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Cytological studies on five families

of

HEMIPTERA-HETEROPTERA

by

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Introduction

The present theory of heredity carries the study of evolution into a wider field of enquiry far beyond the limits hitherto set by morphological criteria. Somatic characters in the phenotype can now be considered in terms of the elaboration and distribution of hereditary factors, the location of which on the chromosomes furnishes a valuable approach to the study of evolutionary problems by linking genetical experiments with cytological observations. The chromosomes provide a visible mechanism for the transmission of hereditary characters. Hence it is evident that chromosome variation must be considered in conjunction with phenotypical characters in differentiating species.

Plants, because of the greater latitude in their mode of reproduction, offer special facilities for a relatively clear understanding of the part played by their chromosomes. In animals, chromosome number and size at meiotic metaphase have been most freely relied upon for the determination of related forms. The first correct evaluation of chromosome number in an animal was made by Flemming in 1882. During the next decade

chromosome numbers for different animal groups were placed on record and collected in a list published by Montgomery (1906) who first appreciated their importance in taxonomy. From the standpoint of size as well as number the Lepidoptera have been studied by Beliajeff (1930), the Odonata by Oguma (1931) and the Hemiptera-Heteroptera by Browne (1916) and Prokofiewa (1933). McClung and his assistants have gone further in comparing structural variations, in particular chromosomes occurring constantly in allied species. They have also pointed out differential behaviour shown by specific variation in the time of pairing during meiotic prophase.

It was originally intended that this thesis should present an account of spermatogenesis in one species of a sub-order of insects, the Hemiptera-Heteroptera, and a comparison of five families of the same sub-order to investigate the degree of correlation between karyology and taxonomy within the group. The chromosome behaviour of the species chosen, Corixa punctata, proved to be so unusual as to justify a detailed study from a viewpoint unconnected with the original theme. The same kind of behaviour, namely the fusion of non-homologous chromosomes, was subsequently

observed in two other species of the same family. One paper is therefore devoted to the description of this phenomenon, while a second deals with the comparative cytology of the Cimicidae, Anthocoridae, Capsidae and Corixidae.

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Non-homologous association of chromosomes in Corixidae (Hemiptera-Heteroptera).

Introduction.

Karyological studies on spermatogenesis in species of aquatic bugs of the family Corixidae have brought to light several examples of chromosome behaviour during the course of meiosis which is of an unusual type. It is considered to be the association of non-homologues in a manner unexampled in any other animal species. The nearest approaches to this type of association seem to be the non-homologous fusion in grasshoppers described by Corey (1933, 1937) and polarisation of bivalent ends reported by Darlington (1936) and other authors.

Prokofiewa (1931, 1933) has described spermatogenesis in Corixidae, giving a detailed account of one species, Corixa distincta, Fieb., and comparing eleven other species of Corixa, Callicorixa White and Macrocorixa Yatsch. In extending this study of the Corixidae non-homologous association was found in species not described by Prokofiewa. The nature and effect of this association on the chromosomal changes during the first meiotic division form the subject of this paper.

Material and Methods.

Testis preparations have been examined of Scottish specimens of the following species of Corixidae:-

Genus Corixa Geoff. (Macrocorixa Yatsch.): C. punctata Illiger (geoffroyi Leach), C. dentipes Thoms.

Genus Sigara Fab. (Corixa Geoff.): S. linnaei Fieb., S. striata Fieb., S. distincta Fieb., S. fallenii Fieb., S. castanea Thoms., S. semistriata Fieb., S. fabricii Fieb., S. fossarum Leach., S. scotti Fieb., S. carinata Shlb., S. germari Fieb.

Genus Callicorixa White: Ca. praeusta Fieb., Ca. wollastoni D. & S., Ca. caledonica Kirk., Ca. concinna Fieb.

Genus Glaenocorisa Thoms.: G. cavifrons Thoms.

Genus Cymatia Flor.: Cy. bonsdorffi Shlb.

To obtain all stages of spermatogenesis, males in the last nymphal instar and early imaginal state were dissected in Ringer-Locke physiological saline and the testes fixed immediately after removal. Fixation for eight hours in Allen's Picroformol A3 or Langlet's Navashin mixtures gave consistent and satisfactory results for the meiotic phases of spermatogenesis. Where fixation of the pre-meiotic spermatogonial phases was desired, two hours in Langlet's Nava-

shin or La Cour's 2BE was found to be preferable.

Sections were cut 20 micra in thickness after double embedding by the method of Peterffi (1924) and were stained by Newton's Gentian Violet method. Smear preparations stained with Zirkle's Aceto-carmine and Feulgen technique were used to assist the analysis of special structures.

Description.

Of the twenty species examined, Corixa punctata, Sigara carinata and Cymatia bonsdorffi were found to have the paired autosomes and sex chromosomes associated non-homologously during the first meiotic division. This condition was seen particularly well in C. punctata and will be described in detail in this species.

The pre-meiotic division.

In Corixidae spermatogonial divisions take place in the last nymphal instar (Prokofiewa 1933), but in C. punctata this phase is not complete until early imaginal life. Nuclei at the apices of the tubules of young adults still showed spermatogonial divisions. An accurate analysis of these divisions was rendered uncertain by the difficulty attending satisfactory fixation. Several phases of the pre-meiotic division have been observed. Prophase stages show the diploid

number of chromosomes as irregular threads of which the longer tend to be polarised at a condensed body (Fig.I.).

This condensed body seems to represent the large nucleolus combined with the precocious X and Y chromosomes, later seen to be characteristic of the first meiotic division. As the chromosomes spiralise they contract to short thick rods; the larger elements being slightly curved. The diploid number (2n) of chromosomes is now shown to be twenty-four, there being twenty-two autosomes and the X and Y chromosomes. This number is characteristic of the Corixidae. At present there is only one known departure from it, the exceptional species being Cymatia bonsdorffi with 2n = 26. Contraction reaches its maximum at metaphase where there is a tendency for pairs of chromosomes of similar size and shape to lie together (Fig.2).

Such distribution on the metaphase plate is an indication of somatic pairing of the homologous chromosomes. Somatic pairing during mitotic metaphase has been found in various Diptera, e.g. in Drosophila (Metz 1916) and Culex (Moffet 1936). The pairing in Culex

is so close that the homologous chromosomes were mistaken by Taylor (1914) for sister chromatids and lead her to an erroneous interpretation of the spermatogonial divisions. In Drosophila also, Stern (1931) demonstrated "somatic crossing-over" genetically, involving reciprocal exchange of segments between homologous chromosomes. From the behaviour during mitotic metaphase in C. punctata it seems that the homologous chromosomes tend to associate, but the case for somatic pairing cannot be more clearly defined than this owing to the small size and strong contraction of the chromosomes. Indications of a similar apposition of homologues which might be regarded as somatic pairing may also be seen in figures given by Prokofiewa (1933) of spermatogonial metaphase in C. dentipes.

Meiosis.

In the resting nuclei of the primary spermatocytes about twelve chromatic aggregates appear which are scattered within the nucleus at random. These bodies have been termed "pro-chromosomes" in C. distincta by Prokofiewa (1931) and in Lygaeus and Oncopeltis by Wilson (1928) and, as they correspond in number to the haploid chromosome complement, may represent their proximal

parts (Geitler 1934), the chromosomes being already paired. Some of them may represent "anlagen" of attraction centres (vide infra) or nucleolar material. They have a wide variation is size and form, ranging from sub-spherical bodies to oblong masses and short thick threads, which even at the earliest stage observed show a few fine thread-like connections. With increase in the size of the nucleus these bodies enlarge and elongate to thickened threads with an anastomosis of finer filaments. In the centre of the resting nucleus lies the large nucleolus already referred to, distinguished from the rest of the complement by its lower staining power. Attached to one side of this nucleolus is a chromatic body larger than the other "pro-chromosomes". This characteristic configuration represents the nucleolus and the sex bivalent, seen to be in association throughout the prophase of the first meiotic division. (Figs. 3-6).

Increase in size of nucleus and cell continues until approximately twice the size of that at the earliest phase of the resting stage is reached. At the same time the presence of a haploid complement of paired chromosome threads becomes increasingly evident. The chromosomes

are seen as slender paired threads in which it is possible to determine similar chromomeres in apposition. The absence of progressive phases of pairing suggests that the chromosomes have been in close apposition since the previous division and are now at the end of the Zygotene stage. All nuclei at this and later stages show a marked degree of polarisation of the chromosomes of a peculiar form. (Figs.7-9).

All or most of the bivalents are intimately united either by their ends or by their sub-terminal regions. In exceptional cases an apparent lateral union occurs, but this is not typical in character and is probably due to fixation. The chromosomes exhibit therefore a property of non-homologous association of specific parts.

For the purpose of discussion, there being no fundamental difference in structure between the classes, the types of association may be arbitrarily classified into:-

(a) attraction centres, where the ends of more than two bivalents are polarised at one point.

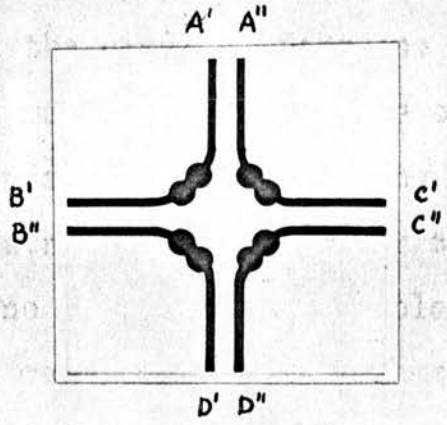
(b) junctions, in which ends of two bivalents are associated by a terminal or sub-terminal union.

The extent to which these strudtures are artifacts cannot be precisely stated, but that they are no more so than the chromosome threads is evident. They present a similar appearance irrespective of the fixative used in preparing

the material, so far as concerns the fact of union of non-homologues. On the other hand differences due to technique exist which may be used to analyse the nature of the associations.

With fixation by Langlet's Navashin or Allen's Picroformol A3 and Gentian Violet staining, the attraction centres and junctions appear to be formed by the union of the ends of bivalents by a ring-shaped or solid mass of chromatic material. At first the material constituting these masses stains intensely throwing the centres into strong relief. Later as the chromosomes contract and thicken their staining becomes more like that of the centres and the difference is lost. Material fixed for two hours in Langlet's Navashin mixture and stained by Feulgen's method gave precisely similar results as with Gentian Violet, the chromosomes and masses of uniting material were stained to the same extent. Treatment of smear preparations with Zirkle's aceto-carmine reveals in greater detail the structure of these associations and it is seen that each chromosome end is enlarged into a rounded knob of chromatic material. For example, in an attraction centre comprising four bivalents, the ends of the homologous chromosomes A' and A"

are associated with those of the neighbouring chromosomes B' and C'; while B" and C" are similarly associated with the ends of the fourth bivalent D' and D" in the manner illustrated in the diagram. (Diag.I., Plate 17 (a)).



Junctions may take the form of end-to-end contacts or the association of one end of a bivalent with the sub-terminal region of another which also appears to possess an aggregation of chromatic material.

Some experiments have been carried out to test the relative durability of these attachments of non-homologues. Exposure of last instar nymphs and of imagines to X-rays produced no observable effect on them. X-ray doses of 5, 10 and 15 minutes at 50 kilo volts, 5 milleamps and a target distance of 13 cms. were employed. Translocations indicated by the appearance of anaphase bridges occurred five to seventy two

hours after X-raying with exposures of 10 to 15 minutes, but in all cases no change was noted in the non-homologous associations.

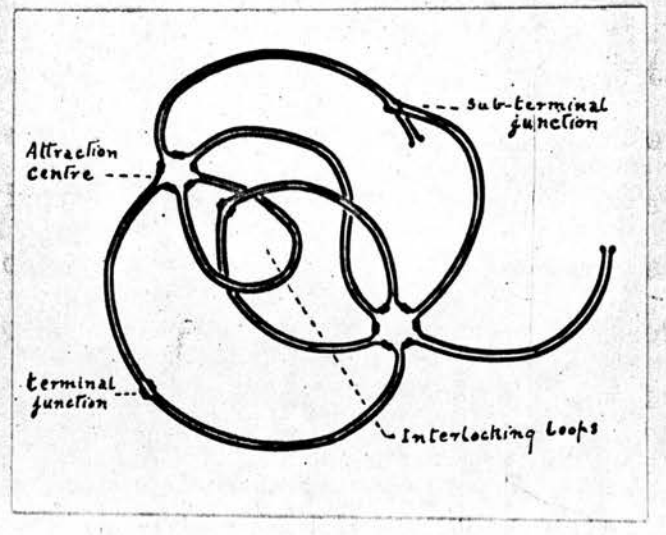
This property of non-homologous attraction characterising meiosis of C. punctata results in a variety of configurations in the prophase nucleus. In the simplest form one end of a bivalent may make contact with an end of a second, opposite ends in each case being free, but generally structures of greater complexity are found. One bivalent may be polarised at each end at two centres or at the same centre. If polarised at two centres it may also be associated at a subterminal point with the end of a second bivalent. Two or more bivalents may unite into a chain by simple junctions and the ends of the chain enter attraction centres. When both ends of a bivalent or chain of bivalents enter the same centre a loop is formed (Plate I (b)), which frequently interlocks with a similar loop polarised at a second centre. Figure 10 and Diagram 2 illustrate the different types of association observed.

Table I.

No. per nucleus of Attraction centres, Junctions, and Free bivalent ends.

		0.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
No. of nuclei with each class of:-	Attraction centres.....	0	1	8	10	3	1	0	0	0	0	0	0	0
	Junctions.....	3	8	6	2	1	2	1	0	0	0	0	0	0
	Free bivalent ends..	0	0	1	7	6	3	1	3	1	0	0	1	0

Table showing segregation of 23 nuclei into classes having different numbers of Attraction centres, Junctions and Free bivalent ends at pachytene and early diplotene stages.



A small nucleolus occurs during pachytene on one bivalent in an interstitial position and at late pachytene may be found free in the nucleus. (Figs. 10 and 12). The bivalent which bears it is thus recognisable and its behaviour may be followed. In most cases this bivalent forms associations by simple junctions and in one nucleus with an attraction centre and a junction, but in no instance does the interstitial nucleolus fuse with the uniting material developed by other bivalents since interstitial associations have not been found.

Table 1. illustrates the extent of polarisation and non-homologous union, though allowance must be made for possible error arising from the low number of cases on which the table is based.

The degree of polarisation varies, but is generally well developed. In all nuclei at least one attraction centre occurs. The frequency of attraction

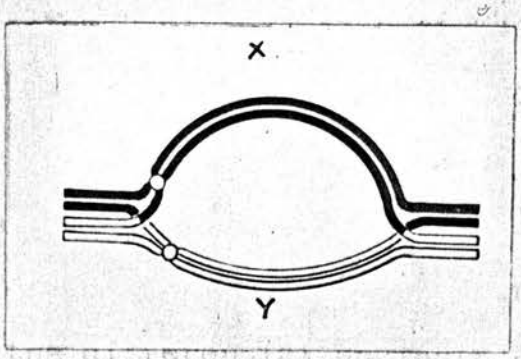
centres in each nucleus ranges from one to six and shows a modal value of three. Since the mode coincides with the mean a random distribution of the centres is indicated. The frequency of junctions is correspondingly low, 60% of the total number of nuclei examined having one or two such associations. These remarks refer to both end-to-end and subterminal relationships, the latter having a frequency of 43% for one subterminal junction and 4% for two, in individual nuclei. Loop bivalents were found in 70% of the nuclei examined.

Where bivalents remain unpolarised, either wholly or partially, the distribution of the different numbers of free bivalent ends given in Table 1 illustrates their frequency. This distribution, which does not include short free ends in cases of sub-terminal contact, shows a major peak of 30% for nuclei with three free ends and minor peaks for those with seven and eleven.

The orientation of the centres is at random except for a tendency to take up a peripheral position. Where two centres occur they usually lie at opposite sides of the nucleus and where three are present their loci are separated by approximately one-third of the nuclear circumference.

The striking dissimilarity of the XY bivalent from the autosomes engendered by its precocious condensation and close association with a large nucleolus makes it the most out-standing body in the prophase nucleus. It is free from association with autosomes in about 70% of the nuclei (Figs. 9, 12), but does frequently form an attraction centre with one or more. (Fig. 8).

The structure of the sex bivalent first becomes clear during pachytene owing to progressive opening out of the condensed mass taking place through the relaxation of the intimate association with the nucleolus, an opening out similar except for its precocity to that of the autosomes at diplotene. In the typical form two sub-terminal chiasmata are found in short pairing segments separated by a long intercalary differential segment in both X and Y. (Fig.13, Diag.3).



The two chromosomes differ but little in length, but the X is recognisably the longer. When autosomal attachments occur they are located proximal to one chiasma and close to it. This typical appearance of X and Y is often obscured by interconnecting strands which seem to be artifacts due to poor fixation of the degenerating nucleolus. (Fig. 14).

One chiasma may become terminal before the end of pachytene, but the time at which this occurs varies and it may not take place until early or even late diplotene. The terminalisation of one chiasma before the other is characteristic and is probably that of the short arm. Types may be found in which no chiasma forms at one end and in exceptional instances pairing appears to have failed entirely; the nucleolus alone serving to hold the X and Y together. (Fig. 15).

The nucleolus generally disappears during the opening out of the sex bivalent, remaining longer in atypical figures where pairing is incomplete. The heteropycnosis of the sex bivalent and large size of the nucleolus, which it bears, engenders an intimate association of the two, involving the greater part of the bivalent, often the whole of it. The rate at which extension and separation of the differential segments proceeds tends therefore to

be retarded in relation to the autosomal changes.

During the pachytene stage the nucleus undergoes synizesis and passes into a phase where fixation fails to preserve the normal structure of the chromosomes. They clump together and cannot be clearly distinguished. Because at all other stages the chromosomes do fix satisfactorily, such a failure suggests the occurrence of important physico-chemical changes within the nucleus at this time.

With the onset of diplotene a progressive opening out of the loops in the paired homologous autosomes commences owing to repulsion between them. Relational coiling between the chromosomes of the individual bivalents can be clearly recognised when this occurs. (Figs. 16-20, Plate 1. (d)).

With few exceptions all the autosomal bivalents are seen to be relationally coiled. The degree of coiling does not seem to show any direct relationship to the length of the bivalent. Both long and short chromosomes frequently show the same amount in the same nucleus. Free bivalents do appear to show a greater degree of coiling relative to their length than those which are completely polarised and this also applies to those with one free end. In some cases coiling is not consistently developed throughout the length

of a polarised bivalent, but fails towards one end, and finally instances occur where relational coiling and interstitial chiasma formation are absent; pairing being maintained only at the ends. Though coiling may be determined it has not been possible to demonstrate in all cases at this stage the difference between simple passage of one chromosome over its partner and actual chromatid crossing-over between the two.

A second kind of coiling has been observed where two re-entrant or loop bivalents interlock (see p.14,&Fig. 16). If these are polarised at diametrically opposite centres and are pulled out owing to their combined length, being approximately equal to the distance between the poles (i.e. attraction centres), then a further coiling may take place between the two arms of the looped bivalent. This is opposite in direction to that of the relational coiling. It bears a resemblance to the doubling back and coiling of the univalent inert B chromosomes observed in polysomic complements of Zea mais (McClintock 1934) and in salivary gland chromosomes of Drosophila (Koller 1935). In this case the doubling is of a bivalent and the coiling may be an expression of unsatisfied tension produced by the combined effects of relational coiling and the attachment of the ends at attraction centres.

Table 2.

Stage	(a) Mean No.of free bivalents per nucleus.	(b) Mean No. of free sex bivalents per nucleus.	(c) No.of nuclei counted.
Pachytene & early diplotene.	I.I82	0.727	II
Mid-diplotene.	I.477	0.762	21
Late diplotene.	4.77I	0.690	23
Early diakinesis	7.800	0.600	I0
Diakinesis	8.936	0.886	I9
Prometaphase	II.484	0.954	I6
Metaphase	I2.000	I.000	20

At later diplotene stages the polarised bivalents enter into a phase in which progressive liberation from attraction centres and junctions takes place. (Figs. 21-29). This breaking up of the association complex is not usually completed until metaphase. The number of free bivalents at each stage of the first meiotic division given in Table 2 illustrates this process.

At pachytene and early diplotene the numbers of free bivalents represent those which have never been associated with the polarised elements in the nucleus. From mid-diplotene to late diakinesis the increase in mean number of free bivalents per nucleus indicates a rapid release of the individual bivalents, until at prometaphase, most, and at metaphase all of them are free. The mechanism which brings about this separation of the haploid complement into its components is that which normally operates in the nucleus during the passage from diplotene to metaphase.

In the first place internal spiralisation, now actively taking place, contracts the paired chromosomes until, at metaphase, the length has been reduced to approximately one-seventh of that at diplotene shortly before any liberation of associated elements occurs. Secondly the mutual repulsion of paired homologues and attraction centres, already seen at pachytene and early diplotene, still continues. These two forces, the one internal the other external, act concurrently to draw away the associated ends of bivalents from one another. As they separate the material forming the union is drawn out into fine threads. Each chromosome is seen to connect with a non-

homologous chromosome of another bivalent by one thread while no such connection exists between homologous partners. Once one end of a completely polarised bivalent or chain of bivalents is freed from an attraction centre, contraction can play no further part in causing separation of the units from the remaining centre and junctions, if the latter be present. Two further forces are brought to bear on the associated complex. These are the repulsion forces acting between homologous partner chromosomes and between their centromeres. At a late phase of the diplotene stage interstitial loops, in bivalents having more than one chiasma, widen and assist in shortening the distance between the ends. Distal ends possessing no terminal chiasmata tend to separate as do ends having terminal or sub-terminal centromeres. Under the influence of these forces the threads joining non-homologous chromosomes are stretched still further and ultimately break freeing the bivalents from their associations. Complete dissociation is not achieved at once. Frequently the first to break is one thread of the union between two bivalents leaving the second joining thread intact. This type of breakage is found in the liberation of bivalents having unpaired end segments strongly repulsed

and the remaining connection persists until broken by the mutual repulsion of all bivalents which completes the diakinesis stage. Terminal or sub-terminal chiasmata allow the connections between both pairs of chromosomes of two bivalents to exist until a later stage by preventing this separation of homologous end segments. This is well shown in the association of the XY bivalent with an autosome. Here the sub-terminal chiasmata of the XY allow no separation of the ends and connection with the autosome may endure longer than any other non-homologous association as may be seen from the frequency of free sex bivalents (Table 2) at successive stages where the sudden rise does not commence until early diakinesis.

At late diplotene instances of false interlocking occur where one bivalent passes through the loop formed by the opening out of the partner chromosomes of another. (Fig.30). It probably took place at an early stage before the completion of pairing when strong repulsion forces were not operating to prevent the interlocking. Fixation of the bivalents at attraction centres would subsequently play a part in maintaining the positional relationship.

In several nuclei an association of four

bivalents seems to depart from the rules governing non-homologous associations observed by all other complements examined. Three of these bivalents are united by chromatic threads in a manner which can only be analysed as a union of one chromosome with the chromosomes of two other bivalents by a double thread. (Fig.31).

The interpretation of this configuration is obscured by the combination of terminal and sub-terminal associations and the contraction of the chromosomes.

In some nuclei the union of non-homologous chromosomes occasions the partial breakage of a chiasma (Fig.32). Here the ends of chromatids of partner chromosomes A^{I}, $A^{I^{1}}$ of bivalent A are united with the ends of chromatids of B^{I} and B^{II} of bivalent B by separate strands. Repulsion of the bivalents has set up sufficient tension in the connecting strands to cause breakage of the homologous association of these chromatids at the chiasma. It is important to note in this case that chromatids and not whole chromosomes are united by separate strands in the non-homologous union. From this structure it may be inferred that the association of non-homologous chromosomes so far seen to be effected by single chromatic

strands is in reality an association of individual chromatids. If this view be taken, each chromosome is connected by two parallel strands as a result of division of the homologues into daughter chromatids. This may well have occurred if the two bivalents were closely approximated at the time and the uniting material condensed into a compact mass; repulsion of the bivalents then drawing it out into a pair of strands. Such behaviour indicates a further character of the uniting material, namely that it has a predetermined cleavage plane along the axis joining the points of contact with the non-homologous chromosomes. In a few instances bivalents seem to show this partial breakage of a chiasma after the lapse of non-homologous union at metaphase.

At diakinesis the bivalents show maximum repulsion and lie for the most part near the nuclear membrane. (Figs.33-37).

At this stage non-homologous association has relaxed until only two elements remain united as a rule, but occasionally three or four are still conjoined. All members of the complement have now contracted to a marked extent and appear as short rods, crosses or rings according to the number and degree of terminalisation of chiasmata.

Contraction is accelerated from diplotene onwards in the autosomes relative to that in the sex bivalent which becomes difficult to recognise in many nuclei; its former precocious contraction now no longer serving as a distinguishing character.

In some preparations with optimum fixation and staining the position of the centromeres and their relation to chiasma distribution can be determined. The product of advanced contraction and strong repulsion of the sub-terminal centromeres in certain autosomes forms a characteristic structure. The short proximal arms of these chromosomes, represented by minute spherical bodies, are drawn away from the long arms and remain separated by thread-like constrictions. The resultant structure bears a close resemblance to a trabant. The position of this structure varies according to chiasma distribution. Where the chiasmata are in the long arms the "trabants" stand at opposite ends of the terminalised bivalent (Fig.38). A chiasma in the short arm (i.e. in the "trabant") brings them together so that they are placed on an axis perpendicular to that of the long arms (Fig.38 b). In a few instances terminal non-homologous association still remaining between the short arms of two or more bivalents may be seen to draw out the constrictions to a length equal to

that of the remainder of the bivalent. (Fig. 38 c)

At the prometaphase stage when formation of the spindle and congression of the bivalents at its equator take place, very few cases of bivalents remaining in connection have been found. (Figs. 39 - 43). Occasionally two or three are still linked by fine threads and appear to be retarded in their movement to the equatorial plane in consequence.

The ensuing metaphase of the first meiotic division marks the final dissappearance of any indication of non-homologous association of the chromosomes in Corixa punctata. (Fig. 44).

In all other species of Corixidae of which the pachytene and early diplotene stages have been examined, attachment of the XY bivalent to one or more autosomal ends was found.(Plate 1. h). The percentage frequency of this attachment varies from 12% of the nuclei in Sigara fabricii to 81% in Callicorixa concinna. There is also a marked tendency for high frequencies of XY attachment to be correlated with an increased number of autosomal ends to which the sex bivalent is attached.

Additional evidence of non-homologous association of autosomes not involving the XY has been found in only two species other than C. punctata. In Sigara carinata and Cymatia bonsdorffi pachytene and diplotene nuclei bear a close resemblance

to the equivalent nuclei of C. punctata with respect to the appearance of attraction centres (Plate 1 (f)); but the phenomenon in these two forms has not yet been studied in detail.

This account is brought to a conclusion with some observations on the further progress of the maturation divisions in Corixa punctata. In related genera (Sigara and Callicorixa) orientation at metaphase is of the type known as a "hollow spindle". All bivalents lie on an equatorial ring with the exception of the small micro-chromosomes (m chromosomes)(1st metaphase) or the XY (2nd metaphase) which occupy a central position. The development of a hollow spindle is imperfect in Corixa, both in C. punctata and in C. dentipes (Prokofiewa 1933). The number of elements seen to be lying on the equatorial plate at first metaphase varies from twelve to fourteen. (Figs.44-48). Based on counts of ninety one nuclei, the percentage frequency of the occurrence of twelve elements is 7.9: of thirteen elements, 60.4: and of fourteen elements 31.7. This variation in the number of chromosome elements is the result of the peculiar behaviour of the X and Y chromosomes and the smallest pair of autosomes, the "m" chromosomes. In nuclei giving counts of thirteen or fourteen (91.1% of the

total) it is found that the X and Y have disjoined prior to metaphase and now appear as two univalent chromosomes orientated in the same manner on the spindle as the bivalent autosomes. Where there are fourteen elements the 'm' chromosomes, in addition to the X and Y, are unpaired and also appear on the plate as univalent chromosomes showing no special mode or orientation. At anaphase (Figs.49, 50) in these cases chromatids of the X and Y and of the similarly unpaired 'm' chromosomes segregate to each pole, while the behaviour of the remaining autosomal bivalents is normal, each disjoins and homologous partners pass to opposite poles. Where there are twelve elements the whole complement is disjunctional at this division. There is a tendancy for the largest pair of autosomes to lag behind the rest of the complement.

First telophase is short. The daughter nuclei in the second spermatocytes quickly reform a spindle and enter second metaphase (Figs.51-53). All the autosomes which disjoined normally at first anaphase are now univalent mitotic chromosomes.

The X, Y and 'm' chromosomes are univalent or bivalent, the reverse of their condition at first metaphase.

Finally at second anaphase (Figs.56-59) the

autosomes divide mitotically, the X and Y and 'm' chromosomes divide or separate according to their condition and reduction of the whole complement is complete.

During second anaphase cell division commences, forming daughter cells at telophase whose nuclei reorganise into the resting stage of the spermatids. This is a stage of long duration occupying 30% of the period between pre-meiotic resting stage and the formation of spermatozoa.

In one specimen three nuclei were found in which four autosomes remained associated at second metaphase (Fig. 54, Plate 1.f). This seemed to be a quadrivalent having one triple chiasma. The interpretation of the structure as a quadrivalent implies non-disjunction of two homologues A_1, A_{11} at the first division. The total number of chromosomes in the complement excludes the possibility of the presence of super-numary chromosomes, carrying with it the implication that a reciprocal failure of disjunction of a second homologous pair B_1, B_{11} took place at the same time. The reduplicated autosomes B_1, B_{11} in the sister second spermatocyte nucleus would have two expected modes of behaviour; either to form a similar structure or to separate and divide normally.

In a neighbouring nucleus to each one in which this abnormality was found the whole chromosome complement had degenerated into irregular chromatin masses. If this represented the sister nucleus concerned there seems to be no reason why this degeneration should have occurred unless the further assumption is made that, while reduplication of chromosome A has no deleterious effect on the meiotic division, reduplication of B completely destroys the structure of the nucleus. Degeneration following reduplication suggests that the chromosomes B_I, B_{II} are heterozygous for a gene which is lethal in the homozygous condition.

Discussion.

In the maturation divisions of the male germ cells of Corixa punctata two phases of the first meiotic division have not been observed. The chromosomes appearing during the early stages in the development of the primary spermatocytes never at any time had the appearance of a diploid set of single threads. Nor, in consequence, was the pairing of these to form a haploid set of bivalents observed.

In the light of the evidence of somatic pairing during the pre-meiotic spermatogonial division, it is probable that attraction is exhibited by the homologous chromosomes in a precocious degree so that they segregate in close proximity at anaphase. Thus the homologues would be closely apposed at the ensuing resting stage. Such behaviour might well result in the elimination of visible leptotene and zygotene stages and ensure pairing at meiosis.

The most striking feature of meiosis in C. punctata is the non-homologous association of chromosomes at pachytene and its persistence throughout the greater part of the first meiotic division. The long duration of the phenomenon is one of the characters by which it differs from the fusion of non-homologues in grasshoppers (Corey 1933, 1937).

The nature and behaviour of attraction centres and junctions (as judged by the study of preparations fixed and stained by methods other than Feulgen's technique) strongly suggests that the union of non-homologous chromosomes seen at prophase and subsequent stages of meiosis is a fusion of nucleolar material (Darlington 1936). This implies that all chromosomes develop or may develop nucleoli of which the organisers are terminal or sub-terminal in position and present at both ends of each chromosome. Constrictions indicating the position of such organisers (cf. Dearing 1934) have not been found in this material. Each chromosome terminates in a knob as can be seen where chromosome ends have failed to fuse in competition with the aggregates of the successful attraction centres. These terminal knobs resemble the "polar granules" of Phrynotettix which have the power of expanding into "plasmosomes" (Wenrich 1916). Such a process would have to be a facultative property of both ends of each chromosome in C. punctata to produce the observed associations. If nucleolar fusion be assumed, it may be a secondary reaction due to, or at least facilitated by, a primary polarisation such as occurs in Chorthippus and Stethophymia (Janssens 1924). A primary attraction centre, bearing perhaps some relation to the centromere,

as Darlington suggests, which causes an accumulation of all bivalent ends to one point in the nucleus, would thereby enhance the formation of secondary associations of these ends by fusion of nucleoli. At the same time the possibility of interstitial associations taking place would be reduced and this accords with the evidence. On the other hand the observed phenomena of polarisation in C. punctata give no support to this hypothesis. Unless the occurrence of a bouquet stage in C. distincta, a related species (Prokofiewa 1931) can be admitted as evidence of an initial primary pole, it must be inferred that several centres are formed primarily in each nucleus.

It is possible that the centromeres play some part in bringing non-homologous chromosomes together. Darlington observed a tendency for centromeres to be mutually attracted in Agapanthus and Stauroderus and suggests that this should be regarded as evidence of the essential homology of all centromeres by virtue of a common evolutionary origin rather than as non-specific attraction between them. (Darlington 1937).

If this view of Darlington is adopted together with the assumption that nucleolar organisers are situated near to sub-terminal centromeres, then the attraction of the centromeres would serve the

same purpose as a primary centre, and the absence of association of terminal with sub-terminal regions of the same bivalent would be explained. On this assumption association of sub-terminal centromeres of different bivalents should also occur, but this has not been found to be the case.

The behaviour of the XY complex, both in C. punctata and in other Corixid species, upholds the theory of nucleolar fusion and is probably the strongest support for it. When the sex bivalent has attached autosomes its extension and opening out does not as a rule take place until the autosomal association lapses at diplotene and the bivalent remains until then in the condensed mass characteristic of the earlier phases. This breaking of the fusion of the autosomal connection with the sex bivalent is not necessarily to be regarded as a trigger mechanism instigating further development of the XY complex but may be regarded as an expression of the dissolution of nucleolar material which by liberating the chromosome elements allows extension to take place (Darlington 1936). It is necessary to decide in this case whether the liberation of the XY from the nucleolus or whether both are a function of the dissolution of the nucleolus. Since the general procedure seems to be for the nucleolus to disintegrate in advance of

the autosomal liberation it may be concluded that it is an independent process which collaborates with the non-homologous union to bring about the delay in the opening out of the XY.

The evidence provided by the application of Feulgen's technique (p. 12) is certainly contrary to the hypothesis that nucleolar material is responsible for the union of non-homologues. This reaction seems to be the most reliable microchemical test for the presence of thymonuclein and although instances are known where chromosomes do not give a positive result while the nucleoli do (e.g. "lampenbürsten" chromosomes of certain growth stages of egg-nuclei of Salamandra are negative and nucleoli of growing eggs of Stegomyia are positive with respect to Feulgen technique (Hartmann 1933)), it may generally be assumed that nucleoli do not stain by this process. As already stated, both chromosomes and the material uniting their ends gave positive results, and on these grounds the latter cannot be accepted as nucleolar in nature.

In the salivary gland nucleus of Drosophila the centromere regions of chromosome pairs are heterochromatic and fuse together to form a chromocentre. This attraction is non-specific unless considered from the point of view of Darlington's suggestion. Bauer (1936) regards the hetero-

chromatic material as consisting of modified chromomeres, "heterochromomeres", differing from the "euchromomeres" in their reaction to nuclear dyes. To these heterochromomeres he accords the special property of non-specific attraction. Moreover Bauer postulates a non-specific affinity of terminal chromomeres in these chromosomes which exist in a condition of permanent prophase. The application of similar properties to the chromosomes of C. punctata makes possible a different analysis of the attraction between non-homologues. Association at centres and end-to-end junctions may be a function of Bauer's "non-specific affinity of terminal chromomeres" and sub-terminal junctions a function of "non-homologous attraction of heterochromomeres". In this respect it may be pointed out that all the observed types of association can be analysed as being the union of two and only two non-homologous chromosomes (c.f. pairing in polyploids with homologous segments). This is illustrated by the characteristic ring formation of centres concerning four or more bivalents (see Diag. 1).

Furthermore the material uniting non-homologues persists up to metaphase and is stretched out under the influence of chromosome repulsion at late diplotene, whereas nucleoli disintegrate at an earlier stage. Some difference therefore must exist between this uniting material and the material of nucleoli.

McClintock (1933) described knobs of deeply staining material on the prophase chromosomes in pollen mother-cells of Zea and Longley (1937) reported similar knobs in other grasses, namely Euchlaena, Euchlaena-Zea hybrids, and Tripsacum, and observed their fusion to produce non-homologous associations. Longley suggests that these knobs are large chromomeres and that they represent genetically inert regions of the chromosomes which possess the power of sticking together. The association of many chromosome ends bearing knobs results however in a large undifferentiated mass and does not produce the ring-formation characteristic of pachytene chromosomes of Corixa punctata. On these grounds the two phenomena are not comparable. Non-homologous association in C. punctata appears to be regulated by a special type of behaviour which does not govern the similar association in Euchlaena and its allies.

Distinct from the problem of the nature of polarisation during prophase is the consideration of orientation of centres and junctions within the nucleus. Evidence in favour of some force operating on the centres is forthcoming from the behaviour of loop or re-entrant bivalents (see page 14). Where two such bivalents, associated with diametrically opposite centres, interlock the loops are

pulled out indicating a movement of the attraction centres towards the periphery of the nucleus although the number of bivalents which could cause this movement mechanically is reduced owing to the formation of the loops.

It is noticeable that the peripheral position of the centres is reflected in that of the sex bivalent and that those centres possessing the largest masses of uniting material are those which show the greatest regularity in taking up a position near to the nuclear membrane. This orientation suggests the action of an external force leading to a peripheral position of condensed elements in the nucleus. The action of an electrodynamic force (c.f. Lillie (1905), Cannon (1923), Kuwada (1929)), in the form of a surface charge carried by the chromosomes would tend to the mutual repulsion of all members of a complement. Here however the bivalents are restricted in their range of movement by the polarisation of their ends while the attraction centres bearing large masses of uniting material might be supposed to exhibit stronger repulsion by virtue of a greater surface charge and hence assume equidistant peripheral positions, leaving single or conjoined bivalents associated with them to be mechanically arranged within the nucleus. As in the case of the sex chromosomes,

Table 3.

	Chiasmata 1	2	3	4	5	No. of cells	Total Xta.	Total Xta. Terminalised.	Mean no. per cell	Mean no. per bivalent	Terminalisation coefficient
Diplotene	17	36	4	2	0	5	107	45	21.4	1.76	0.470
Late diplotene	22	24	1	1	0	4	77	26	19.25	1.61	0.338
Early diakinesis	82	37	1	0	0	10	159	44	15.9	1.32	0.277
Diakinesis	85	33	1	0	0	10	156	40	15.6	1.30	0.256
Late diakinesis	29	7	0	0	0	3	43	27	14.33	1.19	0.627
Prometaphase	32	3	0	0	0	3	38	38	12.66	1.05	1.000

free autosomes usually show a peripheral orientation in accordance with this hypothesis.

With the separation of the bivalents and their opening out at late diplotene determination of chiasmata becomes possible.

From the determination of chiasma frequencies at successive stages from late diplotene to metaphase unexpected results emerge with respect to the terminalisation coefficient. As is to be expected the number of chiasmata per bivalent falls owing to terminalisation until this is complete at metaphase. The sequence of terminalisation coefficients does not reciprocate the fall in frequency of mean number of chiasmata per bivalent. From late diplotene until diakinesis the terminalisation coefficient also falls and thereafter rises rapidly up to unity, denoting complete terminalisation at metaphase. (Table 3).

The degree of terminalisation recorded at diplotene may be partly due to the ends of paired homologues being held together through tension of the strands linking them to other bivalents. From late diplotene to diakinesis the non-homologously associated bivalents are breaking away one from the other. When they become free, centromere and body repulsions separate the ends of the paired chromosomes of those which do not possess terminal

chiasmata. Hence this process progressively affects the observed terminalisation coefficient in a negative direction. From diakinesis to metaphase only true terminalisation remains and the coefficient rises in the expected manner since the lapse of non-homologous association now allows a valid analysis.

The persistance of the union of at least two of the bivalents up to pro-metaphase in some nuclei leads to the inference that the final expression of the non-homologous association is to be found in the imperfect formation of a hollow spindle at first metaphase, a characteristic of most members of the Corixidae (Prokofiewa 1933). This conclusion is invalidated however by the behaviour of the chromosomes at second metaphase when they still fail to from a perfect hollow spindle and by the similar conformation of both spermatocyte metaphase stages in C. dentipes in which non-homologous unions do not occur.

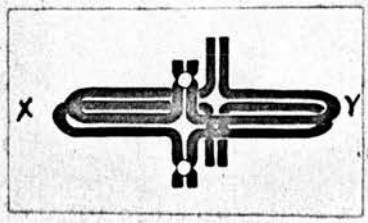
Precocious condensation or heteropycnosis observed in C. punctata is a well known feature of the heteromorphic sex chromosomes in animals and is especially frequent in Orthoptera and Hemiptera e.g. in Leptophyes (Mohr 1915), Chortippus and Stauroderus (Darlington 1936), Pyrrhocoris (Henking 1891), Oncopeltis and Lygaeus (Wilson 1928).

Karpoff (1926) considers that heteropycnosis in Cleonus punctiventris results from the close association of the sex chromosomes and the plasmosome. It may also be related to the differential segments of the XY.

The peculiar form of post-reductional division of the X and Y chromosomes is characteristic of the Hemiptera-Heteroptera and of almost universal occurrence in the sub-order. The time of actual separation after prophase pairing may be set as being between diakinesis and pro-metaphase.

Exceptional first anaphase figures (Fig. 55), show the separating chromatids of X and Y in close proximity as they approach the poles, as though they were paired. Either this indicates that secondary pairing occurs before the establishment of second metaphase or that these are instances where the X and Y do not separate at the first division. The latter supposition allows a different interpretation of the first meiotic division which involves the location of the centromeres in the pairing segments. If crossing-over does not occur between the centromeres and the differential segments division will always be disjunctional. Given a sufficient length of pairing segments between the centromere and the differential segment to permit crossing-over to

take place, the sex bivalent may divide equationally as a result of crossing-over in this region. (Diag. 4).



Reduction of the paired X and Y chromatids obtained in this manner would follow at the second division without secondary pairing .

Summary.

1. The study of twenty species of aquatic bugs (Hemiptera-Heteroptera) of the family Corixidae has revealed the occurrence in Corixa punctata, Sigara carinata, and Cymatia bonsdorffi of non-homologous association of the paired chromosomes during the first meiotic division in spermatogenesis.

The pre-meiotic and first meiotic divisions in C. punctata are described showing the appearance and effects of this property of the male germ-cell chromosomes. Its possible nature is discussed.

Reference is made to a similar form of non-homologous association in S. carinata and Cy. bonsdorffi but these species have not been studied in detail.

2. In the pre-meiotic spermatogonial division of C. punctata there is evidence of somatic pairing at prophase and metaphase. Leptotene and all but late zygotene stages not being found, in the following meiotic prophase. It is supposed that the tendency for somatic pairing leads to the close apposition of the chromosomes when they become visible at the commencement of meiosis.

3. All nuclei exhibit a form of non-homologous association involving all or most of the chromosomes at pachytene and this association is maintained until late diplotene. It then commences to break up and finally disappears at diakinesis or pro-metaphase, leaving free bivalents at metaphase.

4. This non-homologous association concentrates the ends of bivalents into a limited number of loci within the nucleus and may be looked upon as a form of polarisation. It is an association of non-homologues restricted to specific parts of chromosomes which are either terminal or sub-terminal in position. It appears to be a fusion of knob-like enlargements of each chromosome resembling "polar granules", as in Phrynotettix and to

some extent the "knobs" found in Zea, Euchlaena and Tripsacum chromosomes. Variations in fixation and staining technique which still give satisfactory images of the chromosomes do not cause a significant variation in the nature of the non-homologous association.

5. To facilitate description the types of terminal or sub-terminal fusion have been grouped under two headings viz: "attraction centres" and "junctions" according to whether more than two or only two bivalent ends associate at one point. Association at an attraction centre may be briefly described as being analogous to a multiple chiasma.

6. An account is given of the various configurations formed by this association and of the degree to which it extends in the primary spermatocyte nuclei. The breaking up of these configurations by the forces operating on the chromosomes from diplotene onwards is shown to draw out the uniting material into fine threads joining the non-homologues until they finally break leaving all the bivalents free at metaphase. The influence of this process on the apparent terminalisation of chiasmata produces an atypical sequence of terminalisation coefficients probably due to the impossibility of determining true terminalisation owing to its being obscured by the non-homologous fusion.

There is evidence also that relational coiling is partially interrupted by immobilisation of the ends of the chromosomes at attraction centres.

7. Several possible causes of this association are discussed *viz*: that it is due to the fusion of nucleoli or of inert regions of the chromosomes; or to the non-specific attraction of heterochromomeres.

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Legend to Figures.

Fig.1. Pre-meiotic Prophase showing polarisation and tendency to somatic pairing.

Fig.2. Pre-meiotic Metaphase showing tendency to somatic pairing.

Figs.3-6. Growth period of meiotic Prophase preceeding the appearance of determinate chromosomes.

Fig.7. Meiotic Prophase at late Zygotene stage.
c.- attraction centre.
(autosomes partly represented).

Figs.8-10. Pachytene nuclei of meiotic Prophase.

Figs.11, 12. Meiotic Prophase at early Diplotene stage.
L_1 - simple loop bivalent
L_2 - interlocking loop bivalents
s.j. - sub-terminal junction.
(XY in outline in Fig. 11).

Fig.13. XY bivalent at Diplotene with attached autosomes.

Fig.14. Forms of XY at Diplotene.

Fig.15. XY at Diplotene showing partial failure of pairing.

Figs.16-20. Meiotic Prophase at mid-diplotene.
f.a. - free autosome.
t.j. - terminal junction
Other lettering as in Fig.11.
(Inset XY and remains of nucleolus in Fig.16).

Figs.21-30. Later Diplotene stages showing progressive separation of the bivalents.

Fig.31. Complex union of four bivalents (A,B,C,D,) due to non-homologous association.

Fig.32. Early Diakinesis. Partial breakage of a chiasma in each of two bivalents due to the tension in the strands uniting their ends. (For explanation of lettering see text, p. 25).

Figs.33-37. Nuclei at Diakinesis illustrating the persistance of a few attachments.

Fig.38. Bivalents showing "trabants" at Diakinesis.
(a) chiasma in long arm.
(b) chiasma in short arm.
(c) non-homologous fusion of short arms.

Figs.39-43. Prometaphase.

Figs.44-48. 1st Metaphase.

Figs.49, 50. 1st Anaphase.

Figs.51-53. 2nd Metaphase.

Fig.54. Nucleus at 2nd Metaphase to show the pairing of four autosomes by a multiple chiasma (q) and secondary pairing of X and Y.

Fig.55. 2nd Anaphase with apparent equational division of paired X and Y.

Figs.56-59. 2nd Anaphase.

Legend to Photographs.

Plate 1.

Corixa punctata Ill.

a. Attraction centre involving four bivalents (A,B,C,D.) X 5500.

b. Attraction centre in part side view showing two re-entrant or loop bivalents (L) X 3200.

c. Attraction centre in side view to show paired homologous chromosomes (A_1, A_{11}) associated with non-homologues on either side. X 3200.

d. A bivalent autosome with each end entering centres at opposite sides of the nucleus. X 3200.

e. A bivalent autosome still attached to the XY at late Diplotene stage. X 3200.

f. A multiple chiasma formed by four autosomes at 2nd Metaphase. X 3200.

g. Secondary pairing of the XY at 2nd Metaphase. X 3200. Cymatia bonsdorffi Sahlb.

h. Nucleus with one bivalent autosome attached to the XY. X 3200.

i. Attraction centre formed by the union of four bivalents. X 3200.

Photographs a, b, c, h, and i represent nuclei at the Pachytene stage: d, and e at Diplotene: f, and g, at 2nd Metaphase.

Note with Reference to Figures.

Differences in magnification are due to failure to carry out instructions on the part of the commercial photographer who reproduced the drawings.

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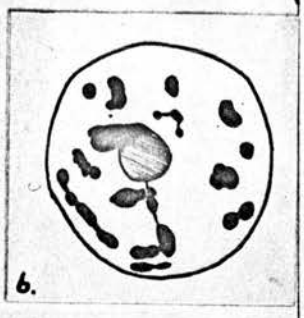

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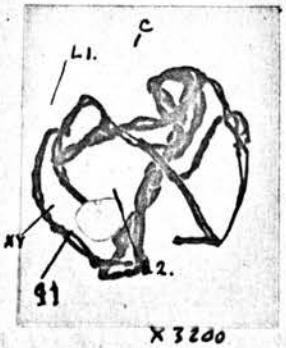

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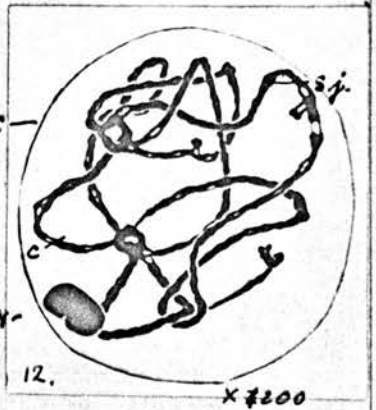

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X 3200

Nucleolar Strands

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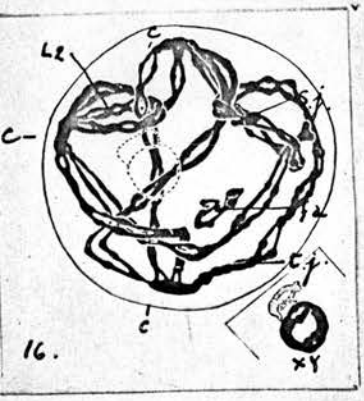

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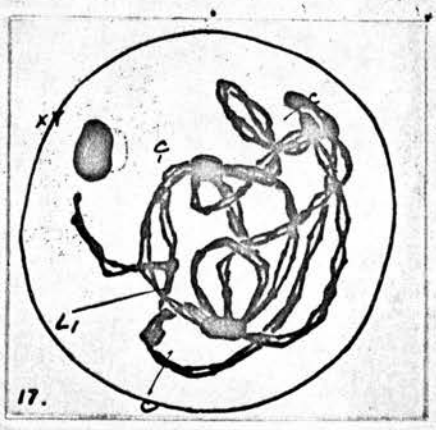

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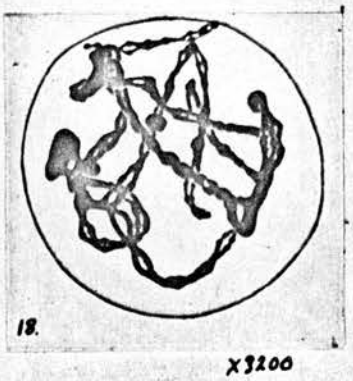

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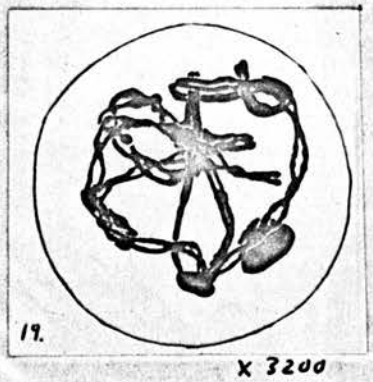

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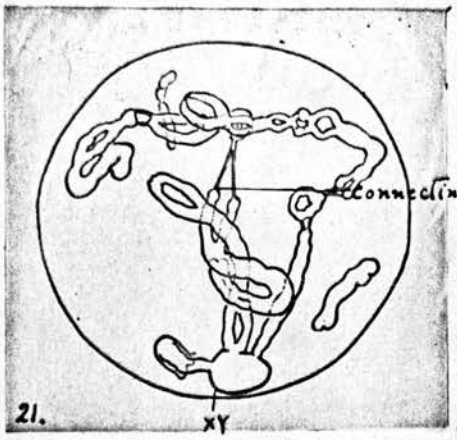

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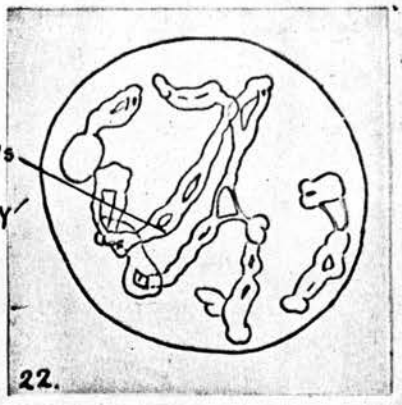

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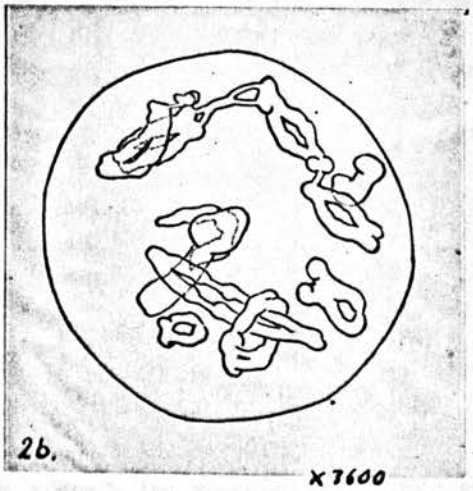

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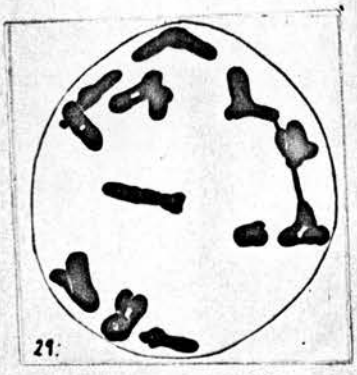
XY—

28.

X 3200



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30

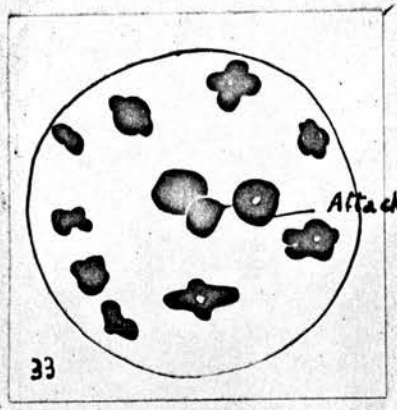
X 2200

31

X 2600

32

X 2600



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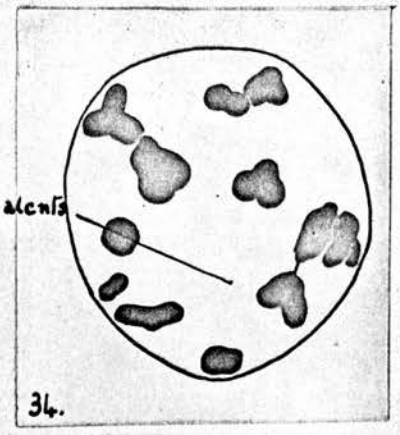

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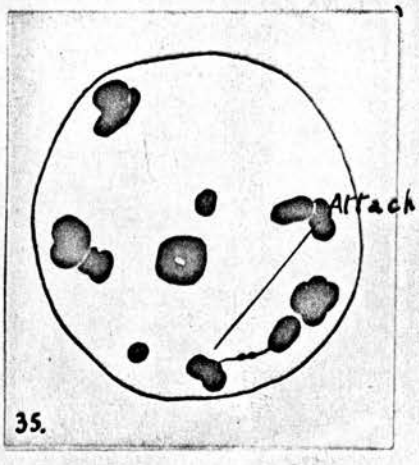

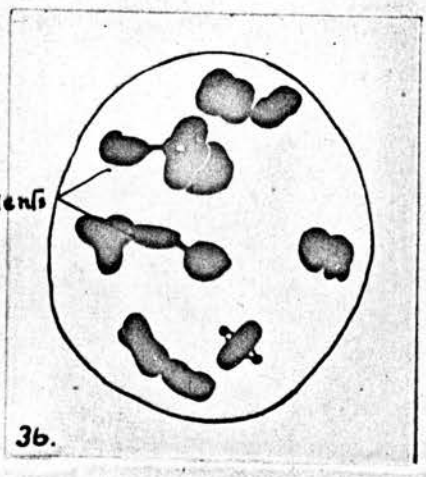

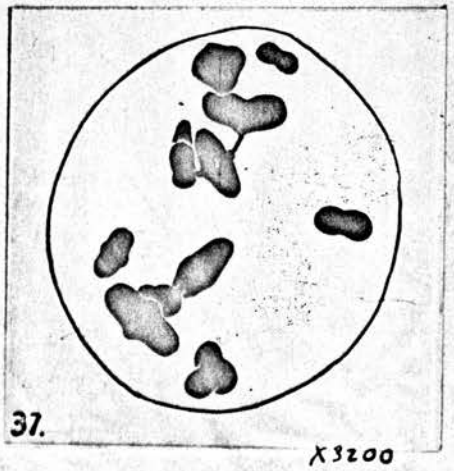

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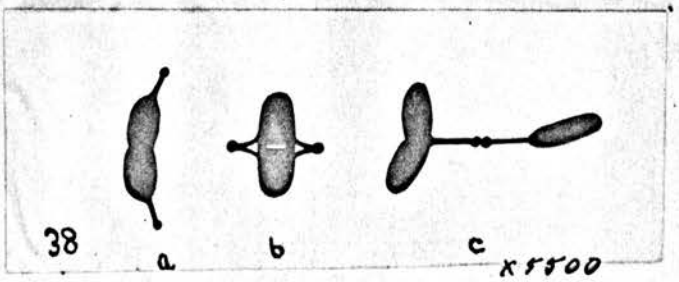

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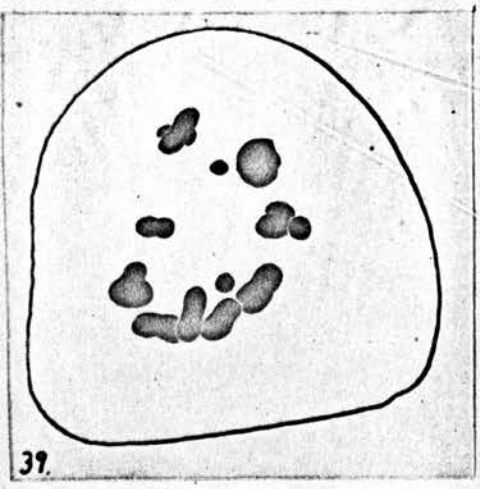

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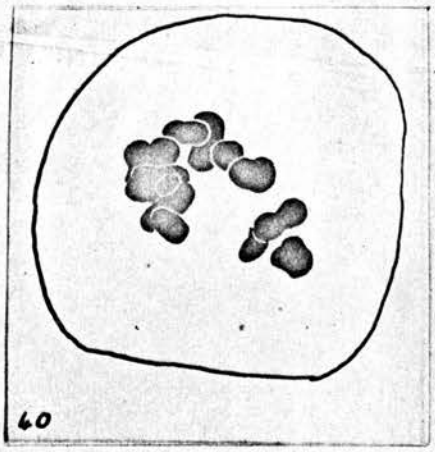
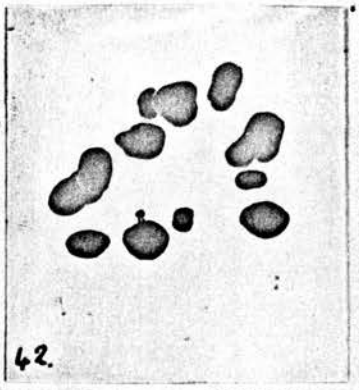


40

X 3200

41.

X 3200



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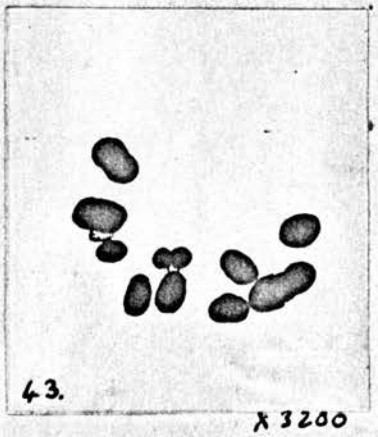

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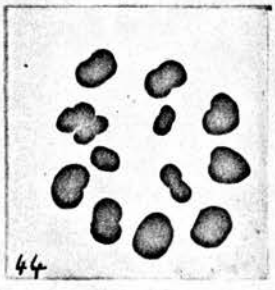

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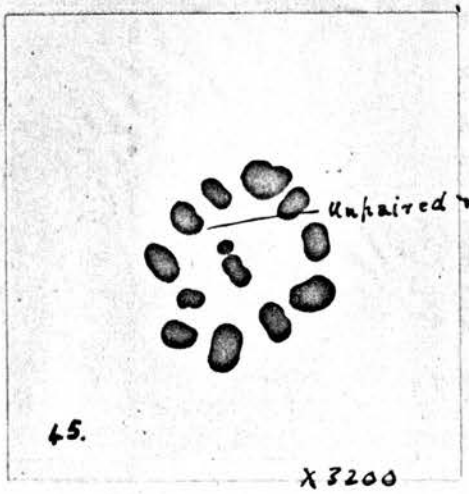
X 3200



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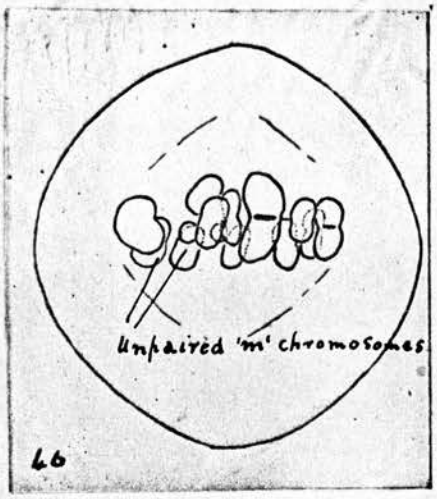

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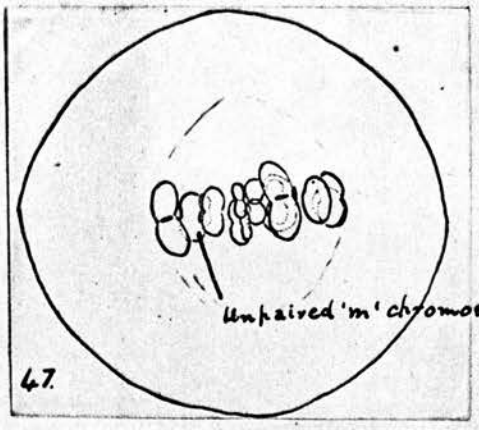

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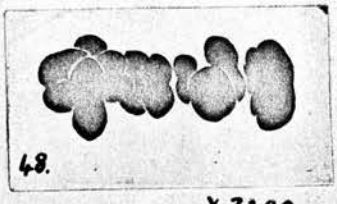

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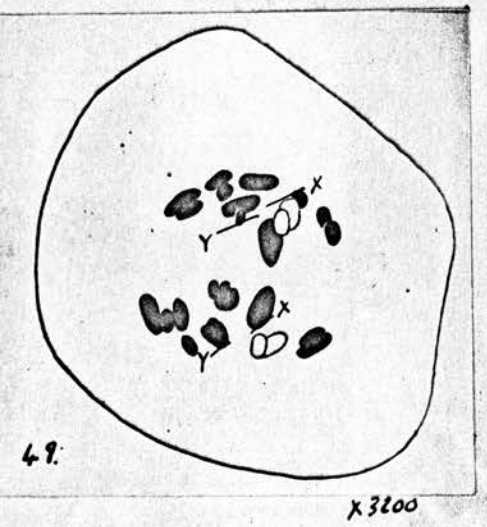
X 3200



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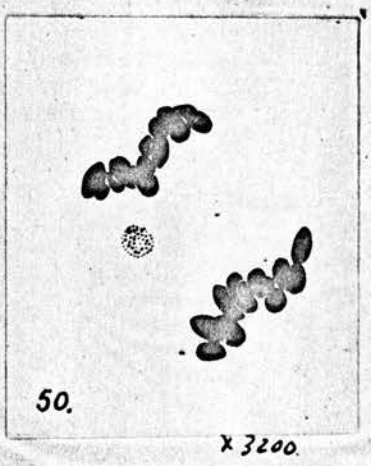

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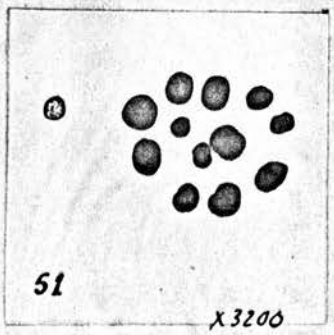
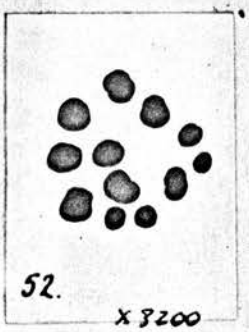
X 3200.



51

X 3200



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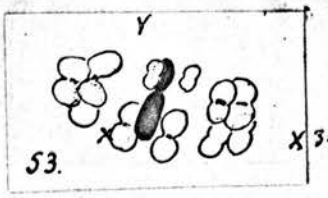
X 3200



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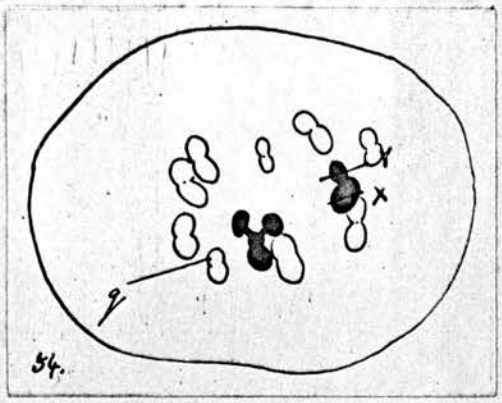


54.

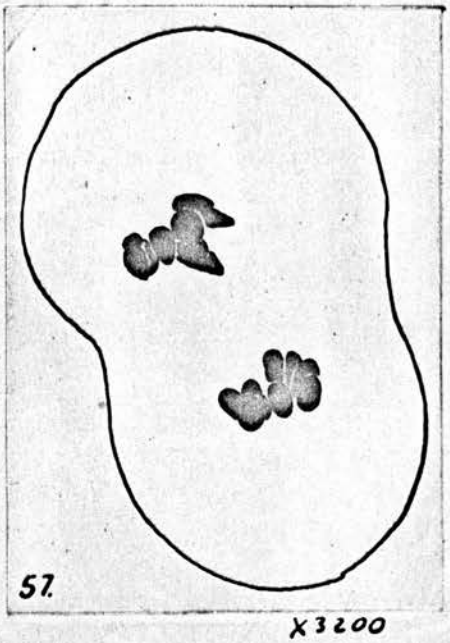
×3200

55

×3200

56

×3200



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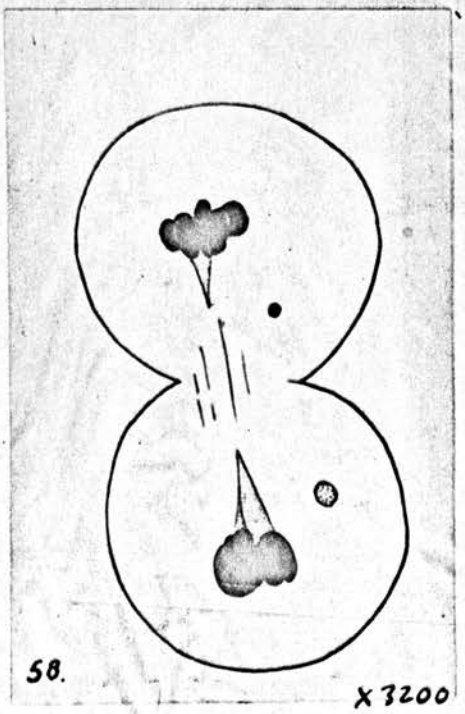

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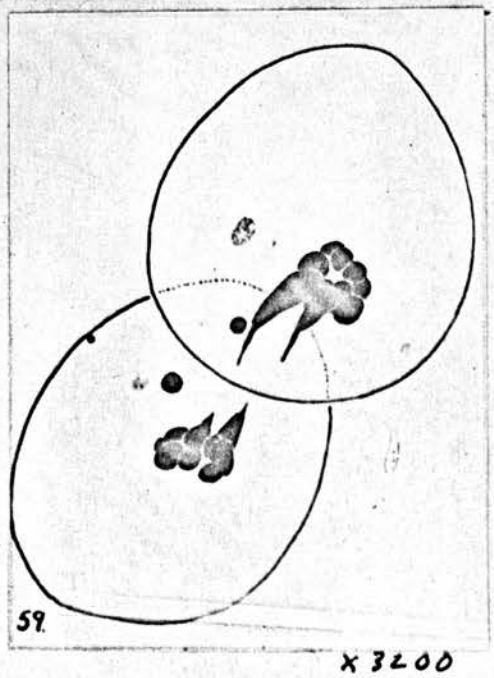
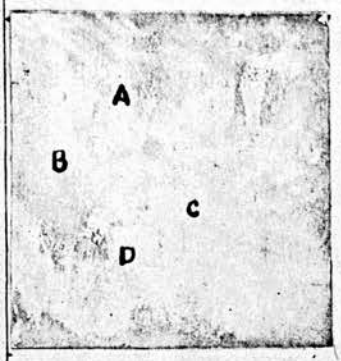


59.

×3200

Plate 1.

Corixa punctata Ill.



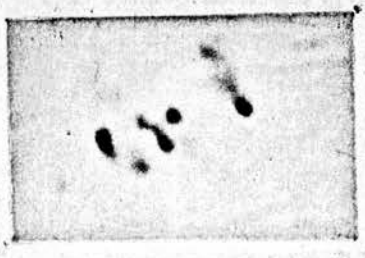
a.

b.

c.

d.

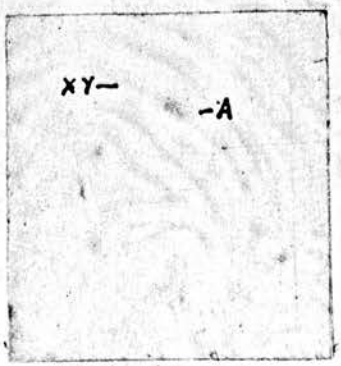
e.



f.

g.

Cymatia bonsdorffi Sahlb.



h.

i.

Chromosome behaviour and taxonomic groups with special reference to five families of Hemiptera-Heteroptera.

Introduction.

Since chromosomes are permanent structures normally transmitted in constant form from generation to generation in living organisms, the problem of the role of chromosome behaviour in taxonomy centres upon the means by which the various chromosome complements, or karyotypes, have been evolved. As bearers of the genes responsible for somatic characters by which one species is distinguished from another, they cannot be regarded as having arisen with their present constitution, but must have been built up in stages of increasing complexity from simpler forms.

A number of studies on wild populations exist which emphasize the significance of the karyotype in relation to morphological differences of taxonomic value.

Among insects, Oguma (1931) has compared the chromosome complements in species of Odonata. Beliajeff (1930), from records of chromosome numbers in ninety four species of Lepidoptera, suggested the probable stem number and showed an agreement between karyological and phylogenetic affinities of

Lepidoptera and Trichoptera. Browne (1916) investigating the spermatocyte divisions of six species of American Notonectidae concluded that the only connection between chromosome number and taxonomy lay in body size and suggested that two groups of species differing by one chromosome in the haploid complement attained maturity at different rates. Dobzhansky and Sturtevant (1938) attempted to trace the history of geographic races of Drosophila pseudo-obscura from a study of inversion, while Helwig (1929) correlated geographic distribution with the behaviour of multiple chromosomes in Circotettix verrucosa.

Many references may be found to chromosome number and behaviour in Hemiptera-Heteroptera, especially in the older literature. (Harvey 1916, 1920). Of the two primary divisions, the first (Gymnocerata) has received attention in descriptions of species belonging to the following families:- Pentatomidae (Montgomery 1901, 1906, Wilson 1907, etc.): Tingitidae (Montgomery 1901, 1906): Pyrrhocoridae (Henking 1891, Wilson 1907, 1909: Coreidae (Montgomery 1901, 1906, Wilson 1932, 1909 etc.): Reduviidae and Nabidae (Montgomery 1901, 1906, Payne 1912): Gelastocoridae (Payne 1909): Hydrometridae (Wilke 1907): Lygaeidae (Wilson 1912, etc): Phymatidae and Capsidae (Montgomery 1901, 1906).

In the second primary division (Cryptocerata) the families of which species have been investigated are:- Naucoridae (Divaz 1914, Poisson 1921, Steopoe 1929): Nepidae (Spaul 1923, Steopoe 1930): Belostomatidae (Chickering 1918, 1927, Montgomery 1901, 1906): Notonectidae (Browne 1916, Poisson 1927) and Corixidae (Prokofiewa 1931, 1933).

The present paper deals with chromosome form and behaviour during spermatogenesis in British species of the families Cimicidae, Anthocoridae, and Capsidae, of the Gymnocerata: Corixidae and Micronectidae of the Cryptocerata. These species were collected principally in the neighbourhood of Edinburgh during the summers of 1936 and 1937 and were identified by the author who is indebted to Mr. W. E. China, British Museum (Natural History) for the confirmation of certain species.

Differences in time of maturation of the germ cells existing between some species called for the examination of many specimens before satisfactory material was obtained. As an example, meiosis seemed to extend through a longer period of imaginal life in Corixa and Sigara than in Callicorixa and the whole course of meiosis was less readily obtained in this genus.

To bring the comparison of forty five species within the scope of a discussion of their comparative

karyology, description of spermatogenesis is restricted to brief accounts of metaphase stages in primary and secondary spermatocytes. Reference to other phases of meiosis is made only where these stages were absent from the material examined or to elucidate specific characteristics.

Technique.

The testes of the larger species were dissected out in Ringer-Locke physiological saline and fixed in Allen's Picroformol A3 or Langlet's Navashin solutions for eight hours. In the case of small species the whole abdomen was cut off and immersed in the fixative. Sections were cut 15 to 20 micra in thickness and stained with Newton's Gentian Violet.

Drawings were made with a X15 ocular and 1/12 inch oil immersion objective using a Zeiss Abbe camera lucida. These drawings were enlarged X2 by an optical apparatus the details of which have been published (Slack 1938).

All chromosome areas referred to in the following description were obtained by measuring the areas of drawings of metaphase chromosomes and expressing them on an arbitrary scale which is only of value for the purpose of comparison of the species discussed.

Description.

During the maturation of the male germ cells the chromosomes behave in a characteristic manner in the Hemiptera-Heteroptera, different from the usual course of events. Reduction of the whole complement does not occur at the first meiotic division. As a rule only the autosomes separate reductionally at this time. The sex chromosomes conjugate during prophase in the primary spermatocyte but do not remain paired up to metaphase. They separate precociously and enter metaphase as univalent chromosomes, often being close together as though paired, but not orientated parallel to the spindle axis. When the autosomes separate the X and Y divide equationally into their component chromatids so that each secondary spermatocyte also possesses both an X and a Y. At the second division these come together to pair secondarily at metaphase and separate to opposite poles. While the first division is reductional and the second equational for the autosomes, the process is reversed for the X and Y chromosomes, where the first is equational and the second reductional. This entails a difference in chromosome number between the two divisions. In the primary spermatocyte there is one more element at metaphase (two

more in Cimex since this has two X chromosomes) than in the secondary spermatocyte owing to the separation of the sex chromosomes in the one case and their union in the other.

Frequently in the haploid complement, one autosome is much larger than any of the others and may be distinguished as the macrochromosome or "M" chromosome (Browne 1916). Similarly, the smallest chromosome may be so much smaller than the rest of the complement as to merit its distinction as the microchromosome or "m" chromosome. This discrimination is not entirely arbitrary. The "m" chromosome often behaves in a manner akin to the X during meiosis or differs from the other autosomes either in orientation or time of division. With regard to the species described, this chromosome can always be distinguished in the Cryptocerata by such differential behaviour. In the Gymnocerata, if it exists at all, size is the only guide to its presence. Significant small size has been deemed sufficient to denote an "m" chromosome in this paper.

In order to avoid unnecessary repetition and abbreviate description some characteristics of the karyotype are categorically recorded in the following manner:-

(1) n - haploid number of chromosomes

(2) Relative total area = the sum of the areas of each chromosome in the haploid complement seen in polar view at second metaphase (first metaphase where stated). This total area includes the X chromosome but not the Y. In Cimex only the X lying in the same plane as the autosomes is taken into account.

(3) Size frequencies. This formula relates the chromosomes within the complement by recording the numbers of groups of equal areas. The number forming a group of approximately equal size is expressed by the figure within brackets and the number of such groups by the figure outside the brackets. Thus:- 9(1) - 4(2) - 2(4) records the presence of nine chromosomes all differing in size, four pairs and two groups of four each having similar areas. As in the case of total area, these values are based on measurements of chromosomes at second metaphase in polar view.

The validity of considering area as equivalent to size for the purpose of comparison is open to objection. It relies upon the similar degree of contraction of the chromosomes of all species bringing them to a spherical of sub-spherical form. Cymatia bonsdorffi is an exception to this rule and is accorded separate treatment.

Although the polar view of the X is included

in the foregoing measurements, contraction of both X and Y is typically less than that of the autosomes. The difference is not considered to materially affect the measurements.

(4) Ratio of X:Y The size relationship of X and Y can be judged most conveniently from the spindle view at second metaphase. This view has been adopted in comparing the area of the Y relative to that of the X, expressed as a ratio in which X = 1, and not the polar view as in the case of all other measurements.

Section 1. Gymnocerata.

Family Cimicidae

Cimex columbarius?* (Figs. 1, 2, Diag. 1.).

n = 26 or 25.

Relative total area = 38.

Size frequencies = 9(1) + 4(2) + 2(4)

Ratio of $X_1:X_2:Y$ = 1:0.8:0.62

1st Metaphase.

Twenty-seven elements are distributed at random on the equatorial plate. Of these 24 are bivalent autosomes and 3 univalent sex chromosomes.

2nd Metaphase.

The diameter of the spindle is approximately two thirds of that at first metaphase. Twenty five elements are present, one representing the X_1X_2Y complex. Since the sex chromosomes pair end-to-end in the axis of the spindle only the terminal X lies in the same plane as the autosomes and can be seen in polar view. The macrochromosome is sufficiently discontinuous from the series of autosome sizes to be recognized but there is no distinct "m" chromosome.

* This species has not the true phenotypic characters of C. columbarius. The length ratio of the third and fourth antennal joints places it between C. lectularius (the human bed bug) and C. columbarius (which infests birds), but closer to the latter than to the former. It was obtained from laboratory white rats. Mr. W. E. China, in a personal communication, suggests that it may have been C. columbarius originally and that its morphology has changed following the assumption of parasitic life on rats.

A change of orientation at second metaphase introduces a partial regularity into the chromosome configuration. Typically 13 of the larger autosomes lie in a ring at the periphery of the spindle and enclose a group of 11 smaller autosomes and the sex chromosome complex.

At second anaphase the separation of the sex chromosomes is retarded relative to the division of the autosomes, causing the complex to lie extended in the spindle between the two groups of daughter chromosomes.

C. columbarius? (Figs. 37, 38).

n = 18 or 17.

One specimen was found to possess an abnormal number of chromosomes but did not show any marked difference in the phenotype from the other specimens examined. Throughout the whole testis, 19 elements occurred at 1st metaphase and 17 at second. The reduction in number is due to the loss of 8 autosomes which belong to the central group of the second metaphase figure in the normal form, the two types being alike in all other respects. Efforts to find further specimens with this number have been unsuccessful.

Family Anthocoridae.

Anthocoris nemorum L. (Figs 3, Diag. 2).

n = 15

Relative total area = 29 (First metaphase)

Size frequencies = 6(1) + 2(2) + 1(6) (First metaphase)

Ratio of X:Y - 1:0.37 (Diakinesis)

A. nemoralis F. (Fig. 4, Diag. 3)

n = 15

Relative total area = 30 (First metaphase)

Size frequencies = 7(1) + 3(2) + 1(3) (First metaphase)

Ratio of X:Y = 1:0.53 (Diakinesis)

1st metaphase.

This was the only metaphase observed and measurements are chiefly of value for the comparison of the two species and not for their relation to other genera. Sixteen elements are distributed at random in the equatorial plane. The chromosomes of A. nemorum show a slightly smaller absolute size and greater uniformity than those of A. nemoralis. In the former species however, the "M" chromosome is distinct but there is no conspicuous "m". A. nemoralis on the other hand has no clearly defined "M" but has a small element which might be regarded as the microchromosome.

Late anaphase nuclei gave an indication of the orientation at the ensuing second metaphase. In both species a peripheral ring of 12 chromosomes encloses the XY pair and 3 autosomes.

Family Capsidae.

sub-family Mirina

tribe Miraria

Stenodema calcaratum Fall. (Figs. 5, 21, Diag. 4).

n = 17

Relative total area = 30

Size frequencies = 10(1)+ 2(2) + 1(3)

Ratio of X:Y = 1:0.40

1st metaphase.

Orientation of the 16 bivalent autosomes and univalent X and Y is random except that the clearly defined "M" chromosome lies outside the plate formed by the remainder of the complement.

2nd metaphase.

Distribution is still irregular but with a tendency for the larger autosomes to lie near the edge of the plate, the XY near the centre, and the "M" in the position it occupied at first metaphase. There is sufficient difference between the smallest autosome and the next in size to warrant its determination as the "m".

Miris dolabratus L. (Figs. 6, 22, Diag. 5).

n = 17

Relative total area = 40

Size frequencies = 10(1)+ 2(2) + 1(3)

Ratio of X:Y = 1:0.35

1st metaphase.

Orientation resembles that of the foregoing species except that the X is here the largest chromosome and occupies a position at the edge of the plate.

2nd metaphase.

The larger autosomes tend to form an ill-defined ring enclosing the XY pair and usually 5 autosomes. Arranged in order of size, the first 6 chromosomes show progressive reduction to half the size of the largest (X) after which there is only a gradual decrease throughout the remainder of the genom.

tribe Capsaria.

Phytocoris ulmi L. (Figs. 11, 28, Diag. 6).

n = 16

Relative total area = 20

Size frequencies = 7(1)+3(2)+1(3)

Ratio of X:Y = 1:0.25

1st metaphase.

The 15 bivalent autosomes and the Y are disposed at random; the X, a chromosome almost twice the size of the largest autosome, lying at the edge of the plate as in M. dolabratus.

2nd metaphase.

There is a tendency towards the formation of a ring surrounding the XY and 3 or 4 autosomes,

but in this species the enclosed autosomes are not the smaller members of the complement. The chromosomes are not only smaller than those of M. dolabratus, but vary less in size. The "m" chromosome is particularly small.

Calocoris norvegicus Gml. (Figs. 7, 23, Diag. 7).

n = 16

Relative total area = 26

Size frequencies = 8(1) + 4(2)

Ratio of X:Y = 1:0.69

1st metaphase.

Ofientation is irregular with a large "M" chromosome at the edge of the plate.

2nd metaphase.

A peripheral ring of 11 autosomes enclose a group of 3 and the XY pair. The inner group includes a microchromosome and the largest autosome with the exception of the "M" which lies outside the ring.

C. fulvomaculatus De G. (Figs. 8, 24, Diag. 8).

n = 17

Relative total area = 18

Size frequencies = 7(1) + 2(2) + 2(3)

Ratio of X:Y = 1:0.56

1st metaphase.

Distribution is not entirely random. The

chromosomes exhibit a slight inclination to move towards the periphery of the spindle and form a ring enclosing a group of 7 or 8. The X is the largest member and is peripheral in position.

2nd metaphase.

The incipient formation of a peripheral ring is again in evidence but with the XY in the centre. A microchromosome occurs but, unlike C. norvegicus, no distinct "M"; while all the chromosomes are smaller than in that species and vary less individually.

C. sexguttatus F. (Figs. 9, 28, Diag. 9).

n = 16

Relative total area = 18

Size frequencies = 6(1)+2(2)+2(3)

Ratio of X:Y = 1:0.38

1st metaphase.

While no peripheral ring and central group are formed, the chromosomes generally congregate towards the edge of the spindle plate leaving a central space unoccupied. The X chromosome is the largest element and always peripheral in position.

2nd metaphase.

Orientation resembles that of the equivalent stage in C. fulvomaculatus in the development of an outer ring but 4 autosomes are included with a larger XY pair in the central group. Size relationships of the two species are closely similar,

C. fulvomaculatus differing chiefly in the addition of one middle-sized chromosome.

Stenotus binotatus F. (Figs. 10, 26, Diag. 10)

n = 16

Relative total area = 17

Size frequencies = 7(1)+3(2)+1(3)

Ratio of X:Y = 1:0.71

1st metaphase.

The arrangement of chromosomes is very similar to that of C. sexguttatus in the production of a central space and the position of the X.

2nd metaphase.

S. binotatus advances much further in the formation of a peripheral ring comprising all the autosomes and leaving the XY in the centre of the spindle. Of the two species, S. binotatus has the smaller complement, as a whole, and an even gradation in size exists between the chromosomes.

Capsus ater L. (Figs 27, Diag. 11).

n = 17

Relative total area = 36

Size frequencies = 9(1)+4(2)

Ratio of X:Y = 1:0.9

1st metaphase

Unobserved.

2nd metaphase

A regular outer ring of 11 autosomes encloses a group of 6 elements, the largest of which represents

the XY. The size of the whole complement is greater than that of any species of the tribe Capsaria and chromosome size more uniform.

sub-family Bryocorina.

Monolocoris filicis L. (Figs. 12, 13, 29, Diag. 13).

n = 17

Relative total area = 10

Size frequencies = 1(1)+4(2)+2(4)

Ratio of X:Y = 1:0.98

1st metaphase.

Sixteen bivalent autosomes form an irregular plate with no indication of a hollow spindle. The X and Y lie outside this plate, unpaired, and both are larger than any of the autosomes.

During first anaphase the equational division of the sex chromosomes is delayed relative to the reductional separation of the autosomes. The Y is the first to divide, followed by the X. The process takes place between the two separating plates of autosomes, the sex chromosomes having moved inwards from their metaphase positions.

2nd metaphase.

A ring of 12 chromosomes surrounds the relatively large XY pair and 4 of the smaller autosomes.

sub-family Macrolophina.

tribe Macrolopharia.

Dicyphus epilobii Reut. (Figs. 14, 30, Diag. 14).

n = 24

Relative total area = 33

Size frequencies = 8(1)+ 2(2)+ 4(3)

Ratio of X:Y = 1:0.24

1st metaphase.

The first metaphase pattern is an irregular grouping as in the majority of the foregoing species but the unusually large X does not lie at or beyond the edge of the autosomal group. It is placed well within the margin and may be near the centre. In some nuclei a thread of faintly stained material unites it with the Y, although this chromosome may be situated at a distance from the X equal to the latter's width.

2nd metaphase.

A well defined ring of 19 autosomes encloses a group of 4 and the XY pair. The range of size of the autosomes shows little discontinuity but the difference between the X and the largest autosome is exceptionally great. In polar view the area of the former is more than four times that of the latter. Secondary pairing is accomplished in two ways. The X touches the Y either at one end or at an interstitial point midway along its length.

D. stachydis Reut. (Fig. 39, Diag. 12)

n = 24

Relative total area = 25

Size frequencies = 4(1)+2(2)+3(3)+1(7)

Ratio of X:Y = 1:0.38

1st metaphase.

Unobserved.

2nd metaphase.

Distribution resembles that in D. epilobii. In this case 15 autosomes form the outer ring and 8 lie within it, also arranged in a ring with the XY pair in the centre. Absolute size of the genom is less than that of D. epilobii. There is also less variation between individual chromosomes.

sub-family Heterotominа.

Orthotylus ericetorum Kb. (Figs. 15, 31, Diag. 15).

n = 12

Relative total area = 23

Size frequencies = 10(1)+1(2)

Ratio of X:Y = 1:0.17

Although first metaphase nuclei were absent from the sections examined, diakinesis in the primary spermatocyte showed 11 bivalent autosomes and univalent X and Y chromosomes; the latter widely separated from one another.

2nd metaphase.

Ring formation of the autosomes is not well defined. Usually a ring of 8 can be determined with difficulty, surrounding a group of 3 and the XY. There is a return in O. ericetorum to the type of complement with a large "M" chromosome which exceeds the X and a very small "m" micro-chromosome occurs. The range of size is such that only two autosomes are approximately equal.

sub-family Phylina

Onychumenus decolor Fall (Figs. 16, 32, Diag. 16).

n = 16

Relative total area = 20

Size frequencies = 6(1)+2(2)+2(3)

Ratio of X:Y = 1:0.60

1st metaphase.

There is evidence of a departure from the usual irregular distribution and a slight advance in the direction of hollow spindle formation. The X and Y lie closely apposed, usually within the weakly developed outer ring in spite of their being the largest elements.

2nd metaphase.

Orientation is similar to that of first metaphase with the XY now at the centre of the spindle. Secondary pairing of the sex chromosomes

is not necessarily end-to-end in the same axis. Their long axes may meet at an oblique angle.

Conostethus brevis Reut. (Figs. 17, 33, Diag. 17).

n = 16

Relative total area = 15

Size frequencies = 5(1) + 2(2) + 1(3) +1(4)

Ratio of X:Y = 1:0.51

1st metaphase.

Orientation resembles that of O. decolor with a closer approximation to two concentric rings consisting of 11 outer and 6 inner components. The sex chromosomes take part in the inner ring.

2nd metaphase.

Two concentric rings are clearly defined with the inner ring now reduced to 5 elements as a consequence of the secondary pairing of the XY.

Psallus varians H.S. (Figs. 18, 34, Diag. 20).

n = 16

Relative total area = 26

Size frequencies = 6(1) + 2(2) + 2(3)

Ratio of X:Y = 1:0.25

1st metaphase.

The 15 autosomes tend to become arranged in a double ring with the XY near the centre. These last are closely apposed, approximately side by side. After equational division they become orientated in the spindle axis at early anaphase and

are then secondarily paired in preparation for reduction at the second division.

2nd metaphase.

The formation of a hollow spindle is carried to an advanced degree and may consist of a single ring of autosomes encircling the bivalent XY, either alone or with several autosomes.

Ps. variabilis Fall. (Fig. 40, Diag. 21).

n = 15

Relative total area = 11

Size frequencies = 4(1)+1(2)+1(4)+1(5)

Ratio of X:Y = 1:0.82

1st metaphase.

Unobserved.

2nd metaphase.

Most nuclei fail to show any regularity of distribution and have the XY situated either centrally or towards one side of the spindle plate. In some cases a peripheral ring may be determined around the XY and a group of 2 or 3 autosomes. The size of the chromosomes as a whole is much less than in Ps. varians but the range of size somewhat similar.

Plagiognathus arbustorum Wlff. (Figs. 19, 35, Diag. 18).

n = 17

Relative total area = 22

Size frequencies = 8(1)+1(4)+1(5)

Ratio of X:Y = 1:0.41

1st metaphase.

Distribution of the chromosomes is random with the XY lying far apart from one another. The X is usually near the centre of the spindle, a fact readily determined in faded gentian violet preparations in which it appears as a less deeply stained body than any of the other chromosomes.

2nd metaphase.

The irregularity of the first metaphase orientation is still apparent but to a lesser degree. The autosomes are generally disposed at the periphery of the spindle leaving the XY pair in a central position. Variation in size is greater than that of the two Psallus species and an "M" chromosome clearly defined.

Pl. chrysanthemi Wlff. (Figs. 20, 36, Diag. 19).

n = 15

Relative total area = 17

Size frequencies = 5(1)+2(2)+2(3)

Ratio of X:Y = 1:0.46

1st metaphase.

The chromosomes are arranged close together and form a plate of little more than half the size of that of Pl. arbustorum. Orientation is more symmetrical, usually a double ring with the X

chromosome a member of the inner ring.

2nd metaphase.

A definite ring of 11 chromosomes develops with greater regularity than in Pl. arbustorum. It surrounds 3 autosomes and the XY.

Chlamydatus evanescens Boh. (Fig. 41, Diag. 22).

n = 17

Relative total area = 16

Size frequencies = 6(1)+ 4(2) +1(3)

Ratio of X:Y = 1:0.27

1st metaphase.

Unobserved.

2nd metaphase.

Both the chromosomes and the diameter of the spindle are smaller than those of Plagiognathus. Orientation is completely random except for the XY which takes up a central position.

Section 2. Cryptocerata.

Family Corixidae.

Sub-family Corixinae.

Corixa punctata Ill. (Figs. 42, 53, Diag. 23).

n = 12

Relative total area = 44

Size frequencies = 7(1)+1(2)+1(3)

Ratio of X:Y = 1:0.51

1st metaphase.

The large chromosomes of this species are, as a rule, irregularly distributed in the equatorial plane but may orientate as an ill-defined ring. Typically the X and Y and "m" chromosomes behave in the manner characteristic for the Heteroptera but the usual sequence of divisions may be reversed. In some nuclei these chromosomes appear as four univalent elements which divide equationally; in others either the sex chromosomes or the "m" are univalent.

2nd metaphase.

Orientation differs but little from that of first metaphase and the XY is inconstant in position. X, Y and "m" chromosomes which were univalent at the first division separate reductionally to restore the haploid number in the spermatids.

Sigara hieroglyphica Duf. (Figs. 43, 54, Diag. 25).

n = 12

Relative total area = 19

Size frequencies = 10(1)+1(2)

Ratio of X:Y = 1:0.51

1st metaphase.

The bivalent autosomes are widely separated from one another in a single peripheral ring whose

diameter is a little larger than the diameter of the first metaphase plate in C. punctata although the individual chromosomes are very much smaller. The "m" chromosome lies within this ring, generally towards one side. Univalent X and Y, while taking part in the ring, are so close together as to resemble a bivalent except that they are situated side by side and not end to end parallel to the spindle axis.

2nd metaphase.

The diameter of the spindle is strongly reduced being only two thirds of that of the first metaphase figure. In addition to the XY the autosomal ring encloses two small chromosomes, one of which is the "m".

S. castanea Thoms. (Figs. 44, 55, Diag. 28).

n = 12

Relative total area = 38

Size frequencies = 10(1)+1(2)

Ratio of X:Y = 1:0.33

1st metaphase.

The formation of the peripheral ring is less regular than in S. heiroglyphica and the much larger chromosomes approach the dimensions presented by those of Corixa. The microchromosome is small in relation to the rest of the complement and occupies an excentric position within the ring.

The sex chromosomes lie apart.

2nd metaphase.

In contrast to the first division figure, the ring of autosomes is regular and includes all but the "m" and XY pair which lie within it. The latter are approximately central in position.

S. scotti D & S. (Figs. 45, 56, Diag. 34).

n = 12

Relative total area = 36

Size frequencies = 8(1)+2(2)

Ratio of X:Y = 1:0.37

1st metaphase.

In its symmetry the first metaphase figure agrees with that of the related S. fossarum (q.v. Prokofiewa 1933). An unbroken ring of chromosomes encircles the central, relatively large "m" bivalent. The autosomes are equidistant from one another while the X and Y are closely apposed and arranged radially with X distal to Y.

2nd metaphase.

The peripheral autosomal ring now includes the "m" chromosome and two larger autosomes accompany the XY within it.

S. carinata Sahlb. (Figs. 46, 57, Diag. 36).

n = 12

Relative total area = 37

Size frequencies = 3(1)+3(3)

Ratio of X:Y = 1:0.48

1st metaphase.

The large chromosomes of this species form a regular ring. The enclosed microchromosome components may either be paired to separate reductionally or unpaired and equational as in C. punctata. The sex chromosomes lie together in the peripheral ring but divide equationally.

2nd metaphase.

The spindle is reduced in diameter to about two thirds that of first metaphase, causing a crowding together of the chromosomes. One of the medium sized chromosomes lies within the ring with the XY.

S. germari Fieb. (Figs. 47, 58, Diag. 37).

n = 12

Relative total area = 33

Size frequencies = 6(1)+3(2)

Ratio of X:Y = 1:0.55

1st metaphase.

Arrangement is similar to that of S. carinata and the diameter of the spindle is slightly smaller. The "m" bivalent is central and the sex chromosomes placed close together side by side.

2nd metaphase.

The spindle has now approximately the same diameter as at second metaphase in S. carinata but

orientation is less regular. Several autosomes, including the "m", may comprise a central group in addition to the XY.

Figs.

Callicorixa wollastoni var. caledonica Kirk (48, 59, Diag. 40).

n = 12

Relative total area = 35

Size frequencies = 12(1)

Ratio of X.Y = 1:0.41

1st metaphase.

The diameter of the spindle is the same as that of Ca. wollastoni (q.v. Prokofiewa 1933) and the arrangement of chromosomes also similar. While the "m" always lies within the ring its position is not constant and may be central or towards one side. X and Y chromosomes are situated close to oneanother.

2nd metaphase.

Reduction of the spindle diameter is not marked, being five sixths of that at first metaphase. The autosomal ring loses the symmetry of the first division and encloses one autosome in addition to the XY. The chromosomes are larger than those of Ca. wollastoni or Ca. praeusta (Prokofiewa 1933) and show considerable variation in size. The "m" bivalent is unusually large and generally peripheral, though both "m" homologues

y occur unpaired within the ring following
uational division in the primary spermatocyte.
ch passes to the opposite pole at second ana-
ase.

Ca. concinna Fieb. (Figs. 49, 60, Diag. 41).

= 12

lative total area = 21

ze frequencies = 12(1)

tio of X:Y = 1:0.58

t metaphase.

As in other members of the genus Callicorixa
e first metaphase ring is almost symmetrical in
st nuclei, with the X and Y lying side by side.
some cases the sex chromosomes pair and in doing
move into the ring displacing the bivalent "m"
a lateral position.
mpared with that of Ca. wollastoni the diameter
the spindle is reduced to five sixths.

d metaphase.

Loss of symmetry characterises orientation
in Ca. wollastoni and the spindle has a diameter
about four fifths of that at first metaphase.
e chromosomes are smaller than in any other species
the genus and vary in size to a greater extent.

aenocorisa cavifrons Thoms. (Figs. 50, 61,
ag. 42).

= 12

lative total area = 16

ize frequencies = 8(1)+ 2(2)

atio of X:Y = 1:0.45

st metaphase.

A well defined ring encircles the central
m" bivalent, the sex chromosomes lying adjacent
ut not closely apposed.

nd metaphase.

A ring again forms with little change in
iameter. While generally included as a member
f the ring, the "m" or one of the other autosomes
ay lie within it. The XY pair occupies a central
osition and occasionally this position is main-
ained where the two components are unpaired owing
o pre-reduction. The chromosomes are unusually
mall and vary to a marked degree from the distinct
M" to the very small microchromosome.

ub-family Cymatinae.

Cymatia bonsdorffi Sahlb. (Figs. 51, 52.)

= 13

elative total area ----------

ize frequencies ----------

atio of X:Y = 1:0.72

st metaphase.

It is not practicable to apply measurements
f areas of chromosomes as seen in polar view to
he comparison of Cymatia with other Corixid species
ince several bivalents differ from the typical

shape found throughout the Corixinae. Two of these atypical bivalents do not contract to a sub-spherical form but remain elongate with their axes in the equatorial plane, due either to localised chiasma formation or to terminalised chiasmata coupled with reduced contraction. The other two bivalents of abnormal shape are asymmetrical, each component being unequally bilobed as though composed of long and short chromatids. This asymmetry may be due to translocation. The fact that one unequal bivalent is larger than the other rules out the possibility of reciprocal translocation between two pairs of chromosomes of different lengths. It suggests that a distal segment of one of the smaller pair has been transferred to the end of one of the larger homologues. The validity of this analysis should be proved at second metaphase by the occurrence of two chromosomes dividing into unequal chromatids on the grounds that the first division is equational and the second reductional. Unfortunately very few second metaphase nuclei have been found to show spindle views. At least one chromosome fulfilled the required conditions in that it appeared to be dividing unequally. The form of the bivalent does not imply a marked discrepancy in chromatid lengths and the difference might well be more

ifficult to detect at second metaphase, especially
the small chromosomes typical of the Heterop-
era. While therefore there is evidence of
ranslocation its occurrence remains unproven.
matia is also unique in another respect. It
the only species of the Corixidae known to have
different number of chromosomes. The haploid
mber of 13 is probably due to the addition of a
all chromosome approximately equal in size to
e "m", though differing in behaviour. The "m"
valent itself consists of elongate components
ich separate in advance of the other chromosomes
the primary spermatocyte and are usually a
ort distance apart at metaphase. Orientation
the complement conforms with the usual Corixid
pe, the peripheral ring is regular at both meta-
ase stages and changes but little in size. At
e first division the "m" bivalent occupies the
ntral position and at the second the XY pair.

mily Micronectidae

Micronecta poweri D & S (Figs. 52, 63, 64,
ag. 44).

= 12

elative total area = 22 (First metaphase)

ze frequencies = 6(1)+3(2)

tio of X:Y - ----------

t metaphase.

Only two nuclei have been examined at this

stage and in both the orientation was random. At early anaphase however the autosomes form a ring with the X and Y in a central position. These lie side by side and closely apposed. At later anaphase they move apart but still retain the same orientation relative to the spindle axis. Each appears to divide at the same time as the autosomes separate. The daughter sex chromosomes then move apart at a greater rate, so that atmid-anaphase in the primary spermatocyte they lie approximately half way between the autosomes and the poles. Size relationships based on measurements of first metaphase figures show a general small size of complement without great variation between individual chromosomes and with no clearly indicated "m" chromosome.

Discussion.

Metaphase orientation.

The formation of a hollow spindle at meiotic metaphase is typical of the Hemiptera-Heteroptera. In the primary spermatocyte, most or all of the chromosomes, including the X and Y lie in a peripheral ring at the equator of the spindle while at the second division the sex chromosomes occupy a central position within the ring. This characteristic arrangement of the chromosomes is developed in varying degrees in the twenty two species of

Table 1.

		Orientation at First Metaphase: Random	Incipient Ring	Single Ring	Double Ring	Orientation at Second Metaphase: Random	Incipient Ring	Single Ring	Double Ring	10	11	12	13
F.Cimicidae	Cimex columbarius	X						X					
F.Anthocoridae	Anthocoris nemorum	X						(X)[A]					
	A.nemoralis	X						X					
F.Capsidae													
s.f.Mirina													
t.Miraria	Stenodema calcaratum	X				X							
	Miris dolabratus	X					X						
t.Capsaria	Phytocoris ulmi	X					X						
	Calocoris norvigicus	X						X					
	C.fluvomaculatus	X					X						
	C.sexgutatus		X				X						
	Stenotus binotatus		X					X					
	Capsus ater							X					
s.f.Bryocorina													
	Monalocoris filicis	X						X		X			
s.f.Macrolopharia													
	Dicyphus epilobii	X						X					
	D.stachydis								X				
s.f.Heterotomina													
	Orthotylus ericetorum						X						
s.f.Phylina													
	Onychumenus dicolor		X				X						
	Conostethus brevis		X_2						X				
	Psallus varians		X_2					X					
	Ps.variabilis						X				X		
	Plagiognathus arbustorum	X					X						
	Pl.chrysanthemi		X					X					
	Chlamydatus evanescens				X			X					

$(X)^A$ = First Anaphase.

X_2 = Incipient double ring.

39 40	Ratio of X:Y (Y= 1.0) .2	.3	.4	.5	.6	.7	.8	.9	1.0	Groupings of Equal Areas. 1	2	3	4	5	6	7	Haploid No. (n)
					X		X			9	4	-	2	-	-	-	25,26
			D (X)							(6	2	-	-	-	1	1 -)	15
				D (X)						(7	3	1	-	-	-	1 -)	115
			X							10	2	1	-	-	-	-	17
X		X								10	2	1	-	-	-	-	17
	X									7	3	1	-	-	-	-	16
						X				8	4	-	-	-	-	-	16
					X					7	2	2	-	-	-	-	17
			X							6	2	2	-	-	-	-	16
						X				7	3	1	-	-	-	-	16
								X		9	4	-	-	-	-	-	17
									X	1	4	-	2	-	-	-	17
	X									8	2	4	-	-	-	-	24
			X							4	-	3	1	-	-	1	24
	X									10	1	-	-	-	-	-	12
					X					6	2	2	-	-	-	-	16
				X						5	2	1	1	-	-	-	16
	X									6	2	2	-	-	-	-	16
							X			4	1	-	1	1	-	-	15
			X							8	-	-	1	1	-	-	17
				X						5	3	2	-	-	-	-	15
		X								6	4	1	-	-	-	-	17

$(X)^{D}$ Ratio of X:Y at Diakinesis.

Gymnocerata here described. (Table 1.)

Random distribution of chromosomes at both metaphase stages occurs in:-

Stenodema calcaratum

Random distribution at 1st and ring formation at second metaphase occurs in:-

Cimex columbarius C. fulvomaculatus
Anthocoris nemorum Monalocoris filicis
A. nemoralis Dicyphus epilobii
Miris dolabratus Plagiognathus arbustorum
Calocoris norvegicus

Ring formation at both metaphase stages occurs in:-

Calocoris sexguttatus
Stenotus binotatus
Onychumenus decolor
Conostethus brevis
Psallus varians
Plagiognathus chrysanthemi

These facts illustrate an advancing tendency towards ring formation in accordance with the taxonomic order. This is especially true in the subfamily Mirina where Stenodema calcaratum with random chromosome distribution at both stages, stands at the beginning of the series and Stenotus binotatus, with an incipient and a definite ring at first and second metaphase, respectively, at the

Table 2.

		15	16	17	18	19	20	21	22	23
F. Corixidae s.f.Corixinae	Corixa punctata									
	C.dentipes (P)									
	Sigara hieroglyphica					X				
	S. salbergi (P)									
	S.linnaei (P)									
	S.striata (P)						X			
	S.distincta(P)					X				
	S.fallenii (P)									X
	S.castanea									
	S.semistriata (P)					X				
	S.fabricii (P)							X		
	S.fossarum (P)									
	S.scotti									
	S.carinata									
	S.germari									
	Callicorixa praeusta (P)									X
	Ca. wollastoni (P)									X
	Ca.caledonica									
	Ca.concinna							X		
	Glaenocorisa cavifrons		X							
s.f. Cymatinae	Cymatia bonsdorffi				—					
F. Micronectidae	Micronecta poweri								X	

(P) = Species described by Prokofiewa.

38 39 40 41 42 43 44 45	Ratio of X : Y (X = 1.0) .1 .2 .3 .4 .5 .6 .7 .8 .9 1.0	Groupings of Equal Areas. 1 2 3 4 5 6 7	Hap num
X	X	7 1 1 - - - -	
X	X	12 - - - - - -	
	X	10 1 - - - - -	
	X	8 2 - - - - -	
	X	8 2 - - - - -	
	X	10 1 - - - - -	
	X	10 1 - - - - -	
	X	8 2 - - - - -	
X	X	10 1 - - - - -	
	X	8 2 - - - - -	
	X	10 1 - - - - -	
	X	10 1 - - - - -	
	X	8 2 - - - - -	
	X	5 2 1 - - - -	
	X	8 2 - - - - -	
	X	10 1 - - - - -	
	X	8 2 - - - - -	
	X	12 - - - - - -	
	X	12 - - - - - -	
	X	8 2 - - - - -	
	X	5 2 1 - - - -	1
	X	6 3 - - - - -	1

end. While it is impossible to assume a similar trend in the sub-family Phylina, it is noted that all three types of chromosome arrangement are represented in this group.

The Cryptocerata are more uniform in chromosome orientation than are the above families of Gymnocerata. A single peripheral ring is present at both metaphase stages in all except two species of Corixidae in which the karyotype is known. These exceptions Corixa dentipes (Prokofiewa 1933) and C. punctata, generally show random distribution but the latter species may occasionally develop an irregular ring. (Table 2.)

Chromosome number and size.

The basic number of autosomes in the Heteroptera appears to be six (Vandel 1937)* since this number and its multiples with variations of ± 2 occur most frequently in the sub-order. A general formula for the haploid number based on these values is:-

$$n = ya \pm z + X(Y)$$

where a represents the basic number (6) of autosomes, y varies from 1 to 4 and z from 1 to 3. It is plain that variations of ± 1 to 3 from the stem number 6 (a) or its multiples generates a complete series of consecutive numbers. If all the numbers

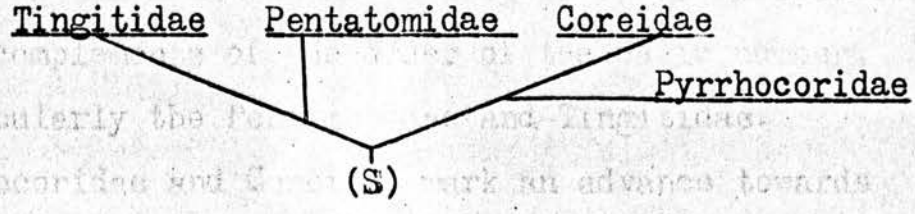
* This conclusion was reached independantly by the author and reported in a paper read before the British Association (Nottingham 1937) previous to the publication of Vandel's paper.

Table 3.

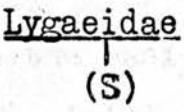
		a-4	a-3	a-2	a-1	a	a+1	a+2	2a-3 a+3	2a-2	2a-1	2a-	2
Gymnocerata													
A.	Pentatomidae	1	1	1	4	6	4					2	
	Tingitidae					1							
	Pyrrhocoridae				1	1					1		
	Coreidae					3				4	1	1	
B.	Lygaeidae				2	2							
C.	Reduviidae									1		2	
	Phymatidae												
	Nabidae							2					
	Hydrometridae								2	2			
D.	Cimicidae												
	Anthocoridae												
	Capsidae										1		
Cryptocerata													
E.	Gelastocoridae												
	Naucoridae												
	Belostomatidae		1.								1		
	Nepidae												
F.	Pleidae										1		
	Notonectidae										3	1	
	Corixidae										20	1	
	Micronectidae										1		
		1	1	1	7	13	4	2	2	7	29	7	
		2	3	4	5	6	7	8	9	10	11	12	

occurred equally throughout the group the formula would have no significance. That this is not the case is shown by Table 3. which classifies the Heteropteran families according to different values for y and z. There are relatively few species having the formula ya±3 (two species of Hydrometridae and eight of Capsidae). A more significant fact brought out by this classification is that increase in chromosome number is correlated with advance in taxonomic order. The more primitive families have low values of a and the more specialised families high values. This statement may be elaborated by comparing the chromosome numbers with the phylogeny of the families given by China (1933). Groups of families arose from a Pentatomoid stock (S) in the following manner:-

A.



B.



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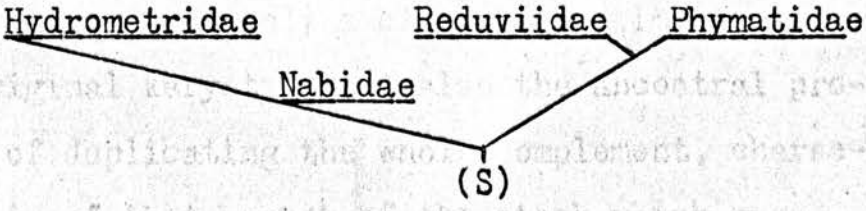

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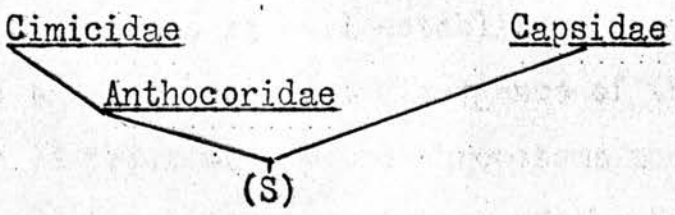

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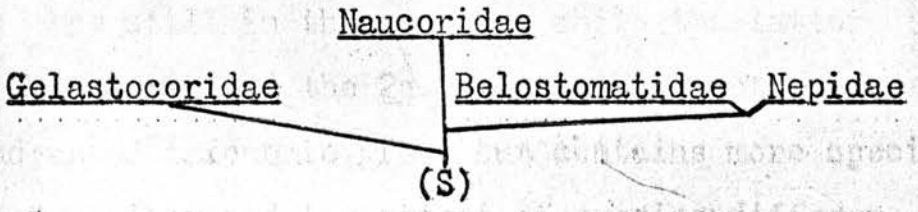

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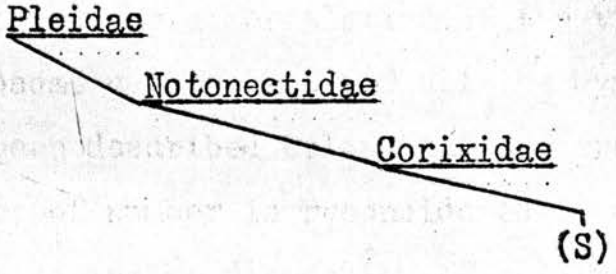


These taxonomic groups show a fairly close accordance with grouping of chromosome number (Table 3.).

Groups A and B show a preponderance of species with complements of the order of the basic number, particularly the Pentatomidae and Tingitidae. Pyrrhocoridae and Coreidae mark an advance towards the 2a class. After Group B there is no return to a karyotype with the basic number or its varieties. These two groups of primitive families appear to have retained not only a closer approximation to the original karyotype but also the ancestral property of duplicating the whole complement, characteristic of that branch of the stock which gave rise to the Pyrrhocoridae and Coreidae.

The 2a class is well established in Group C and here the morphological divergence of the families is reflected by the chromosome numbers. Nabidae, on the line of evolution of the Hydrometridae are still in the a class, while the latter family has reached the 2a. Group D is not only an advanced taxonomic group but contains more species than any other and the extent of species differentiation may be a correlative of the wide range in chromosome number. Since all the Gymnocerata which have been described belong to this group the significance of number is reconsidered in conjunction with size in the discussion of relationships between and within the families.

Almost all the Cryptocerata fall into a group having the value 2a - 1, and it is noticeable that those species which do differ significantly from this number belong to Group E. Group F is remarkably constant and, since the three families concerned form a single evolutionary series from the taxonomic point of view, the whole group may possess a particular constitution which suppresses change in the chromosome number.

In whatever ways variations have been evolved, in the course of time, they have resulted in stabilised karyotypes whose origins cannot now be analysed with any degree of certainty on account

of their long establishment. All that can be done is to examine the available observational evidence and deduce the probable course of evolution.

Vandel (1937) considers that multiples of the stem number (a) in the Hemiptera represent fragmentation of the whole complement. A review of chromosome numbers together with other characteristics within the families described in this paper indicates that primary polyploidy, secondary polyploidy and fragmentation as well as other methods have played a part in differentiating karyotypes.

These methods and the criteria available for inferring them are:-

(a) Polyploidy and polysomy indicated by increase in size of the entire complement and in number of chromosomes without change in their mean size.

(b) Fragmentation shown by increase in number and decrease in mean size without affecting the size of the whole complement.

(c) Loss of chromosomes or their fusion with other members of the complement illustrated by decrease in number, the first case decreasing total size of complement, the second increasing mean size of chromosomes.

(d) Structural change by accumulation of small duplications, deficiencies or translocations enlarging or diminishing certain chromosomes.

(e) Genotypic control which may have operated in cases where all the chromosomes of the genom differ proportionately from those of allied species. (Darlington 1937 a).

Postulate (b) can only be conceded with reservations. In order to avoid the production of acentric fragments, simple fragmentation must either entail transverse division of the centromere or give place to a more complex process. This might be the duplication of small, relatively inert, chromosomes by failure of mitosis (Darlington 1937, b) and the functioning of these as bases of attachment for the translocation of large fragments.

The species of Gymnocerata form the following groups according to autosome formula:-

2a - 1	Orthotylus ericetorum
2a + 2'	Anthocoris nemorum, A. nemoralis, Psallus variabilis, Plagiognathus chrysanthemi.
2a 2a + 3 / 3a - 3	Phytocoris ulmi, Calocoris norvegicus, C. sexguttatus, Stenotus binotatus, Onychumenus decolor, Conostethus brevis, Psallus varians.
3a - 2	Stenodema calcaratum, Miris dolabratus, Calocoris fulvomaculatus, Capsus ater, Monalocoris filicis,

	Plagiognathus arbustorum, Chlamydatus evanescens.
4a - I	Dicyphus epilobii, D. stachydis.
4a	Cimex columbarius?

Polyploidy would account for the fact that the related families Cimicidae and Anthocoridae have chromosome numbers of the orders 4a and 2a respectively. Although not strictly comparable, on account of the absence of second metaphase from Anthocoris (see p.75), size relationships show similarity in mean chromosome dimensions and size frequencies and a much greater size of the whole complement in Cimicidae.

There is strong evidence for this suggestion that Cimicidae are tetraploid with respect to Anthocoridae in the occurrence of one specimen of Cimex which had lost eight homologous pairs (i.e. more than one basic set) without the course of meiosis being affected. This implies that the remaining chromosomes comprise at least one complete set, having some degree of genetic homology with those lost and capable of carrying on their functions.

Within the genus Anthocoris, similarity of somatic characters as well as of karyotypes emphasize the near kinship of A. nemorum to A. nemoralis.

In the Capsidae 2a, 3a, and 4a classes all occur, usually with variations of ±1, 2, or 3 chromosomes. The sub-family Mirina includes three species having fifteen haploid autosomes which may be interpreted as either 2a+3 or 3a - 3. Since the remaining species have seventeen, equivalent to 3a - 2, the entire sub-family is regarded as belonging to the 3a class.

Three karyotypes of the sub-family Phylina are intermediate between the 2a and 3a classes. 2a+ 2 and 3a - 2 complements occur equally so that it is difficult to decide to which class the Phylina should be assigned. The relegation of haploid numbers differing by more than three chromosomes to classes with different multiples or a is entirely arbitrary. It does not necessarily imply relative polyploidy in all cases as there is no reason for supposing that loss or gain of chromosomes by other means cannot exceed three. For example, strict adherence to the scheme would place Plagiognathus arbustorum in the 3a class, Pl. chrysanthemi in the 2a, and consequently the genus becomes polyphyletic. There is no other evidence to justify this conclusion and it must be discarded in favour of loss or gain by non-disjunction which could have effected the change as successfully as polyploidy, especially in view of the fact that all species

ave more than one basic set.

Different methods of species differentiation re illustrated by the Capsaria. Fragmentation f one chromosome in Calocoris sexguttatus or a imilar form may have given rise to C. fulvomaculatus hile intragenic change affecting genom size ccounts for the larger complement of C. norvegicus nd species of Phytocoris, Stenotus and Capsus; he last named also showing fragmentation.

The very small size of the chromosomes in onalocoris filicis (3a - 2) suggests that the ryocorina should be looked upon as a comparitively solated group. Karyology does not stand alone n advancing this suggestion. The British genera re peculiar in their morphology and their restriction to specific food plants.

A second case of tetraploidy in the Gymnoerata is indicated in the Macrolophina (4a - 1). ere the individual autosomes approximate in size o those of some species of Phylina but their number approaches the tetraploid value, with a corresponding increase in size of the whole complement. oth species of the single genus examined have the ame number and if all other species prove to be f the 4a class then the Macrolophina should rank s a group standing apart from other sub-families.

Polyploidy can only have operated in establishing the common 2a - 1 karyotype of Corixidae nd Micronectidae. Relationships within these ryptoceran families must be ascribed to structural hange of the chromosomes or to genotypic control f the whole complement.

Prokofiewa (1933) described eleven species f Corixidae and formed three groups founded on aryological features. The first group is characerised by the regular formation of a hollow spindle, y the comparitively small size of the microchromoome and by the apposition of the X and Y at first etaphase. Members of the second group differ in aving large chromosomes and in the wide separation f the X and Y. The third group is similar to the econd except that the chromosomes are still larger nd are orientated irregularly. The effect of his classification is to segregate Sigara (Corixa) ahlbergi and S. linnaei from the other species of igara which together with Callicorixa form a separate group. Corixa dentipes stands alone in the hird group. Taxonomic relations are not violated y this arrangement of eleven species, but the investigation of nine further species of the family as shown that they cannot be fitted into Prokoiewa's scheme without disturbing the taxonomic rder in an unwarrantable manner. Elaboration of

he scheme by the formation of secondary groups till entails the separation of closely related pecies and it is evident that it must be abandoned. ize is the only character of the chromosomes which an be reconciled with systematic classification f the phenotypes. Measurement of the whole complement (Relative total area of Table 2) brings to ight a variation in accordance with the division f the family into genera and the sub-division of hese genera into smaller groups.

The comparision of the following scheme of llied species with relative total area serves to how this agreement between somatic and cytological haracters:-

Taxonomic groups.	Relative total area.
. Corixa punctata, C. dentipes	43, 44
. (a) Sigara hieroglyphica	19
(b) S.sahlbergi, S. linnaei	31, 31
(c) S.striata, S. distincta, S.fallenii	20, 19, 23
(d) S.semistriata, S.fabricii	19, 21
(e) S.fossarum, S.scotti	31, 36
(f) S.castanea	38
(g) S.carinata, S.germari	37, 34
. Callicorixa praeusta, C. wollastoni, Ca. caledonica, C. concinna	23, 23 35, 21
. Glaenocorisa cavifrons	16

The only marked divergence is shown by Ca. caledonica. This species was identified by Mr. W. E. China who considers it a probable variety of Ca. wollastoni. Dr. L. Lundblad has also examined specimens and reports them to be true Ca. wollastoni, "even if they genetically differ regarding chromosomes". All the specimens of this form were collected from one locality (Loch Leven, Kinross) and have not been found elsewhere by the author. They must be regarded as a local race in which chromosome size has increased to an unusual degree for a Corixid species.

A more important instance of the way in which karyological characteristics indicate phylogenetic relationships refers to Cymatia bonsdorffi. The fact that the haploid number of autosomes is exactly twice the basic number suggests that Cymatia has diverged less from the Corixid archetype than have other species of the family. The size of the nucleus in relation to that of the cell together with the form and behaviour of its chromosomes bears a striking resemblance to the same characters of Notonecta. Some species of Notonecta also resemble Cymatia in having the haploid autosome formula 2a, others have 2a - 1, while Notonecta insulata appears to be an intermediate form in which 2a is becoming 2a - 1 by fusion of two chromosomes (Browne 1916).

It is apparent that there is good reason for supposing that in Cymatia lies the connection between Corixidae and Notonectidae.

This view is postulated on purely cytological grounds independantly of other considerations. It is not however a theory for which other support is lacking since China (1937 unpublished) has arrived at the same conclusion from the standpoints of morphology and physiology.

Size ratio of the sex chromosomes.

The proportional length of the Y chromosome with respect to the X was found by Prokofiewa (1933) to be a characteristic bearing little relationship to the phylogenetic affinities within the Cryptocerata. This is even more noticeable in the three families of Gymnocerata. Tables 1 & 2 show to what degree the X:Y ratio does agree with phylogeny. They illustrate the marked variability of this ratio in the Gymnocerata and its relative uniformity in Cryptocerata where the karyotype is more stable (e.g. chromosome number and orientation).

Throughout the discussion of chromosome number the sex chromosomes have been purposely omitted, on account of their special properties and the necessity for postulating a particular mode of behaviour, which would not disturb their function

ring evolutionary changes. It remains to be
en in what way the normal functioning of these
romosomes can have been preserved. The assump-
on that polyploidy has taken part in the evolution
animal species is faced with the serious obstacle
esented by the disturbance of the interaction
tween autosomes and sex chromosomes which is res-
nsible for the production of two sexes has been
ressed by Müller (1925, 1932) in discussions on
e question of polyploidy in animals.

Tetraploid nuclei in the gonads of otherwise
rmal diploid individuals are not uncommon (c.f.
lson 1932). If doubling of the complement
ok place simultaneously in both sexes and these,
ted together, produced viable offspring, a tetra-
oid form might arise immediately.

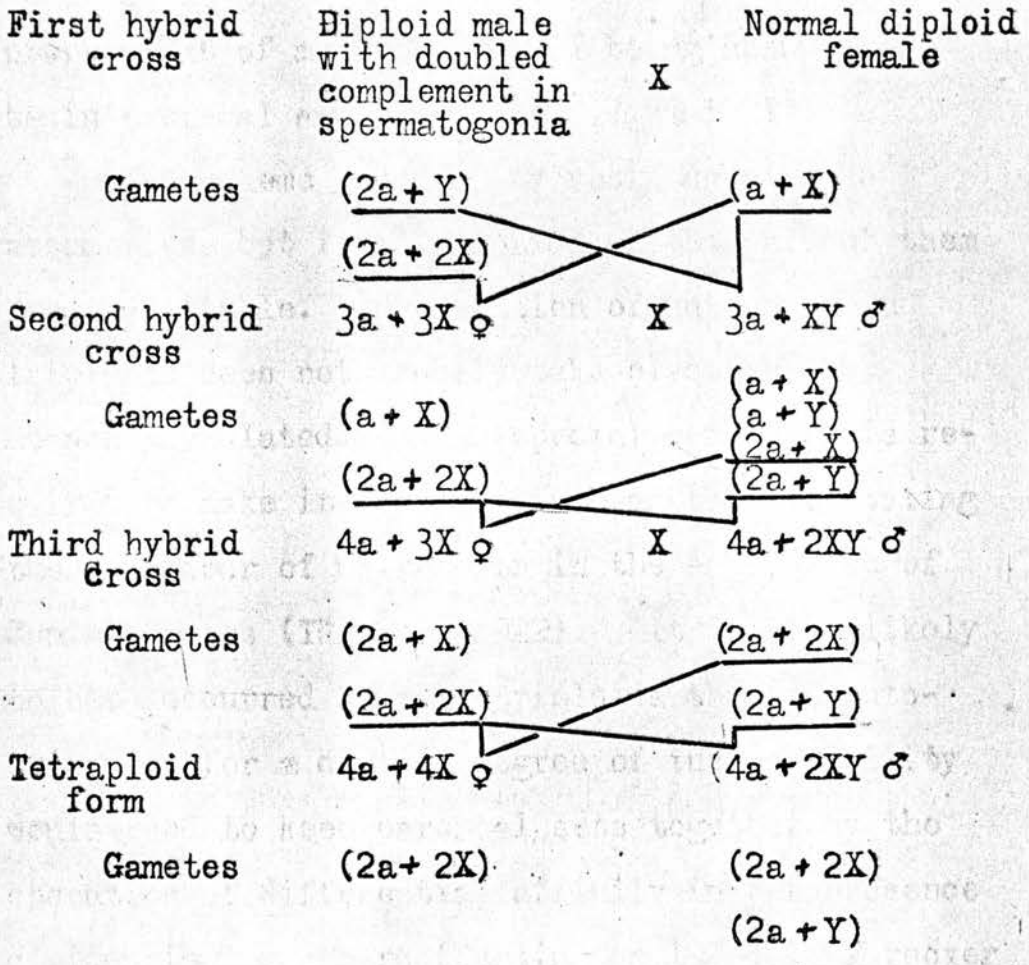
It is an obvious fact that some regulation
mechanical properties of the sex chromosomes
st occur before the polyploid species could be-
me stabilised. The species could not long sur-
ve with random segregation of the multiplied
mber of sex chromosomes. With this fact in mind,
e two genera presented in this paper, which show
gns of polyploid derivation from other types
und in the family, can be seen to possess signi-
cant characteristics. The two X chromosomes of
mex always segregate together, while the enormous

X of Dicyphus may represent the extreme form of regulation attained by fusion of originally separate components.

Muller referred to the unbalanced state and consequent sterility of male triploid hybrids found in Bridges (1921) in Drosophila and Vandel (1937) has recently reopened the subject pointing out that while triploids are usually sterile, normal triploids do occur in occasional species (e.g. in Trichoniscus elisabethae). Since the triploid condition would seem to be a necessary step in the evolution of a tetraploid form following doubling in only one sex, evidence of viable triploids is important.

The doubling of chromosome number (e.g. by syndiploidy) in a male which successfully fertilised a normal female could give rise to a tetraploid form under certain conditions. The following tentative scheme, simplified as far as possible for the sake of clearness, illustrates one possible way of achieving this result:-

P.T.O.



It is assumed in this hypothesis that the course of evolution obeyed certain rules:-

(a) that the crossing of a male having a doubled chromosome number with a normal haploid female produced viable triploid offspring of both sexes.

(b) that regular segregation took place during gametogenesis in the triploid producing diploid gametes at least in some nuclei.

(c) that non-disjunction of two X chromosomes always occurred in multiple X forms

(d) that the autosome: X chromosome balance demanded

roportions of more than 3a:2X being assumed to
e intersexual and sterile (Bridges 1921).

The scheme necessarily rests upon these
ssumptions but it is doubtful whether all of them
re justifiable. Segregation of autosomes in
riploids does not usually take place in the
anner postulated. Some special condition is re-
uired to make it possible such as that regulating
he behaviour of univalents in the embryo-sac of
aninae roses (Täckholm 1922). It is more likely
o have occurred in allo-triploids than in auto-
riploids for a certain degree of incompatibility
ould tend to keep parental sets together by the
peration of differential affinity in the presence
f identical partners (Darlington 1928). Moreover
trict obserance of this type of segregation may
ot be necessary. Species having exact multiples
f the basic number are relatively rare and may
ven have been attained by secondarily by other
eans. Secondary polyploidy (Darlington and Moffet
930) can be brought in without seriously disturbing
he scheme, for the presence of two complete sets
f autosomes plus a fraction of a third set might
till produce a viable gamete; the resulting tetra-
loid then having only an approximately doubled
umber. Such a variation from exact multiples of
he basic number is common throughout the Hemiptera-

Heteroptera.

The resulting karyotype has the haploid number of the 2a class with two X chromosomes which must either become stabilised in their behaviour in the ways suggested for Cimex and Dicyphus or establish a permanent sexual system by loss of sex-determining power on the part of the supernumary Xs and their transformation into autosomes (Gates 1926).

Exception may be taken to loss by non-disjunction or deficiency due to fragmentation as methods of varying chromosome number and size on the grounds that genes essential to the life of the organism might be removed. If such changes are imagined to have been preceded by polyploidy or polysomy, the duplication of the complement as a whole or in part compensates for these disadvantageous gene deficiencies and would enhance the survival of the new form (Muller 1925). The case of Cimex is of interest in this respect, but not conclusive. While the mechanism of meiosis was not disturbed by the loss of eight autosomes it is impossible to predict whether the specimen with the abnormal number could have produced viable offspring.

Incompatibility in hybrids offers a further means of establishing karyotypes with multiples of

the basic number. In Populus simoni hybrids pairing fails between the haploid sets from the two parents resulting in a doubled number in the gametes of the progeny (Meurman 1925). Here X and Y exist singly and the problem of regulation of the sex mechanism is not the same as that which besets true polyploidy. What is required in this case is some degree of homology of the X and Y to ensure their pairing and regular disjunction.

The exact course of events leading to the present differentiation of species must remain the subject of speculative discussion awaiting the result of further study.

In this paper stress has been laid upon the presence of polyploidy since the evidence of chromosome numbers points to this. It is clearly understood however that this question can only be answered satisfactorily in the case of recent polyploids (Darlington 1937 c). Selection of a few characteristics of chromosome behaviour while facilitating the comparison of a large number of species, confines within narrow limits the importance to be placed on the results obtained but certain facts are here presented which may contribute to the ultimate solution of problems relating to the phylogeny of the Hemiptera-Heteroptera.

Summary.

1. While the knowledge of cytological evolution and interrelationships of animals is not as advanced as that of plants, attention has frequently been drawn to these problems in studies on animal groups. In this paper reference is made to those which deal with insects.

2. A brief description is given of some features of spermatogenesis in forty five species of the families Cimicidae, Anthocoridae, Capsidae, Corixidae and Micronectidae, belonging to the sub-order Hemiptera-Heteroptera.

3. An attempt is made to relate the karyological characters observed with taxonomic affinities founded on the morphology of the phenotypes.

4. Within the Capsidae chromosome orientation at metaphase appears to follow a trend towards the development of a hollow spindle, the type of metaphase figure commonly found in Hemiptera.

5. Differentiation of species and species groups according to size and number of chromosomes follows fairly closely the taxonomic sub-division of the families.

6. Two examples are cited where taxonomic hypotheses are supported by cytological data:-

a. The species termed Callicorixa caledonica Kirk is thought to be Ca. wollastoni D. & S. by Lundblad.

Differences in chromosome characters seem to separate the two species.

b. Comparison of karyotype shows that Cymatia bonsdorffi Shlb. links the Corixidae with the Notonectidae, a conclusion reached independantly by China from morphological and physiological considerations.

7. While no proof of the occurrence of polyploidy is claimed, evidence is presented of the derivation of at least two species by this means and the significance of chromosome number in the Heteroptera discussed in the light of this evidence.

8. Suggestions are given for the formation of specific karyotypes by methods other than polyploidy.

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Legend to Figures.

Figs. 1 & 2. Cimex columbarius?, 1st and 2nd Metaphase.

Figs. 3 & 4. Anthocoris spp., 1st Metaphase.

Figs. 5 - 20. Family Capsidae, 1st Metaphase (except Fig. 13, Monolocoris filicis, 1st Anaphase and Fig. 15, Orthotylus ericetorum, Diakinesis).

Figs. 21 - 36. Family Capsidae, 2nd Metaphase.

Figs. 37 & 38. Cimex columbarius? with reduced number of chromosomes, 1st and 2nd Metaphase.

Figs. 39 - 41. Additional Capsidae, 2nd Metaphase.

Figs. 42 - 52. Family Corixidae, 1st Metaphase,

Figs. 53 - 62. Family Corixidae, 2nd Metaphase.

Figs. 63 & 64. Micronecta poweri, 2nd Metaphase and 1st Anaphase.

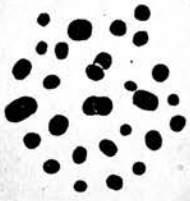
Legend to Diagrams.

The diagrams illustrate the size relationships of the haploid complement of chromosomes at 2nd Metaphase. Each column represents the area of one chromosome in polar view. Areas of X and Y, seen in spindle view are shown at the right of the diagram.

F.12. CIMICIDAE

s.l.(1) Cimicina

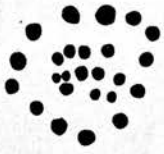
Ist. Metaphase



1.

XY

2nd. Metaphase



2.

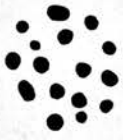
Cimex columbarius Jen.

F.13. ANTHOCORIDAE

XY

XY

Ist.Metaphase



3.

Anthocoris nemorum L.

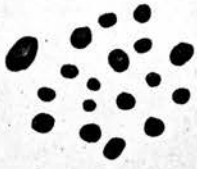
4.

A.nemoralis F.

X3200

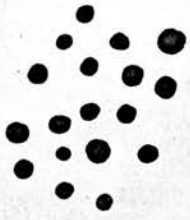
F.14. CAPSIDAE.

s.f.(1) Mirina.



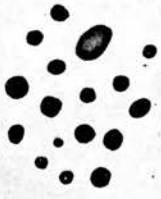
5.

Stenodema calcaratum Fall.



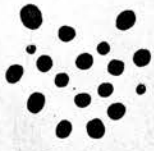
6.

Miris dolabratus L.



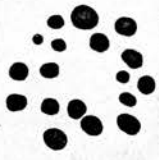
7.

Calocoris norvegicus Gml.



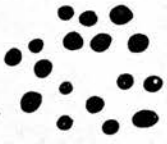
8.

C.fulvomaculatus De G.



9.

C.sexguttatus F.



10.

Stenotus binotatus F.

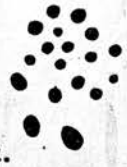
11.

Phytocoris ulmi L.

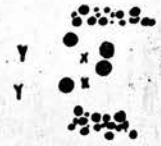
1st. Metaphase.

X 3200

s.f.(3) Bryocorina.



12.



13.

1st. Anaphase

Monalocoris filicicis L.

s.f.(4) Macrolophina.

14.

Dicyphus epilobii Reut.

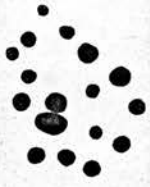
s.f.(5) Heterotomina.

15.

Diakinesis.

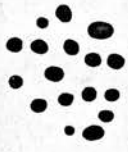
Orthotylus ericetorum Kb.

s.f.(6) Phylina.



16.

Onychumenus decolor Fall.

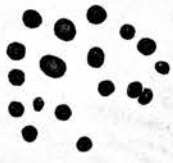


17.

Conostethus brevis Reut.

18.

Psallus varians H.S.



19.

Plagiognathus arbustorum Kirschb.

1st. Metaphase.

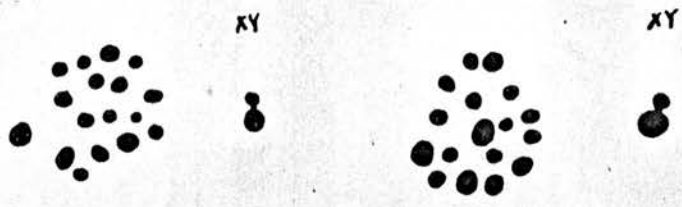
20.

Pl.chrysanthemi Wlff.

×3200

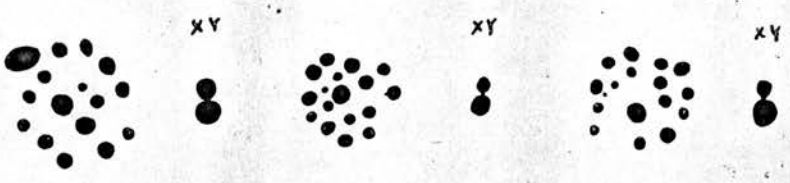
F.14. CAPSIDAE

s.f.(1) Mirina.



21. Stenodema calcaratum Fall.

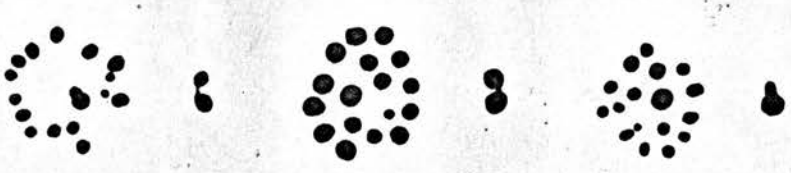
22. Miris dolabratus L.



23. Calocoris norvegicus Gml.

24. C. fulvomaculatus De G.

25. C. sexguttatus F.



26. Stenotus binotatus F.

27. Capsus ater L.

28. Phytocoris ulmi L.

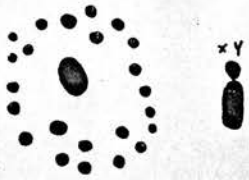
2nd. Metaphase

x3200

s.f.(3) Bryocorina.

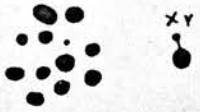
29.
Monalocoris filicis L.

s.f.(4) Macrolophina.



30.
Dicyphus epilobii Reut.

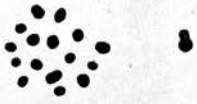
s.f.(5) Heterotomina.



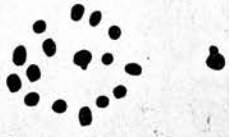
31.
Orthotylus ericetorum Kb.

s.f.(6) Phylina.

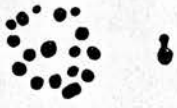
32.
Onychumenus decolor Fall.



33.
Conostethus brevis Reut.



34.
Psallus varians H.S.



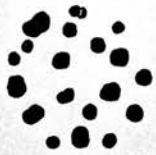
35.
Plagiognathus arbustorum Wlff.

36.
Plagiognathus chrysanthemi Wlff.

2nd. Metaphase

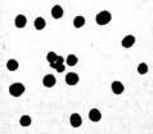
X 3200

F.12. CIMICIDAE



37.

1st. Metaphase



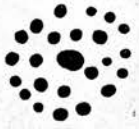
38.

Cimex columbarius Jen. / 2nd. Metaphase

F.14. CAPSIDAE

s.f.(4) Macrolophina.

XY



39.

Dicyphus stachydis Reut.

s.f.(6) Phylina.

XY

40.

Psallus variabilis Fall.

XY

41.

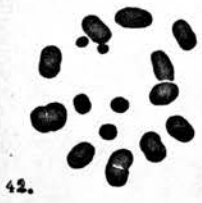
Chlamydatus evanescens Boh.

2nd. Metaphase.

X3200

F. 4 CORIXIDAE.

s.f.(1) Corixinae.



42.

Corixa punctata Ill.

43.

Sigara hieroglyphica Duf.

44.

S.castanea Thoms.

45.

S.scotti DeG.

46.

S.carinata Sahlb.

47.

S.germari Fieb.

48.

Callicorixa calectonica Kirk.

49.

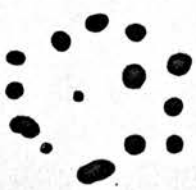
Ca.concinna Fieb.

50.

Glaenocorisa cavifrons Thoms.

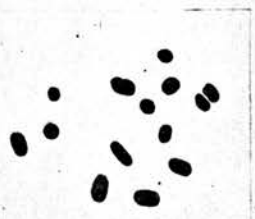
s.f.(2) Cymatinae

F. 5 MICRONECTIDAE.



51.

Cymatia bonsdorffi Sahlb. 1st. Metaphase.



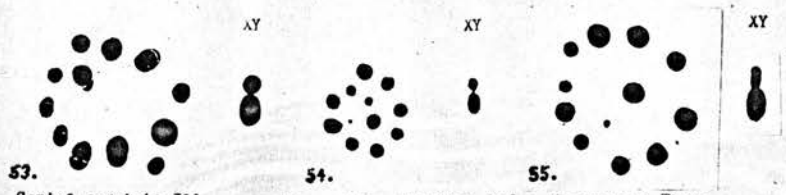
52.

Micronecta poveri DeG.

X3200

F. 4 CORIXIDAE.

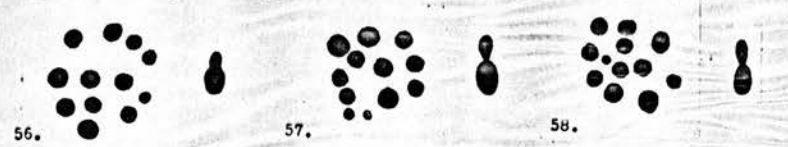
s.f.(1) Corixinae.



53. Corixa punctata Ill.

54. Sigara hieroglyphica Duf.

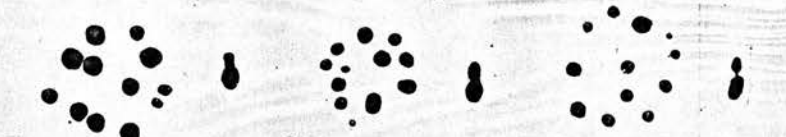
55. S.castanea Thoms.



56. S.scotti D&S.

57. S.carinata Sahlb.

58. S.germari Fieb.



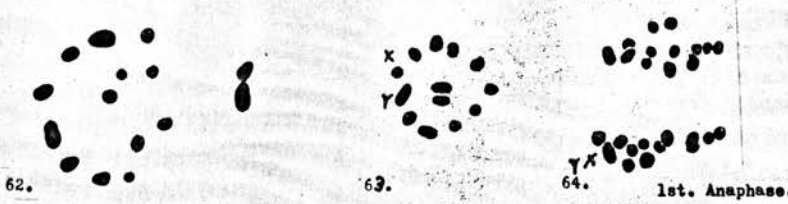
59. Callicorixa caledonica Kirk.

60. Ca.concinna Fieb.

61. Glaenocorisa cavifrons Thoms.

s.f.(2) Cymatinae

F. 5 MICRONECTIDAE.



62. Cymatia bonsdorffi Sahlb.

63. Micronecta poweri D&S. 2nd. Metaphase.

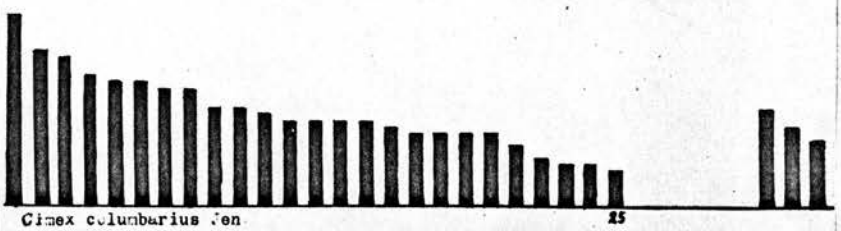
64. 1st. Anaphase.

X 3200

GYMNOCERATA

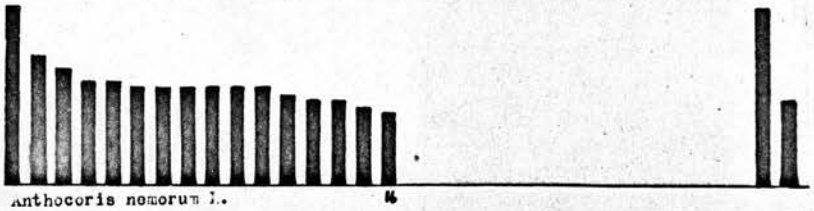
F 12. CIMICIDAE

1. s.l.(1) Cimicina. X Y



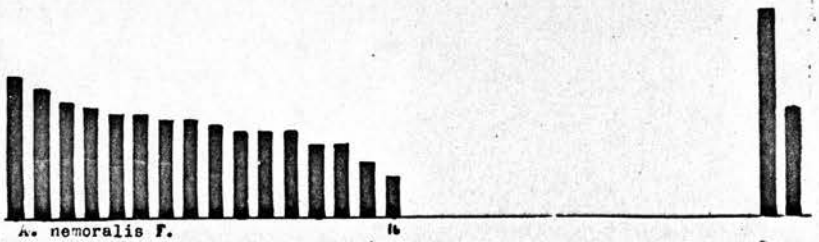
Cimex columbarius Jen 25

2. F. 13. ANTHOCORIDAE

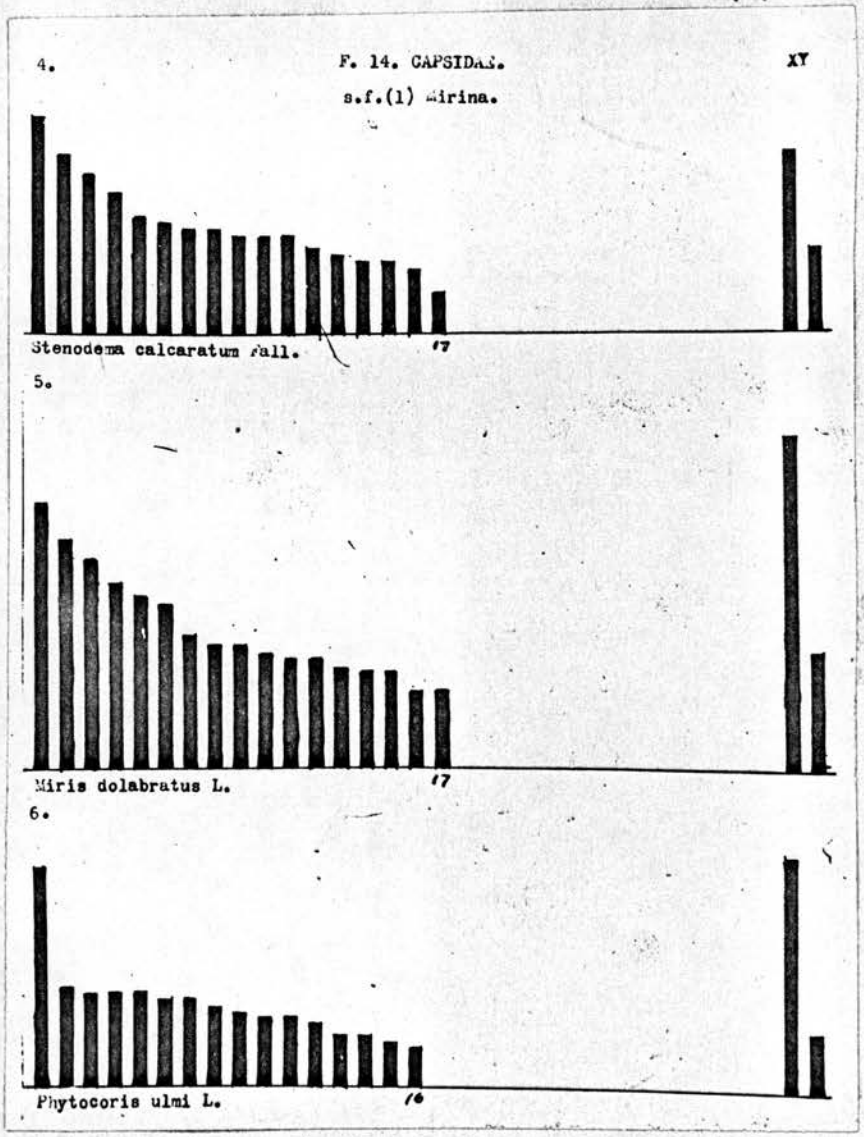


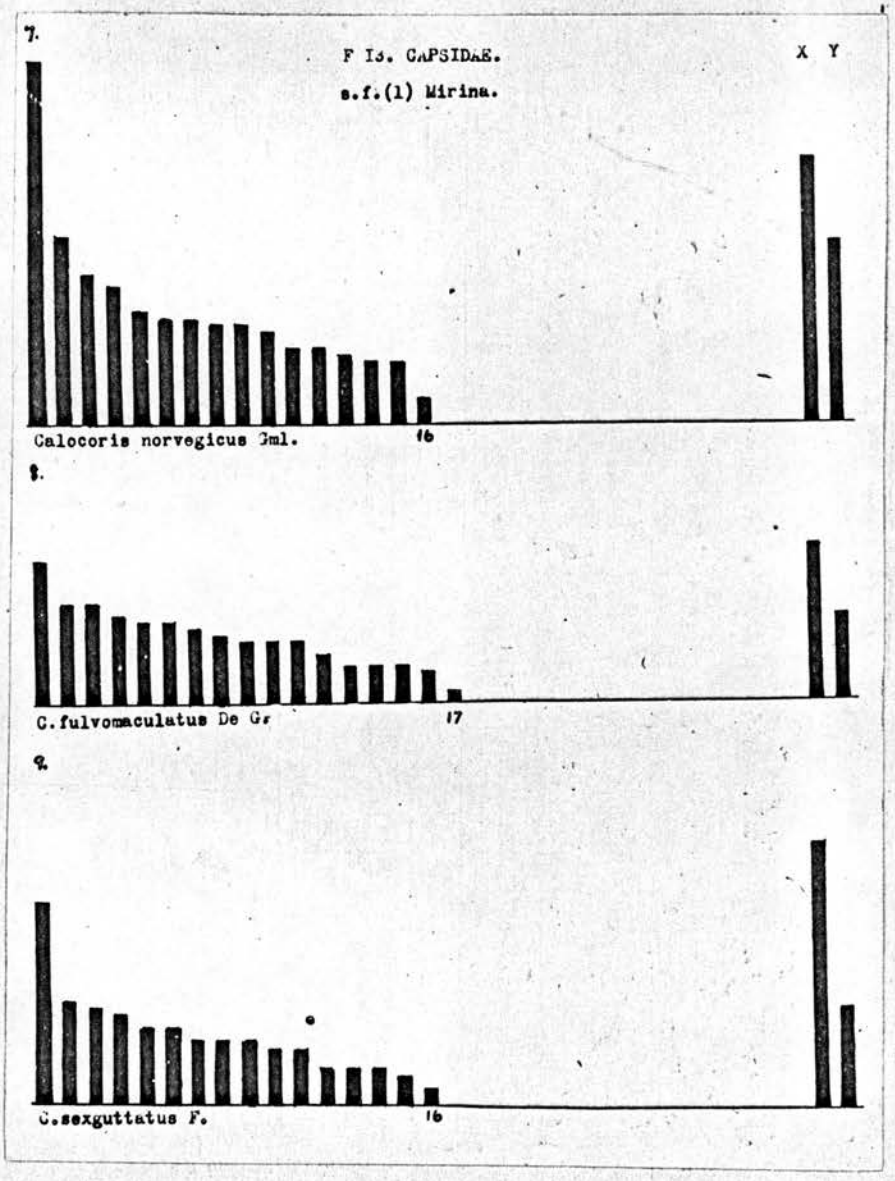
Anthocoris nemorum L. 16

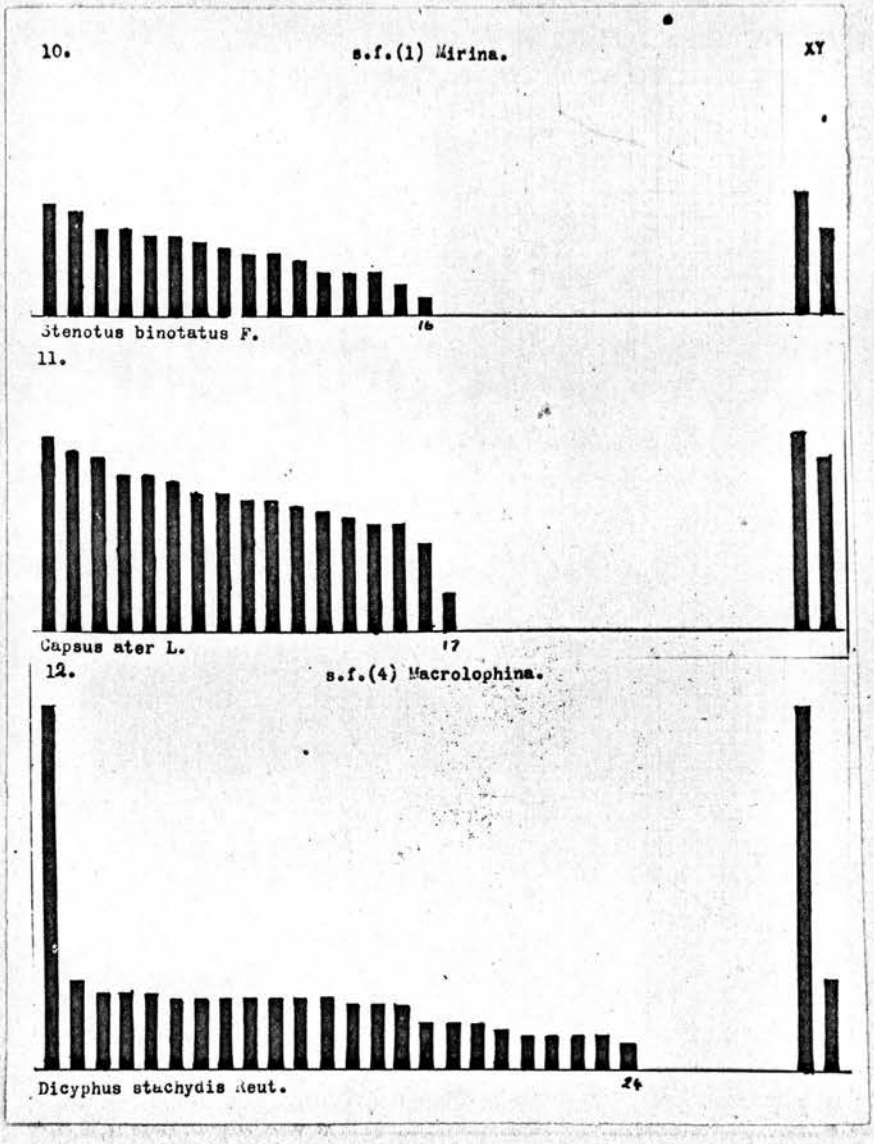
3.

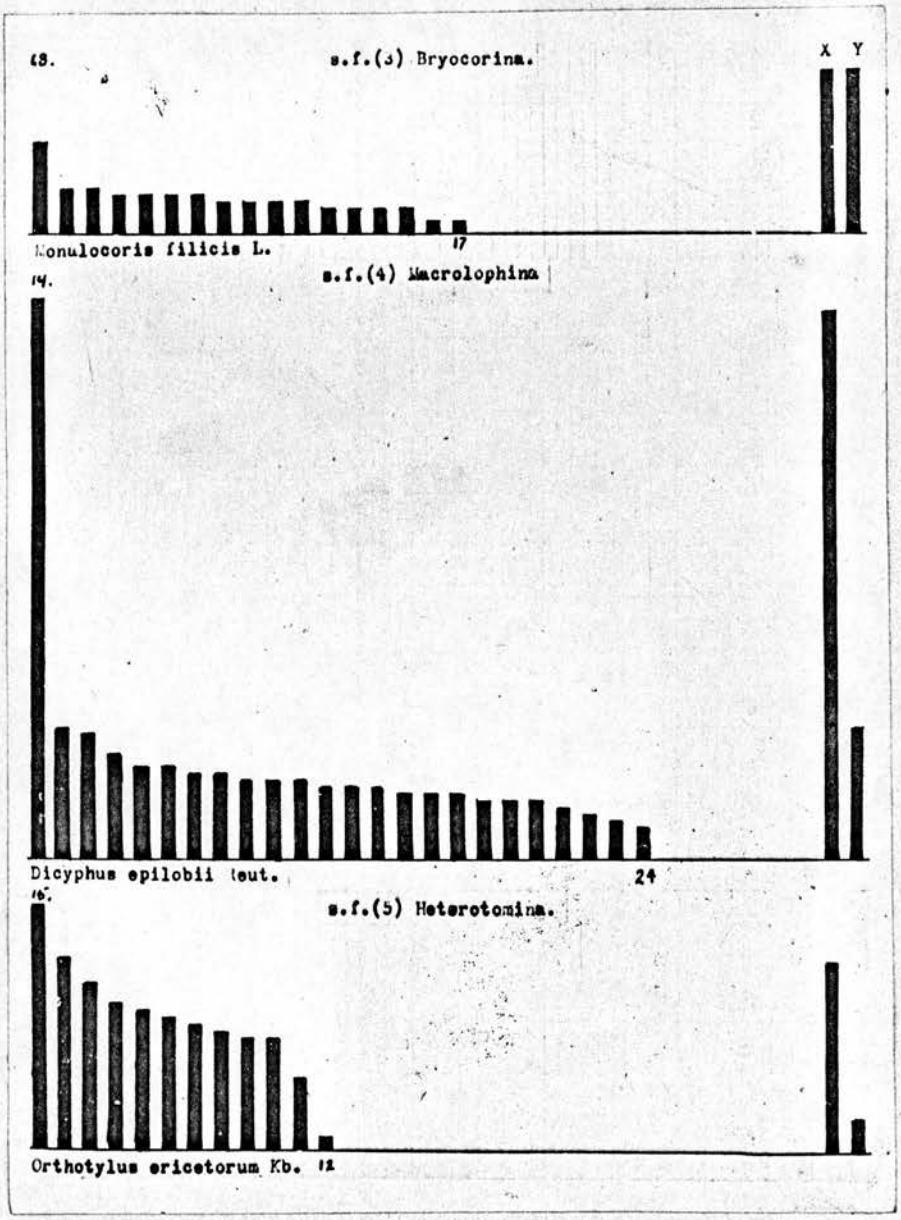


A. nemoralis F. 16


4.
F. 14. CAPSIDAE.
XY
s.f.(1) Mirina.
Stenodema calcaratum Fall.
17
5.
Miris dolabratus L.
17
6.
Phytocoris ulmi L.
16


♂.
F Is. CAPSIDAE.
X Y
s.f.(1) Mirina.
Calocoris norvegicus Gml.
16
♀.
C. fulvomaculatus De G
17
♀.
C. sexguttatus F.
16

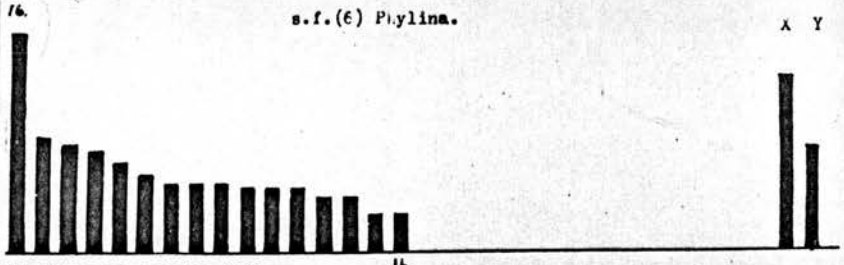

10.
s.f.(1) Mirina.
XY
Stenotus binotatus F.
16
11.
Capsus ater L.
17
12.
s.f.(4) Macrolophina.
Dicyphus stachydis Reut.
24


18.
s.f.(3) Bryocorina.
X
Y
Monulocoris filicis L.
17
14.
s.f.(4) Macrolophina
Dicyphus epilobii Reut.
24
16.
s.f.(5) Heterotomina.
Orthotylus ericetorum Kb.
12

16.

s.f.(6) Phylina.

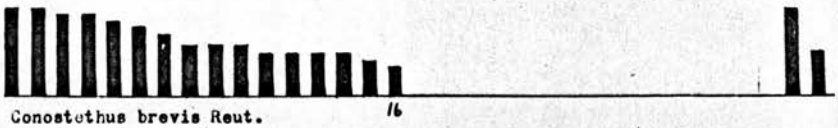
X Y



Onychumenus decolor Fall.

16

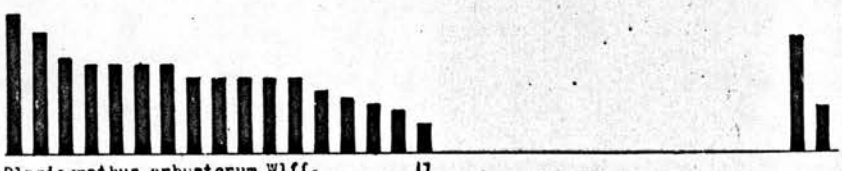
17.



Conostethus brevis Reut.

16

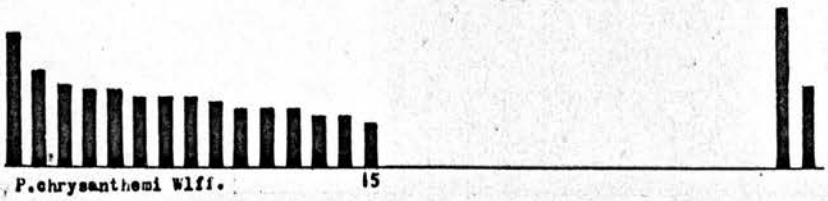
18.



Plagiognathus arbustorum Wlff.

17

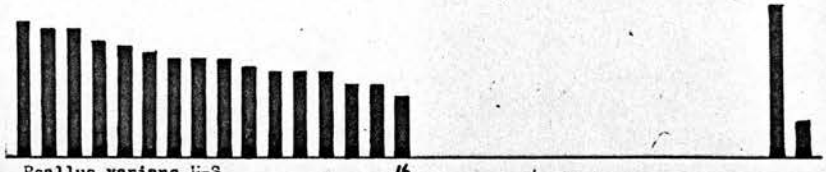
19.



P.chrysanthemi Wlff.

15

20. s.f.(6) Phylina. XY

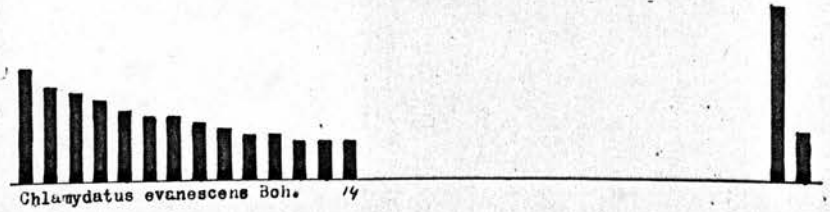


Psallus varians H-S 16

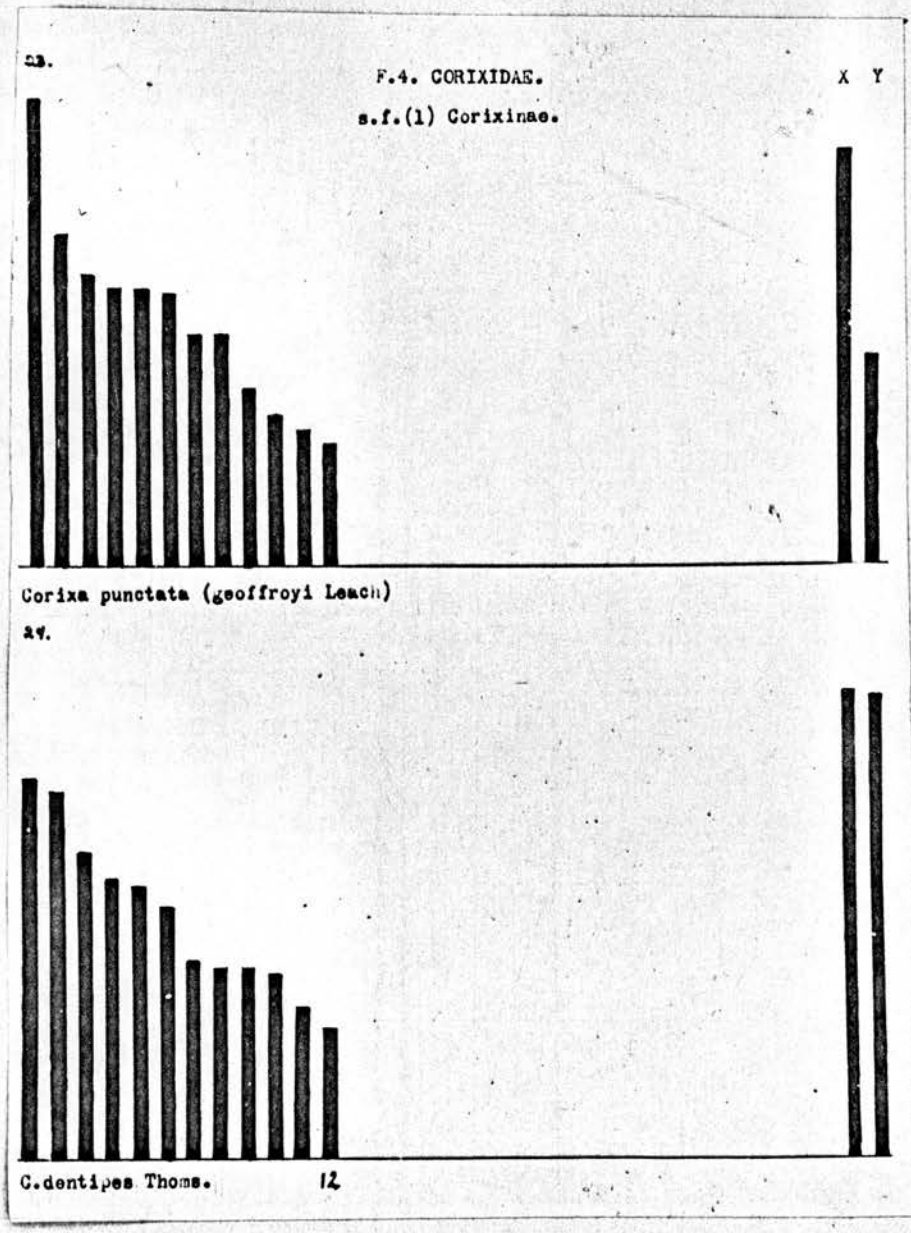
21.

Psallus variabilis Full. 15

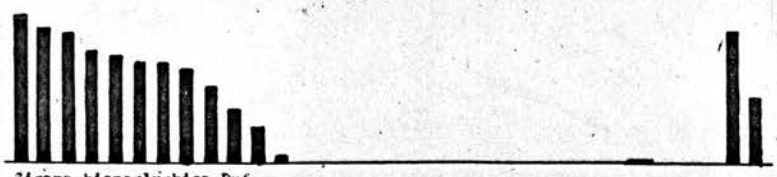
22.



Chlamydatus evanescens Boh. 14

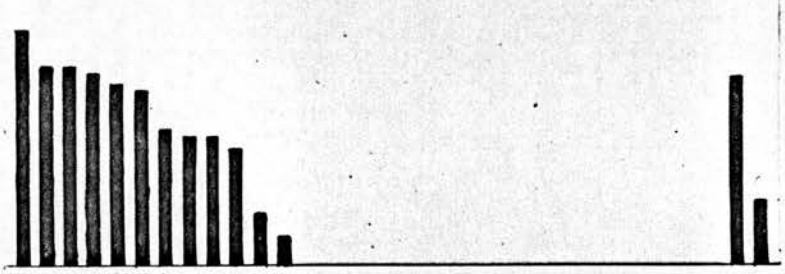

23.
F.4. CORIXIDAE.
X Y
s.f.(1) Corixinae.
Corixa punctata (geoffroyi Leach)
24.
C.dentipes Thoms.
12

25.



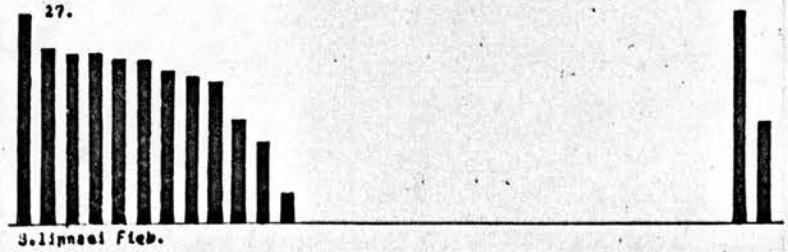
Sigara hieroglyphica Duf.

26.



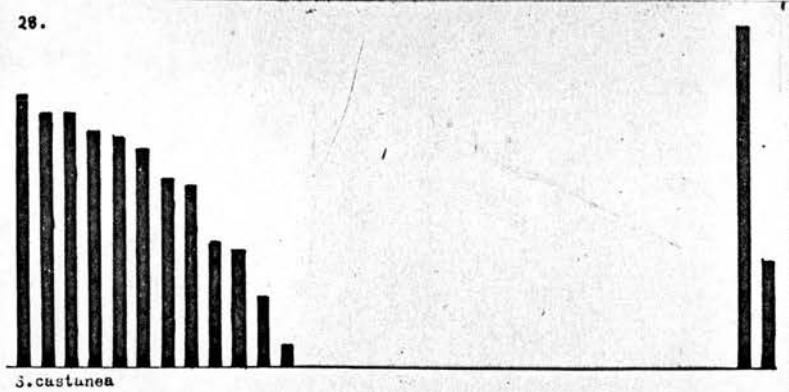
S.sahlbergi Fieb.

27.



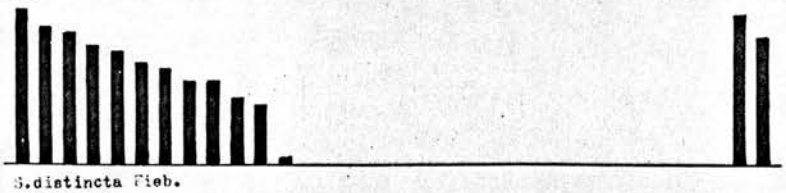
S.limnaei Fieb.

28.



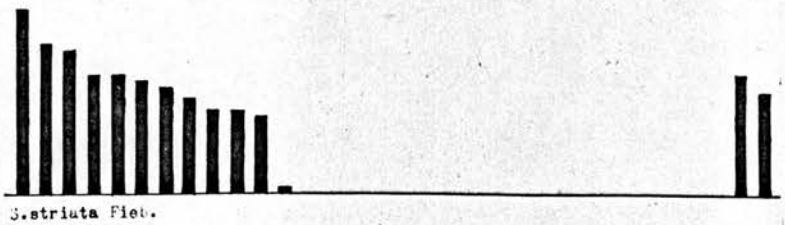
S.castanea

29.



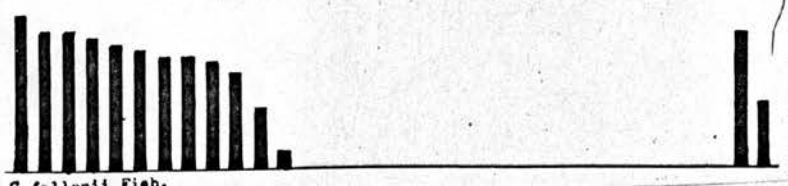
S.distincta Fieb.

30.



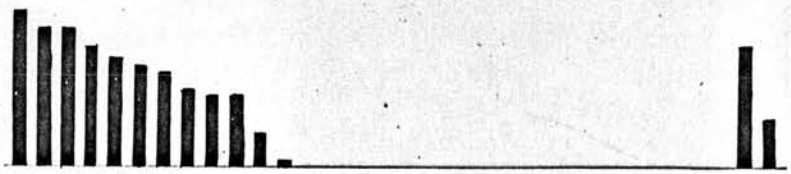
S.striata Fieb.

31.



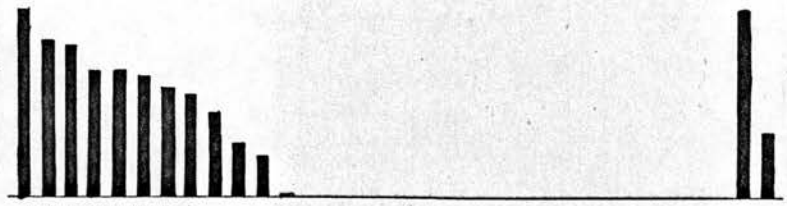
S.fallenii Fieb.

32.



S.semistriata Fieb.

33.

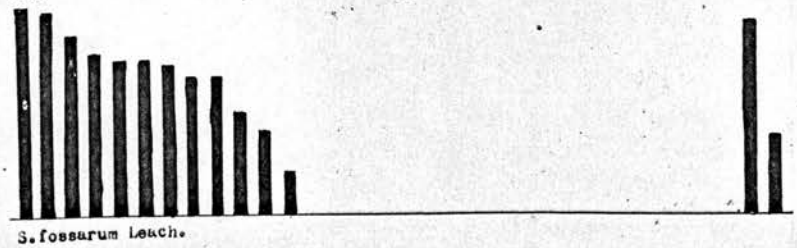


S.fabricii Fieb.

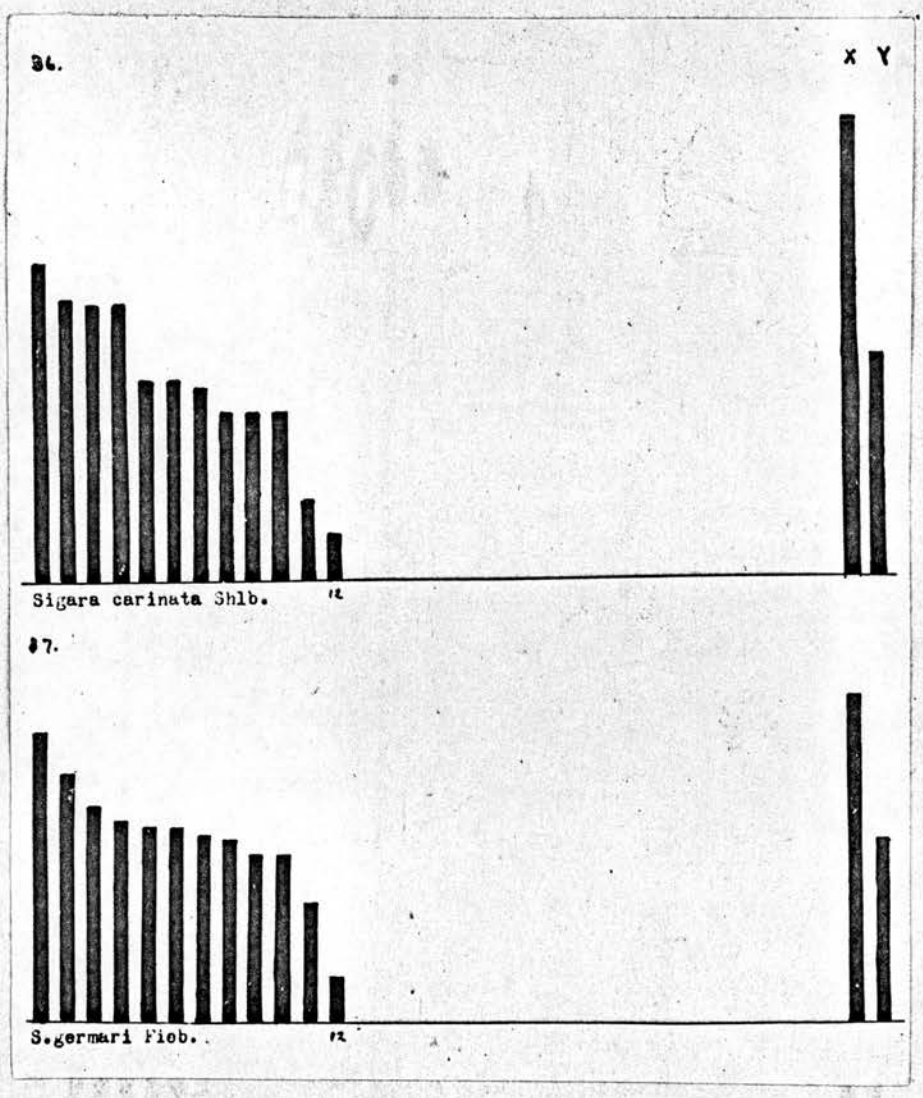
34.

S.scotti Fieb.

35.



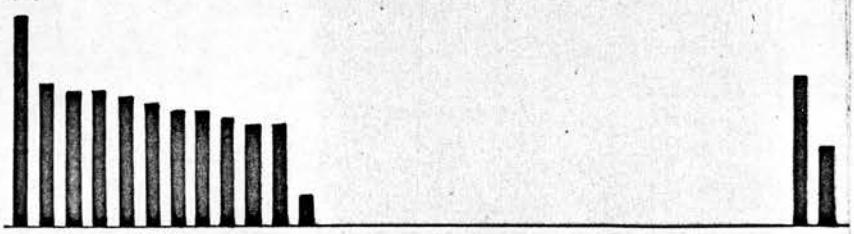
S.fossarum Leach.


36.
X Y
Sigara carinata Shlb.
37.
S.germari Fieb.

38.

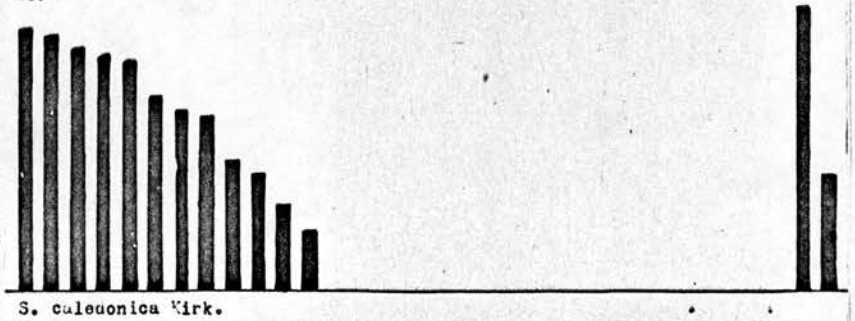
S.praeusta Fieb.

39.



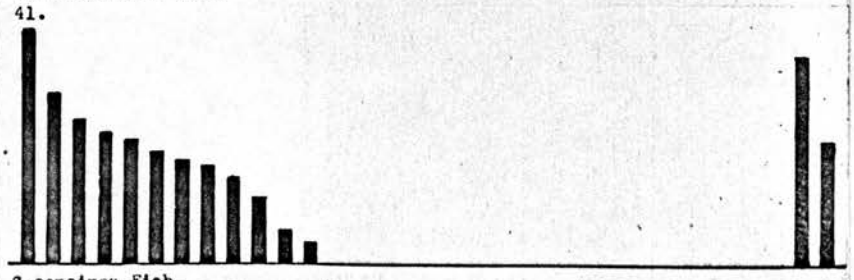
S.wollastoni DdS.

40.



S. caledonica Kirk.

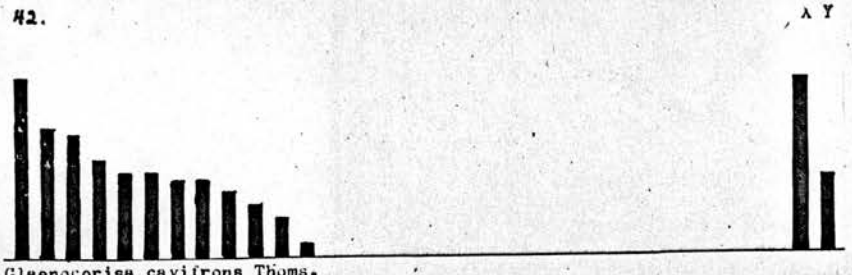
41.



S.concinna Fieb.

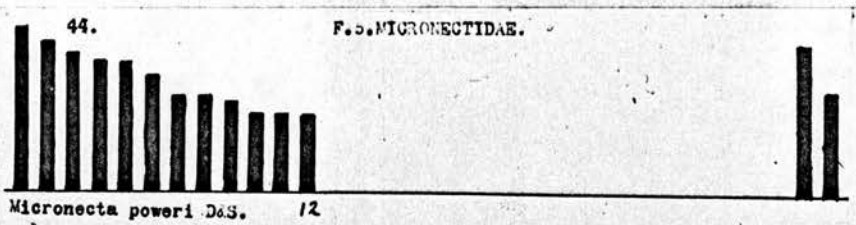
s.f.(1) Corixinae

42. A Y



Glaenocorisa cavifrons Thoms.

44. F.5.MICRONECTIDAE.



Micronecta poweri D&S. 12