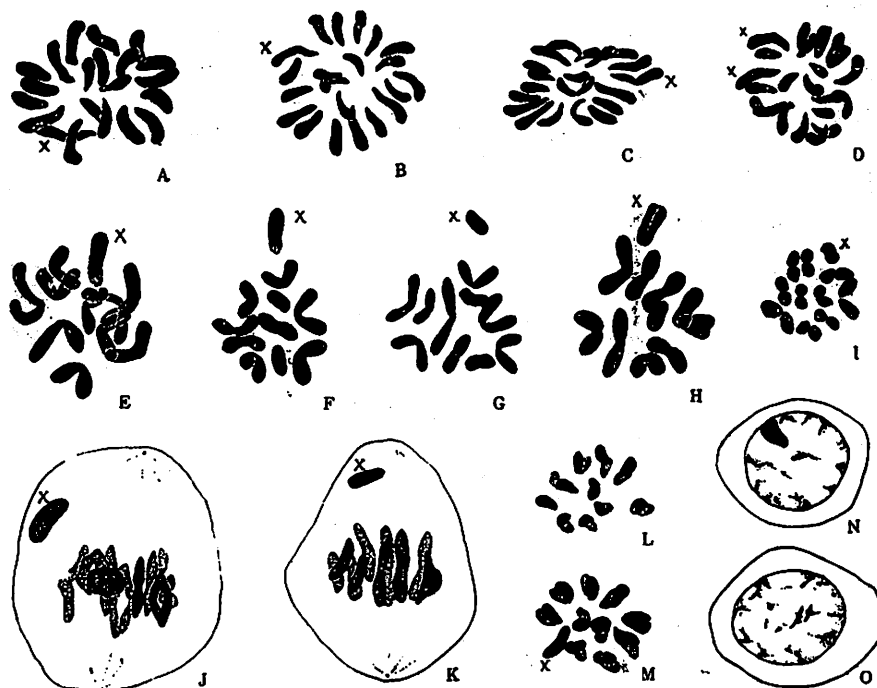


Figure 20. *Oxyopes sertatus*. All drawings at a magnification of 2200 \times (reduced from 2400 \times). A-C, spermatogonial metaphases, showing 21 chromosomes. D, oogonial metaphase, showing 22 chromosomes. E, primary spermatocyte prometaphase, showing 10 bivalents and a single X. F-I, first division metaphases, showing the migration of a single X. J, K, side views of the first division metaphases, showing the migration of X. L, metaphase II with 10 chromosomes. M, the same with 11 ones. N, early spermatid, showing heteropycnotic X. O, the same without X.

The metaphase plate of the primary spermatocyte shows ten autosomal bivalents and an univalent X (Fig. 20 E-H). The bivalents assume V or dumb-bell shape, in which a chiasma is interstitial. When thickly condensed the bivalents show a dumb-bell form with a median non-staining suture (Fig. 20 I). The X-element when viewed from one pole lies on the peripheral region of the metaphase plate. As is shown in the profile of metaphase I (Fig. 20 J, K), it stands usually on the intermediate position between the equatorial plane and one of the poles, parallel to the spindle axis. At that stage it assumes rod shape, but often shows an equational split.

PAINTER (1914) reported the occurrence of an usual X_1X_2O -system

in *Oxyopes salticus*. The two X's shown in his plate (PAINTER's Figs. 116-117) are very much alike the single X which shows a longitudinal split as shown in the present material (Fig. 20 H), moreover, as HACKMAN (1. c.) has already pointed out, PAINTER described nothing on the separation of each X in the course of division, therefore, *O. salticus* also might have a single X-element.

Here also, two sorts of the secondary spermatocytes are produced, one of which contains ten autosomes plus X-element and another, ten autosomes alone (Fig. 20 L,M). In the metaphase plate containing 11 chromosomes, one is markedly distinguished due to its magnitude, and which is considered to be X-element (Fig. 20 M). The X-element is distinguishable in young spermatids also, some are of heteropycnotic X-element and others without such element (Fig. 20 N,O).

22. *Nishina generosa* KISHIDA

(Figure 21 A-C)

The present genus was created by KISHIDA based on the present material, I regret to say, however, that a regular description of the species and genus has never been made public. A single subadult male gathered in April was employed for the present material. The testes was fixed in modified NAVASHIN's solution.

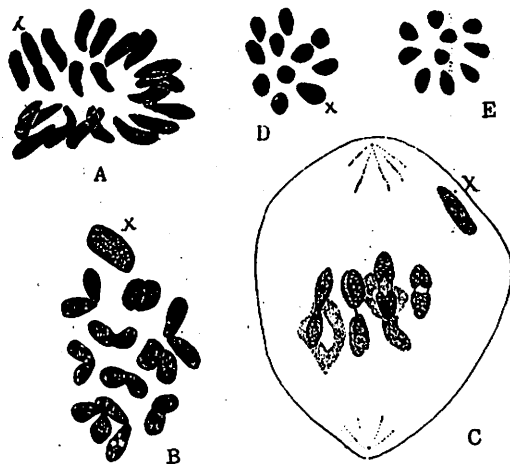


Figure 21. *Nishina generosa*. All drawings at a magnification of 3000 \times (reduced from 4000 \times). A, spermatogonial metaphase, showing 21 chromosomes. B, primary spermatocyte metaphase, showing 10 bivalents and a single X. C, profile view of the first division metaphase, showing X. D, metaphase II, with 11 elements. E, the same, with 10 elements.

This species is closely allied to the preceding species in the taxonomic point of view, consequently as regards the chromosomes marked resemblance is found between the two species. Namely, in the present species male too, the chromosome number is twenty one in diploid and eleven in haploid and XO type of sex determination is found.

The spermatogonial chromosomes are stout rods, with a little size difference (Fig. 21 A). Although the section was stained in more or less deep colour, the X-element has been clearly distinguished in the spermatogonial metaphase. As shown in Fig. 21 A, the X assumes a straight rod and it is one of the largest in the complement and provided with a distinct transverse constriction in the submedian region. The condition is similar to *Oxyopes hindustanicus* studied by GOWDA (1950).

The number, morphology and behaviour of chromosomes in the meiotic divisions are likely to *Oxyopes sertatus*.

DISCUSSION

I. Chromosome number and chromosome morphology of the studied families

In the foregoing pages the chromosomes of twenty two Japanese species of spiders belonging to the four families, Clubionidae, Sparassidae, Thomisidae and Oxyopidae have been dealt with. When already published data are added to the present material, the cytologically studied spiders belonging to these families amount to forty two species. The details of the species are as follows: Clubionidae 11 species, Sparassidae 4 species, Thomisidae 21 species and Oxyopidae 6 species. The numerical relationship among the chromosomes of these 42 species are given in the Table II.

Of these the chromosome number of Sparassidae is markedly larger ($n=22-23$) than that of the remaining three families, in which the number is relatively small ($n=11-15$) and varies within narrow range. So far as the chromosome number is concerned, therefore, considerable difference exists between Sparassidae and the remaining families. The general description of the karyotype in individual families are given below.

1. Family Clubionidae

The chromosomes of this family have been studied in 8 species of subfamily Clubioninae, 2 species of subfamily Micariinae and 1 species of subfamily Corinninae. The chromosome numbers of the studied species of Micariinae and Corinninae are the same, 12 in haploid. In Clubioninae the haploid number is 12 in 4 cases, 13 in 1 case and 14 in 3 cases, of these 14 is found in *Chiracanthium* alone, and 12 and 13 are, in *Clubiona*.

Table II. Chromosome number in Clubionidae, Sparassidae, Thomisidae and Oxyopidae

Species	Sex	Dipl.	Haploid		Reference
			I cyte	II cyte	
Fam. Clubionidae					
Subfam. Clubioninae					
<i>Chiracanthium japonicum</i>	♂	26	12+X ₁ X ₂	12 14	SUZUKI
<i>kompiricola</i>	♂	26	12+X ₁ X ₂	12 14	♂
<i>unieum</i>	♂	26	12+X ₁ X ₂	12 14	♂
<i>Clubiona holosericea</i>	♂	—	10+X ₁ X ₂	— —	HACKMAN 1948
<i>subsultans</i>	♂	—	10+X ₁ X ₂	— 12	♂
<i>phragmitidis</i>	♂	—	10+X ₁ X ₂	10 12	♂
<i>japonicola</i>	♂	22	10+X ₁ X ₂	10 12	SUZUKI
<i>lena</i>	♂	24	11+X ₁ X ₂	— —	♂
Subfam. Micariinae					
<i>Micaria decorata</i>	♂	—	10+X ₁ X ₂	10 12	HACKMAN 1948
<i>unifascigera</i>	♂	—	10+X ₁ X ₂	— —	SUZUKI
Subfam. Corinninae					
<i>Trachelas japonicus</i>	♂	—	10+X ₁ X ₂	— 12	♂
Fam. Sparassidae					
Subfam. Micrommatinae					
<i>Micrommata viridissima</i>	♂	±35	16+X ₁ X ₂ X ₃ ?	— —	HACKMAN 1948
Subfam. Heteropodinae					
<i>Heteropoda nentoria</i>	♂	41	19+X ₁ X ₂ X ₃	19 22	SUZUKI & CKA-
" "	♀	44	—	—	DA 1950
<i>forcipata</i>	♂	41	19+X ₁ X ₂ X ₃	19 22	SUZUKI
Subfam. Sparianthidinae					
<i>Thellicopsis severa</i>	♂	43	—	— —	♂
Fam. Thomisidae					
Subfam. Misumeninae					
<i>Misumena vatia</i>	♂	—	11+X	11 —	HACKMAN 1948
<i>tricuspidata</i>	♂	23	11+X	11 12	SUZUKI
<i>Xysticus triguttatus</i>	♂	—	11+X ₁ X ₂ ?	11 13?	PAINTER 1914
<i>niaticus</i>	♂	23	11+X	— —	HACKMAN 1948
<i>ulmi</i>	♂	—	11+X	11 —	♂
" "	♀	—	12	—	♂
<i>insulicola</i>	♂	23	11+X	11 12	SUZUKI
<i>Xysticus ephippiatus</i>	♂	23	11+X	11 12	♂
<i>Coriarachne fulnipes</i>	♂	23	—	— —	♂
<i>Oxyptila decorata</i>	♂	—	11+X	11 12	♂
<i>Oxylate setosa</i>	♂	—	11+X ₁ X ₂	11 13	♂
" "	♀	26	—	—	♂
<i>Diaea subadulta</i>	♂	—	13+X	— —	♂
Subfam. Philodrominae					
<i>Philodromus laevis</i>	♂	—	13+X ₁ X ₂	— —	HACKMAN 1948
<i>emarginatus</i>	♂	—	13+X ₁ X ₂	13 15	♂
<i>aureolus</i>	♂	—	13+X ₁ X ₂	13 15	♂
<i>aureolus japonicola</i>	♂	27	13+X	13 14	SUZUKI
<i>histrio</i>	♂	—	13+X ₁ X ₂	— —	HACKMAN 1948
<i>roseus</i>	♂	28	13+X ₁ X ₂	13 15	SUZUKI
<i>nigrostriatipes</i>	♂	—	13+X ₁ X ₂	13 15	♂

<i>Thanatus formicinus</i>	♂	—	13+X ₁ X ₂	13 15	HACKMAN 1948
<i>Tibellus oblongus</i>	♂	—	11+X ₁ X ₂	11 13	"
<i>tenellus</i>	♂	28	13+X ₁ X ₂	13 15	SUZUKI
Fam. Oxyopidae					
<i>Oxyopes salticus</i>	♂	—	10+X ₁ X ₂	— —	PAINTER 1914
<i>ramosus</i>	♂	21	10+X	10 11	HACKMAN 1948
<i>hindustanicus</i>	♂	21	10+X	10 11	COWDA 1950
<i>seriatus</i>	♂	21	10+X	10 11	SUZUKI
"	♀	22	—	—	"
<i>Nishina generosa</i>	♂	21	10+X	10 11	"
<i>Peucedelia viridana</i>	♂	28	13+X ₁ X ₂	13 15	COWDA 1950

Although chromosome number varies, the sex chromosome mechanism of X₁X₂O type is uniform within the family, therefore, the difference of chromosome number is caused by the variation of autosome number. The chromosomes of the family are equally acrocentric type and are of terminal or subterminal spindle attachment. And in respect to the morphological characters and behaviour of chromosomes, essentially different characters are impossible to find out in the studied species, though the size and form of chromosome vary. Accordingly, it seems rather difficult to tell how such different autosome number has been derived, in other words, now it is not determined which is the most primitive among 10, 11 and 12 autosome numbers.

2. Family Sparassidae

In the present family four representatives belonging to three sub-families have been studied cytologically. Every one of the studied species shows a comparatively large chromosome number ($n=19\text{--}23$) and that an unusual multiple sex chromosome mechanism of X₁X₂X₃O type exists without exception (though it has not been proved in *Thelcticopis severa* by the direct observation). Although it is not published, McINTOSH's data support the above fact. According to his personal communication, he has also observed forty three chromosome number in diploid and twenty three one in haploid and 3 X's mechanism in the two forms males of *Deleena* and *Olios* genera belonging to the Sparassidae. Thus such a large chromosome number is commonly found in the studied species of the family, accordingly, it is highly probable that the same condition would be proved in the most species of the family, if further studies will be made.

When compared the chromosome number of Sparassidae with that of the closely related families, it will be found that such a large chromosome number as 21 or 23 is known only in the Sparassidae.

The three families of Thomisidae, Aphantochilidae and Sparassidae were grouped in the same Grade Laterigradae by SAVORY(1928). PETRUNKE-

VITCH (1933) also considered that the Sparassidae is closely related to the Thomisidae and Aphanthochilidae, and these three groups represent a fairly homogeneous line. Of these Aphanthochilidae has not yet been studied cytologically, in the Thomisidae the studied species amount to twenty one and all of them showing 12 to 15 haploid chromosome number which is usually happen in numerous modern spiders. In the BRISTOWE's classification (BRISTOWE 1938) the nine families of Prodidomidae, Homalonychidae, Drassidae, Clubionidae, Anyphaenidae, Sparassidae, Platoridae, Thomisidae and Salticidae were arranged in the same section of the Clubionoidea. Except Prodidomidae, Homalonychidae and Platoridae in which no members have been investigated, the remaining six families are known to have the haploid chromosome number 11-15 in all the species studied. Although the grouping of spiders' families is somewhat variable in the different arachnologists, it may be concluded that regarding the chromosome number, marked difference can be found between the Sparassidae and its related families, contrary to the taxonomic relation. Furthermore, it must be worthwhile that the Sparassidae differs from the related families in the size of chromosome and nucleus, namely, that of the former is remarkably larger than that of the latter.

Therefore now in respect to the chromosomes, we meet with a great difficulty in interpreting the relationship between the Sparassidae and its related families. If we accept the present position of the Sparassidae in the spiders' classification of many arachnologists, we should be compelled to presume some sudden changes in chromosomes between them. Whether the Sparassidae-type of chromosomes is more primitive or not? This is very interesting problem, but very difficult to answer. Here we remember the chromosomal relationship between the *Araneus ventricosus* and its allied forms reported in the previous paper (SUZUKI 1951). In *A. ventricosus* present twenty two pairs of autosomes instead of eleven pairs of the allied forms, and the author considered that the *A. ventricosus*-type of chromosomes might be old and possibly from that the modern *Araneus*-type might have been arisen. The similar interpretation may be applicable to the present case also, namely, the Sparassidae-type of chromosomes may be in more primitive condition, from which that of the allied families might have been originated.

3. Family Thomisidae

This family consists of two morphologically distinct subfamilies Misumeninae (=Xysticinae) and Philodrominae, though some authors regard the two subfamilies as two separate families. At any rate, it is true that both groups are closely related each other in the systematic viewpoint. The cytologically studied species of this family amount to twenty one, in which different autosome numbers 11 and 13 (n) are found, of

which 11 is characteristic for ten out of eleven species of the Misumeninae and one species of Philodrominae. On the other hand, 13 is known in nine out of ten studied species of Philodrominae and a single species of Misumeninae. Thus the haploid autosome number 11 and 13 are characteristic for the Misumeninae and Philodrominae respectively, with only a few exceptions. In addition to the autosome number, the sex chromosome mechanism is very characteristic for both subfamilies. Although PAINTER (1914) reported the presence of an usual X_1X_2O -mechanism in *Xysticus triguttatus*, judging from his Figures (PAINTER's Figs. 95-96), the species is very probably has XO-mechanism. Therefore, except a single species *Oxytate setosa* of the present study, all the ten species out of eleven studied species of the Misumeninae possess a single X-element. On the other hand, in Philodrominae 2 X's mechanism is dominant and found in nine species out of ten studied species with the exception of *Philodromus aureolus japonicola*. In terms of the autosome number and sex chromosome mechanism, the two subfamilies show somewhat marked contrast. But the feature is broken in *Oxytate setosa*, *Diaea subadulta*, *Tibellus oblongus* and *Philodromus aureolus japonicola*.

Oxytate setosa, a member of subfamily Misumeninae shows eleven pairs of autosomes and X_1X_2O -mechanism. As stated just above its autosome number is characteristic for the Misumeninae, but the sex chromosome mechanism is unusual in the subfamily, thus in this respect it seems to be closer to Philodrominae. The X_1 and X_2 elements of *Oxytate*, however, are of nearly equal length, so that both elements are clearly distinguishable from that of the Philodrominae. Thus *Oxytate setosa* shows a Misumeninae-type in autosomal feature, and in respect to the sex chromosomes, it bears some resemblance to Philodrominae. So far as the chromosome is concerned, the species is interesting material in the Thomisidae.

Diaea subadulta shows an aberrant chromosome number in the Misumeninae. It possesses 13 autosomes in haploid and a single X-element. Thus the sex chromosomes shows Misumeninae-type and the autosome number Philodrominae-type. In the cytological point of view *Diaea subadulta* may be regarded as intermediate between Misumeninae and Philodrominae.

In the subfamily Philodrominae two abnormalities are found in *Philodromus aureolus japonicola* and *Tibellus oblongus*. The former shows 13 autosomes (n) and a single X-element. Thus in autosomes it accords with and differs in sex chromosomes mechanism from usual *Philodromus*-species and resembles rather Misumeninae. Here also, in respect to the chromosomes, it is likely to show an intermediate position between the both subfamilies. It would be worthwhile to notice that regarding the sex chromosomes, marked difference is found between the Japanese *Philodromus aureolus japonicola* and the Finnish ground form, *P. aureolus*, though

both forms show remarkably similar morphological characters as is described by BÖSENBERG and STRAND (1906). As it will be discussed in the following pages, the XO type of *japonicola* may have been derived from the X_1X_2O -condition of *aureolus*-type by the elimination of either one element.

Tibellus oblongus studied by HACKMAN (1. c.) shows an X_1X_2O -mechanism of *Philodromus*-type, but possesses haploid autosome number 11 of Misumeninae-type. Thus in respect to the chromosomes, it may stand intermediate between the both subfamilies.

4. Family Oxyopidae

The chromosomes of this family have been studied in six species which consist of four species of *Oxyopes* (PAINTER 1914, HACKMAN 1948, SUZUKI 1950a, 1952, Gowda 1950), one species in *Nishina* (SUZUKI 1952) and one species in *Peucetia* (GOWDA 1950). Except *Peucetia*, all the studied species have equal chromosome number of 11 in haploid and an XO-mechanism, though PAINTER reported X_1X_2O -mechanism in *Oxyopes salticus*. As mentioned above, however, it is highly probable that PAINTER erroneously observed the X-element and the species is of true XO type. The single X-element has been demonstrated by the direct observation of the female chromosomes of the *Oxyopes sertatus* too, in the present study. The single XO-mechanism in the male is thus found in the majority of the family and in this respect, the Oxyopidae bears marked similarities with the subfamily Misumeninae of the family Thomisidae.

The characteristic feature of this sex chromosome has been broken by the discovery of the usual X_1X_2O -mechanism in the Indian spider, *Peucetia viridana* (GOWDA 1950). *Peucetia* has 13 autosomes in haploid and 2 X's, which are of different size. So the general feature of chromosomes in *Peucetia* seems to be very similar with that of many *Philodromus*-species belonging to the family Thomisidae. The coexisting of XO and X_1X_2O type within the same family recalls us the similar condition of the family Thomisidae. Such a parallelism seems to throw some lights upon the solution of the problem of the evolution of chromosome number and sex chromosomes.

II. Feature of sex chromosomes

The sex chromosomes of spiders were studied by many authors such as CARNOY (1885), WAGNER (1896a, b), WALLACE (1900, 1905, 1909), BÖSENBERG (1904), MONTGOMERY (1905), BERRY (1906), PAINTER (1914), SOKOLSKA (1925), HARD (1939), REVELL (1947), PATAU (1948), HACKMAN (1948), SUZUKI (1949, 1950a, b, 1951a, b, 1952), SUZUKI and OKADA (1950) and GOWDA (1950) etc. According to the studies of these workers the

two arms of unequal length. And he said that it is not completely clear whether such X-element is metacentric or accidentally, temporarily fused chromosome, but he insisted on the former opinion in his paper, and described as follows: "Sehr wahrscheinlich ist das X als metazentrisch zu betrachten" (HACKMAN 1948, p. 26) and "Das sehr wahrscheinlich metazentrische X bei *Oxyopes ramosus* könnte durch zentrisch Fusion zweier freien X-chromosomen entstanden sein" (HACKMAN 1948, p. 70).

The X-element of *Oxyopes ramosus* seems to be completely similar to that of *O. sertatus*, *Nishina generosa* and some of Misumeninae studied by me. I think that he might have regarded erroneously a constricted X-chromosome as metacentric one. He has recently confessed in his personal communication that he was probably mistaken in interpreting the X-chromosome of *Oxyopes ramosus* as metacentric.

In respect to the morphology and behaviour of a single X in the meiotic divisions, marked similarities have been found in all the studied species. Namely, in the first metaphase it usually takes an eccentric position on the spindle, at anaphase it passes one pole undividedly and in the second division separates equationally. At first metaphase it assumes rod shape, in which a longitudinal split is often visible, but the constriction appeared in the spermatogonium can not be found probably due to the thick condensation. In the second division the X-element is indistinguishable, in some cases, for example in *Misumena tricuspidata*, *Oxyptila decorata* and *Oxyopes sertatus*, however, it has been identified by its larger size.

2. X_1X_2O type

The X_1X_2O type of sex determination is found in twenty two species out of forty two species studied, namely, in eleven species of Clubionidae, one species of Misumeninae (*Oxytate setosa*), nine species of Philodrominae and one species of Oxyopidae (*Peucetia viridana*). Thus the present type is characteristic for the majority of Clubionidae and Philodrominae, on the other hand, its occurrence is rather exceptional in Misumeninae and Oxyopidae.

In respect to the size of X_1 and X_2 elements, several conditions have been observed. The individual X is almost equal in length in all the studied species of Clubionidae, *Oxytate setosa* and *Thanatus formicinus* of Thomisidae, but in Philodrominae except *Thanatus*, and in *Peucetia* of Oxyopidae clear size difference is recognized between the both X's. And careful examination reveals that the degree of its difference varies in the different species. In this point the family Thomisidae, especially the subfamily Philodrominae, is worthwhile.

In *Thanatus formicinus* (HACKMAN 1. c.) and *Oxytate setosa* studied by me each X has approximately equal length, but in the two species

sex determining mechanism of an X_1X_2O type is characteristic for a large majority of spiders. And $X_1X_2X_3O$ and XO type have been found only recently in some particular families. Further occurrence of these sex chromosome mechanisms, particularly that of XO and $X_1X_2X_3O$ type has been demonstrated in the present study. The presence of single X-element has been known only in three families, Thomisidae (HACKMAN 1948, SUZUKI 1950a, 1952), Oxyopidae (HACKMAN 1948, SUZUKI 1950a, 1952, GOWDA 1950) and Salticidae (HACKMAN 1948). The occurrence of 3 X's mechanism is restricted in a few cases and now is found in some species of Agelenidae (SOKOLSKA 1925, REVELL 1947, HACKMAN 1948, SUZUKI unpublished) and Sparassidae (SUZUKI and OKADA 1950, SUZUKI 1952).

In the following the sex chromosomes in the studied material in the present paper and its allied forms will be discussed.

1. XO type

The single X-element is found in 16 species out of 42 studied species, namely, in 2 species of *Misumena*, 5 species of *Xysticus*, 1 species of *Coriarachne*, 1 species of *Oxyptila*, 1 species of *Diaea* (Misumeninae), 1 species of *Philodromus*, 4 species of *Oxyopes* and 1 species of *Nishina*. The occurrence of this type in Misumeninae has been first reported by HACKMAN (I. c.). In the present study the single X-element has been clearly distinguished in the spermatogonial division of *Misumena tricuspidata*, *Xysticus insulicola*, *X. ephippiatus* and *Coriarachne fulvipes*. The X-element of these species is generally alike in the morphological characters, namely, it is one of the largest in the complement and assumes usually rod shape, but sometimes it shows an interstitial constriction. In some cases, particularly in *Xysticus insulicola*, it stains faintly, when compared with autosomes. Thus it is almost always distinguishable from others in the mitotic spindles. The similar morphological character has been proved to be found in the X-element of Oxyopidae too. GOWDA (1950) found three particularly large chromosomes in the spermatogonial metaphase of *Oxyopes hindustanicus* and he considered one of them may be the sex chromosome, furthermore, he recognized a single chromosome showing a distinct non-staining gap in the interstitial region. Such a chromosome seems to correspond with a single X-element demonstrated in *Oxyopes sertatus* and *Nishina genivosa* in the present study. And that the existence of the single X has been proved more definitely by the direct observation of the female mitosis.

As for the single X-element in *Oxyopes*, HACKMAN (I. c.) published a noticeable result. He distinguished a particular chromosome in the spermatogonium of *Oxyopes ramosus*, which is provided with a transverse gap in the interstitial region, by which the chromosome is divided into

of *Tibellus* (HACKMAN 1948, SUZUKI 1952) a slight but distinct size difference can be found between X_1 and X_2 . The ratio of X_1 to X_2 is approximately 3:4. The size difference increases gradually and in the six species of *Philodromus* the ratio shows 2:3. Thus in Philodrominae the length of one of the two X's seems to diminish by and by. The phenomenon would be of great importance in the evolution of the sex chromosomes of spiders.

The identification of X_1X_2 -elements is made usually in the meiotic divisions, but in many cases they have been distinguished in the spermatogonial metaphase also. The two X-elements observed in *Chiracanthium* and *Clubiona* (Clubionidae) are the largest pair in the complements. And they show an interstitial constriction, so that sometimes they exhibit a significant bipartite structure. This feature resembles very much that of the single X in Misumeninae and Oxyopidae. In *Philodromus roseus* and *Tibellus tenellus* one larger X shows characteristic morphological feature as stated above, but it is impossible to find out another smaller one owing to the lack of distinct character. The larger X found in these species seems to be homogeneous with each of the 2 X's present in the Clubionidae.

The morphological character and behaviour of the 2 X's in the meiotic divisions are allied generally to those of the single X.

3. $X_1X_2X_4O$ type

The sex chromosome mechanism of this type occurs very rarely in spiders. Except Sparassidae the type has been known only in the three species of Agelenidae, *Tegenaria derhamii* (SOKOŁSKA 1925, REVELL 1947, HACKMAN 1948), *T. domestica* (REVELL 1947) and *Cryphozca silvicola* (SUZUKI unpublished). The occurrence of this type in Sparassidae was suggested first by HACKMAN (l. c.) in *Micrommata viridissima* and it was fairly demonstrated by SUZUKI and OKADA (1950) in *Heteropoda venatoria*. And the same condition has been found in the related species, *H. forcipata* in the present study. And that *Thelcticopis severa* very probably contains the same mechanism. Moreover, as already mentioned in the preceding pages, further occurrence of this mechanism has been proved by MCINTOSH in the two forms of *Delena* and *Olios* belonging to Sparassidae (MCINTOSH's unpublished data). Thus the multiple sex chromosome mechanism of $X_1X_2X_4O$ type seems to be characteristic for the majority of Sparassidae. But here we have to notice GOWDA's unpublished datum that the Indian undetermined species of *Heteropoda* contains a single X-element.

III. Evolution of sex chromosomes in spiders

As mentioned above three sorts of sex chromosome mechanism, XO,

X_1X_2O and $X_1X_2X_3O$ type are known in spiders. What relation can be found among them? How these three types have been produced? These problems are very intriguing for cytologists. However, it may be impossible to solve the questions completely, unless full data be obtained, and to accomplish this work many difficulties must be overcome. Therefore, the general discussion on the evolution of the sex chromosomes in spiders will be followed in the later paper, here the relationship between the XO and X_1X_2O type in modern spiders will be mentioned.

In modern spiders (suborder Arachnomorphae) about twenty three families (inclusive the author's unpublished data) have been studied cytologically and the sex determining mechanism of X_1X_2O type is characteristic for large majority of those families, on the other hand, the occurrence of a single XO type is limited in some particular families such as Thomisidae, Oxyopidae and Salticidae. In Salticidae only a single case is coexisted with many species of usual X_1X_2O type. In Thomisidae and Oxyopidae alone, XO type is dominant. In this condition it is highly probable that 2 X's condition is more primitive and from this condition the XO-mechanism has been produced.

How has a single X-element originated from 2 X's condition? HACKMAN (1. c.) considered that the single X-chromosome of *Oxyopes* is metacentric and it has been produced secondarily by the centric fusion of the 2 X-elements. As stated above, however, the X-element of *Oxyopes* is not metacentric but acrocentric, so that HACKMAN's view is not correct. Quite recently GOWDA (1950) proposed a new hypothesis that the single X-element in modern spiders has evolved by mutual translocation between the 2 X's, namely, a proximal and a distal break in the 2 X's respectively gave rise to a large acrocentric X and a small centric fragment which was lost in the process. This hypothesis seems to be very ingenious, but it lacks many data which demonstrate the phenomena. It seems that he has not noticed the chromosomal conditions of the family Thomisidae.

The thomisid spiders are complicated in the feature of sex chromosomes and as already mentioned, two kinds of mechanisms, XO and X_1X_2O type are known within the same family. And that as regards the 2 X's, different conditions are observed. In *Oxytate setosa* and *Thanatus formicinus* one X is nearly equal to another one, in *Tibellus tenellus* and *T. oblongus* a slight but clear distinction is recognizable between the both X's, and the difference becomes more clearly in the six *Phlo-dromus*-species studied. Thus it is very probable that one of the 2 X's might have diminished its length gradually in the course of phylogeny. And it seems that individual X-element of the 2 X's was originally of equal length as in *Oxytate* and *Thanatus*, and after that one X began to diminish as in *Tibellus*, the diminution of the length in one X in-

creased gradually as is found in many of the *Philodromus*-species, and finally it was eliminated entirely and thus the present XO condition in *Misumena*, *Xysticus*, *Coriarachne*, *Oxyptila*, *Diaea* and *Philodromus aureolus japonicola* in the same family has been produced, and the evolution from the X_1X_2O to the XO condition is repeated within the same family.

A similar condition is known in the family Oxyopidae, in which *Oxyopes* and *Nishina* possess a single X-element, on the other hand, *Peucetia* shows 2 X's, in which two elements are of different length.

The diminution of the length of one of the 2 X's is observed in other species of the different families. HACKMAN (l. c.) in *Lycosa fluviatilis* and *Trochosa ruricola* belonging to Lycosidae and SUZUKI (1951) in *Araneus opima* belonging to Argiopidae reported that 2 X's reveal clear size difference. Furthermore, the same is observed in the lycosid spiders, *Lycosa T-insignita* and *L. cinereofusca* (SUZUKI's unpublished data). In many of these cases there is a little difference, but in *L. cinereofusca* the distinction is fairly large. Therefore, the size difference of the 2 X's seems to be significant in the evolution of the sex chromosomes of spiders.

SUMMARY

1. The chromosomes of the following twenty two Japanese species of spiders belonging to the four families were studied.

Fam. Clubionidae.....*Chiracanthium japonicum*, *Ch. kompiricola*, *Ch. unieum*, *Clubiona japonicola*, *Cl. lena*, *Micaria unifascigera*, *Trachelas japonicus*.

Fam. Sparassidae.....*Heteropoda forcipata*, *Thelcticopis severa*.

Fam. Thomisidae.....*Misumena tricuspidata*, *Xysticus insulicola*, *X. ephippiatus*, *Coriarachne fulvipes*, *Oxyptila decorata*, *Oxytate setosa*, *Diaea subadulta*, *Philodromus roseus*, *P. nigrostriatipes*, *P. aureolus japonicola*, *Tibellus tenellus*.

Fam. Oxyopidae.....*Oxyopes sertatus*, *Nishina generosa*.

2. The chromosome number of the species studied was given in the Table II. The haploid chromosome number varies within the range from 11 to 23. In the Sparassidae the chromosome number is large and $2n=41$, 43 have been found in the two species. Clubionidae, Thomisidae and Oxyopidae show relatively small chromosome number of 11-15 in haploid.

3. All the chromosomes inclusive of sex chromosomes in the species studied are acrocentrics.

4. In the 22 species examined the male is heterogametic.

5. All the seven species males belonging to the Clubionidae and the four species males of the Thomisidae, i. e. *Oxytate setosa* (Misumeninae), *Philodromus roseus*, *P. nigrostriatipes* and *Tibellus tenellus* (Philodromi-

nae) have two X's and the sex determining mechanism is X_1X_2O type.

6. In the seven species of Thomisidae, *Misumena tricuspidata*, *Xysticus insulicola*, *X. ephippiatus*, *Coriarachne fulvipes*, *Oxyptila decorata*, *Diaea subadulta* (Misumeninae), *Philodromus aureolus japonicola* (Philodrominae) and two species of Oxyopidae, *Oxyopes sertatus* and *Nishina generosa* males, a single X-element has been found and the sex determining mechanism is XO type.

7. In *Oxytate setosa* and *Oxyopes sertatus* the oogonial chromosomes have been exactly counted and the presence of four and two X's respectively in the female has been confirmed.

8. *Heteropoda forcipata* and possibly *Thellicopsis severa* possess three X-elements and the type of sex determination is $X_1X_2X_3O$.

9. The X_1 and X_2 elements in all the studied species of Clubionidae and one thomisid spider, *Oxytate setosa* are of nearly equal length and in all the cases the X-elements seem to be one pair of the largest in the chromosome set. In *Chiracanthium japonicum* and *Ch. unieum* the two X's are distinguished clearly in the spermatogonial metaphase owing to the larger size and a distinct constriction in the interstitial region. The constricted structure of the two X's can not be seen in the meiotic division probably due to the thick condensation. In the first division the 2 X's are distinguished only by the special behaviour.

10. In the three thomisid spiders, *Philodromus roseus*, *P. nigrostriatipes* and *Tibellus tenellus*, remarkable size difference can be found between X_1 and X_2 . The ratio of the length is 3:4 in *Tibellus* and 2:3 in *Philodromus*. Thus in Thomisidae one of the 2 X's tends to diminish gradually, in length.

11. The single X-element of XO-mechanism has been identified in the spermatogonial spindles of *Misumena*, two species of *Xysticus*, *Coriarachne*, *Philodromus aureolus japonicola*, *Oxyopes* and *Nishina*. In all the cases it is one of the largest in the complement, and in favourable cases a constricted structure in the interstitial locus as in the X_1X_2 -elements was revealed. Here too, the single X is easily distinguishable by its behaviour in the first division. In the second division of *Misumena* and *Oxyopes* it is recognizable by the largest magnitude.

12. In the three X-elements of *Heteropoda forcipata*, X_1 and X_2 are approximately of the same length, but X_3 is remarkably larger than X_1 and X_2 . The X_3 -element is always distinguishable in the spermatogenesis, namely, in spermatogonium and two meiotic divisions owing to the largest size. The X_1 and X_2 are identified only in the first division by their behaviour. In *Thellicopsis severa* one remarkably large chromosome which exhibiting particular form and probably represents X_3 -element was found in the spermatogonium.

13. The size of chromosome and nucleus varies markedly in the di-

fferent species studied. *Heteropoda forcipata* and *Thellicopsis severa* belonging to Sparassidae have the largest chromosomes and nuclei, the smallest are found in *Micaria unifascigera* and *Trachelas japonicus*.

14. In all the species examined sex chromosomes are prereducational and they pass one pole undividedly in the first division and separate equationally in the second division.

15. In the three *Philodromus*-species, *Tibellus* and *Xysticus insulicola* the sex chromosomes lag behind the autosomes at first telophase. The same is observed at second telophase of *Misumena tricuspidata*.

16. The autosomal bivalents form at first metaphase one chiasma in the interstitial region and assume usually V or dumb-bell shape.

17. The irregular separation of some autosomes was found in the meiotic division of *Philodromus aureolus japonicola* and *Oxytate setosa*.

18. At first metaphase of *Clubiona lena* several pairs of minute chromatic bodies were found, which are likely to divide, but the origin and fate could not be traced.

19. The chromosome number and morphology of the studied families were discussed.

20. The large chromosome number of Sparassidae seems to be old-type.

21. The XO-mechanism in Thomisidae and Oxyopidae has originated very probably from the X_1X_2O mechanism by the elimination of one of the two X's.

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