GENERAL INTRODUCTION

A significant advance in our knowledge on heteropteran chromosomes has been made since the discovery of "peculiar chromatin element" in *Pyrrhocoris apterus* (Pyrrhocoridae) by Henking in 1891. The substantial contributions made by earlier workers in the formative years of heteropteran cytology and the chromosome counts of different species have been reviewed extensively by Ueshima (1979). The chromosome data of different species have contributed considerably in solving many problems of heteropteran lineology, though the diffuse nature of heteropteran chromosomes (Hughes-Schrader and Schrader 1961) greatly hamper the karyotypic analysis and the detection of chromosomal rearrangements. Recently, study of the heteropteran chromosomes by banding techniques has gained momentum and C- and G-banding patterns have been demonstrated successfully in the chromosomes of some heteropteran insects (Maudlin 1974; Muramoto 1978, 1980; Solari 1979; Camacho et al. 1985). However, further studies are badly needed on more species to solve the problems of the unusual behaviour shown by holokinetic chromosomes during meiosis (Schrader 1940; Piza 1958; John & Lewis 1965) and the relationships between kinetochore and telomere in holokinetic chromosomes. Extension of chromosome data on different families along with banding study will certainly contribute towards understanding mechanism of karyotypic evolution and in establishing interrelationships between various groups of Heteroptera.

Behaviour of meiotic chromosomes

Sex chromosome

The behaviour of sex chromosomes during meiosis in male heteropteran bugs has been reviewed by Manna (1962, 1982, 1984), Takenouchi and Muramoto (1973) and Ueshima (1979). They have classified the sex chromosomes into XY, XO, X_nO and X_nY types. The most important characteristic features of all types of sex chromosomes are that they show positive heteropycnosis in the early prophase stages and become isopycnotic during late diakinesis and metaphase I. In majority of the heteropteran species, the sex chromosomes divide equationally at first metaphase and reductionally in the second (Hughes-Schrader & Schrader 1961; John & Lewis 1965; Ueshima 1963b, 1966b, 1979), and they form pseudobivalent (XY), trivalent or multivalent (X_nY) or an accessory plate like structures during second metaphase (Ueshima 1979; Manna 1982).

Post reductional XY

The post reductional XY type of sex chromosome system is most prevalent among the heteropteran species and was reported in 23 out of 37 families so far investigated (Ueshima 1979; Manna 1982). At the first metaphase, the sex chromosomes orient side by side in the centre of the ring formed by the autosomes and divide equationally in the first anaphase. At the second metaphase, the sex pseudobivalent formed by the X and the Y chromosomes lies in the centre of the autosomal ring and segregate reductionally to opposite poles at second anaphase. Both types of arrangement of sex chromosomes and autosomes are common in Heteroptera and are found not only in taxa with an XY system and no m-chromosomes such as Pentatomidae (Schrader and Hughes - Schrader 1956, 1958; Manna 1956, 1962) and the Lygaeinae of the Lygaeidae (Wilson 1912, ref. Ueshima 1979; Wolfe and John 1965; Ueshima and Ashlock 1980), but also where there is an XY sex chromosome system and m-chromosomes such as the remainder of the Lygaeidae. Depending upon the particular sex chromosome system and the presence or absence of m-chromosomes, there are some deviations from this typical arrangement. The significance of these diverse patterns of chromosome arrangement is not yet clear (Ueshima 1979). On the other hand, in Stenocephalidae (Lewis and Scudder 1958), Corixidae (Peters and Kleba 1971), and Lygaeidae (Ueshima and Ashlock 1980) where m-chromosomes are present the X and the Y chromosomes lie in the periphery with the m- at the centre during the first metaphase, while both the XY pseudo-pair and the m-chromosome lie in the centre of the ring formed by the autosomes at second metaphase. However, some variations in the arrangement of sex chromosomes and m-chromosomes have been observed in *Rhypodes clavicornis* (Orsillinae, Lygaeidae) and in many other species of Lygaeidae (Ueshima and Ashlock 1980). The X, Y and m occupy a central position at the first metaphase, while the XY pseudo-pair lies in the centre of the ring formed by the m-chromosomes and autosomes at the second metaphase. In *Pylorgus colon* (Ischnorhynchinae; Lygaeidae) (Ueshima and Ashlock 1980), the X lies at the periphery with the autosomes, whereas both Y and m- occupy the centre at first metaphase. At metaphase II, the XY pseudobivalent and the m-chromosome occupy the centre of the ring formed by the autosomes. Furthermore, the X and the Y lie on the periphery with the m at the centre during first metaphase, while the X-Y pseudo - pair occupies the centre of the ring formed by the autosomes and the m-chromosome during second metaphase in *Kleidocerys franciscanus* (Ischnorhynchinae, Lygaeidae) (Usehima

and Ashlock 1980). Yet a further modification in the arrangement of sex chromosomes and m-chromosomes has been observed in *Antillocoris minutus* (Rhyparochrominae, Lygaeidae) (Ueshima and Ashlock 1980) where X and Y occupy the centre of the ring formed by the autosomes and m-chromosomes at metaphase I, and the centre of the ring is occupied by the X-Y pseudo-pair and m-chromosome at metaphase II.

Pre-reductional XY

This type is, however, rare among heteropteran species and was recorded in 13 species only (Ueshima 1979). In the family Tingidae, one species in each of the eight genera *Agramma* (Muramoto 1973), *Acalypta* (Southwood and Leston 1959), *Bredenbachius* (Jande 1960b), *Cochlochila* (Takenouchi and Muramoto 1967), *Dasytingis* (Jande 1960b), *Dictyla* (Southwood and Leston 1959), *Leptobyrsa* (Harley and kassulke 1971), two species in each of the two genera *Stephanitis* (Toshioka 1943a, ref. Ueshima 1979) and *Teleonemia* (Harley and Kassulke 1971) and four species of the genus *Tingis* (Southwood and Leston 1959; Montgomery 1901a, 1906, ref. Ueshima 1979, Muramoto 1973) have pre-reductional XY. Moreover, *Lethocerus indicum* of the Belostomatidae also reported to have pre-reductional XY system (Banerjee 1958; Bagga 1959; Jande 1959a; Manna and Deb-Mallick 1984). In *Tingis lasiocera* (Jande 1960b), the X-Y pseudo-pair occupies the centre of the autosomal ring during metaphase I and they separate reductionally at anaphase I. As a result, there are two types of second metaphase plates: those with X and those with Y. They lie along with the autosomes in the periphery of the spindle leaving the inner space empty. The sex chromosomes divide equationally at second anaphase. However, pre-reductional type of sex-chromosome system is common in the organisms having localized centromere (John & Lewis 1965; Ueshima 1979).

Post-reductional XO

This type was encountered in about 189 species belonging to 17 families viz., Dipsocoridae, Nepidae, Naucoridae, Pleidae, Hydrometridae, Hebridae, Veliidae, Gerridae, Saldidae, Miridae, Reduviidae, Lygaeidae, Largidae, Pyrrhocoridae, Coreidae, Alydidae and Rhopalidae (Ueshima 1979; Manna 1982). The arrangement of the sex chromosome is found to be variable in most of the families. In *Lethaeus barberi* (Lethacini, Rhyparochrominae, Lygaeidae) (Ueshima 1979), the m-locates in the centre of the ring formed by the autosomes and the X chromosome at the first metaphase, while the X and m lie in the centre of the autosomal ring during second metaphase. In the Coreidae, the X locates outside the autosomal ring

and m-chromosomes occupy the central position at metaphase I, while the m-chromosome again lies in the centre of the autosomal ring and the X chromosome lies just outside the ring during metaphase II. In *Ambrysus mormon* (Ambrysinae, Naucoridae) and in other aquatic Heteroptera with an XO sex mechanism and a pair of m-chromosomes (Ueshima 1979), the X and the m-pair are located in the centre of the autosomal ring at metaphase I, while the X lies in the centre of the ring formed by the autosomes and the m-chromosome at metaphase II. On the other hand, the sex chromosome arrangement tends to be irregular at metaphase I in the species with high chromosome number, as found in *Merragata hebroides*(Hebridae) (Ueshima 1979). However, the X chromosome invariably occupies centre of the autosomal ring during metaphase II.

Pre-reductional XO

This type was encountered in *Archimerus calcarator* (Wilson 1905a, 1909a ref. Ueshima 1979), *Archimerus alternatus* (Morrill 1910; Wilson 1932, ref. Ueshima 1979), *Pachylis gigas* (Wilson 1909a, 1911; Schrader 1932, ref. Ueshima 1979), *Pachylis lateralis* (Piza 1946b, ref. Ueshima 1979) of the family Coreidae and *Ectrychotes dispar* (Manna 1951) and *Ectrychotes abbreviatus* (Manna & Deb-Mallick 1980) of the Reduviidae. In *A. calcarator*, the X chromosome is located just outside the ring formed by the autosomes, while m-pair occupies the centre at metaphase I. The X chromosome moves to one pole reductionally during anaphase I. As a result, there are two types of second spermatocytes : one with X and another without it. At metaphase II, the chromosome lies on the periphery with autosomes and the m-chromosome locates in the centre. The anaphase II is equational for both autosomes and the X chromosome. However, in the reduviid species *E. dispar* and *E. abbreviatus*, the m-chromosomes are absent and the X chromosome lies outside the autosomal ring during metaphase I. At metaphase II, the X chromosome lies along with the autosomes in the periphery of the spindle or it lies just near the inner border of the autosomal ring.

X_nO sex chromosome system

This type of sex chromosome system was reported in about 35 species belonging to five families viz., Notonectidae, Stenocephalidae, Pyrrhocoridae, Coreidae and Alydidae (Ueshima 1979). No chiasma forms between X_1 and X_2.

Pre-reductional X_nO

This type was reported only in three species of *Anisops* (Notonectidae) (Jande 1961). In *Anisops fieberi*, the fused X_1 and X_2 locates in the periphery along with the autosomes, whereas the m-pair occupies the centre during first metaphase. At anaphase I, the X's move to one pole as a fused mass and therefore at metaphase II two types of nuclei are formed : one with X_1 and X_2 and other without them; the X_1 and X_2 locate in the centre of the ring formed by the autosomes and the m-chromosome. Second division anaphase is equational for both the autosomes and the sex chromosomes.

Post-reductional X_nO

This type was found in rest of the species belonging to four families. In the Coreidae, the X_1X_2O remain fused in the early prophase stages of meiosis though they have bipartite appearance by late diakinesis. At metaphase I, the X_1X_2 locate outside the autosomal ring, while m-chromosomes occupy the centre. This type of metaphase arrangement is found in *Petillia notatipes*, *Cletomorpha hastata* and in other species of Coreidae (Manna 1951). Yet, minor deviation from this typical arrangement has been reported in *Acanthocoris scabrator* (Manna 1951) which lacks m-pair. In this species, at metaphase I, the centre of the ring is usually occupied by a few autosomal bivalents though most of them are involved in the ring formation. The fused X_1X_2 chromosomes, as in other coreid species, locate outside the ring. However, in *Dysdercus* (Pyrrhocoridae), the X_1 and X_2 remain separate and occupy the centre of the autosomal ring during metaphase I. The fusion of X_1 and X_2 takes place during anaphase I. But in both coreid and pyrrhocorid bugs, an accessory plate is formed during second metaphase to ensure reductional division during second anaphase.

X_nY sex chromosome system

This type of sex chromosome system was reported in about 99 species belonging to 12 families viz., Nepidae, Belostomatidae, Gelastocoridae, Mesoveliidae, Miridae, Cimicidae, Reduviidae, Aradidae, Lygaeidae, Largidae, Cydinidae and Pentatomidae (Ueshima 1979; Manna et al, 1985). The behaviour of X_nY type during meiosis in different families is basically the same. All the sex chromosomes are fused into a mass in the early prophase and their individual entity become apparent only during late prophase. The first division anaphase is equational for

the sex chromosomes. Their arrangement at metaphase II is typical with the formation of pseudo-multivalent like structure at the centre. The single Y chromosome lies opposite to the group of different number of X's as the species contained. Second division anaphase is reductional for the sex chromosomes and their movement is regular. Moreover, no chiasma forms between X and Y.

Micro chromosomes

The micro-chromosomes also show distinctive behaviour during meiosis. The m-chromosomes were first described in a coreid bug, *Anasa tristis* by Paulmier (1899) and were subsequently reported in about 12 families of Heteroptera namely, Naucoridae, Notonectidae, Pleidae, Saldidae, Colobathristidae, Lygaeidae, Largidae, Stenocephalidae, Hyocephalidae, Rhopalidae, Coreidae and Alydidae (Ueshima 1979). The term "m-chromosome" was coined by Wilson (1905b, ref. Ueshima 1979). The m-chromosomes behave differently from both the autosomes and the sex chromosomes during meiosis. In defining m-chromosome, however, it's behaviour and not size is critical because in some cases they are of same size as conventional autosomes (Wilson 1911, ref. Ueshima 1979). During meiotic prophase stage, the m-chromosomes do not pair as a result there is no chiasma formation between them, but the m-chromosomes come close together during diakinesis and form pseudobivalent like structure at metaphase I (Ueshima 1979; Manna 1984). The delayed synapsis of the m-chromosomes was first observed by Gross (1904) in *Syromastus* (Coreidae) and was reported afterwards in many other species (Wilson 1905, 1909, 1911 ref. Ueshima 1979). The staining behaviour of m-pair also differs from that of sex chromosome and autosomes (Ueshima 1979). The m-chromosomes are slightly negatively heteropycnotic during metaphase I and persist in this state till the completion of the meiosis. They move precocciously to the poles during anaphase I and usually lie in the centre of the spindle at second metaphase. The achiasmatic m-chromosomes thus separate reductionally at first and equationally in the second meiotic division. However, their behaviour deviates from the typical one with regard to the onset of negative heteropycnosis and their arrangement in the first and the second metaphases (Ueshima 1979).

Chromosome banding

The C- and G-banding techniques have been applied successfully only in few species of Heteroptera. The C-bands are found to be localized in one or both ends of the mitotic chromosomes (Muramoto 1980; Camacho et al. 1985;

Solari 1979), while clear-cut transverse G-bands are found in both mitotic and meiotic chromosomes (Muramoto 1978; Maudlin 1974). Application of these techniques has made possible the recognition of homologous chromosomes, analysis of chromosomal rearrangements and the detection of centromeric heterochromatin to some extent in Heteroptera. However, at present, the information on the banding pattern of holokinetic chromosomes is too inadequate to construct any picture as comprehensive as that of monokinetic ones.

It is clear from the foregoing review that there is a definite pattern in the behaviour of sex chromosomes, autosomes, m-chromosomes and characteristic orientation of chromosomes at metaphase I and II, and so on. Besides these features, spermatogonial chromosome number, rare occurrence of pre-reductional meiosis, types of sex chromosome system also play an important role in the cytological characterizatin of the species. Thus, the value of cytology as an additional tool in the field of taxonomy in undeniable, and is possible, when we have adequate data at hand obtained in a planned way of study (Manna 1956). It is now well known that the taxonomic classification of animals based solely on morphological characters might suffer some limitations and it was rightly pointed out by Manna (1969) that the identification of species should be based on morphology, supplemented with ecological, cytological, genetical and embryological informations. Furthermore, Ueshima and Ashlock (1980) stressed on the fact that chromosome number, its behaviour, morphology along with non cytological characters of the group together will serve as significant phylogenetic indicator. Therefore, the study of the meiotic behaviour of the chromosomes, chromosome number, karyotype and structure of the chromosomes and correlating these data with morphological findings may be useful in the solution of the taxonomical problems. Although a major limitation in this regard is poor cytological knowledge of many families, while in others it is uneven or variable and sometime incomplete (Manna 1984). According to Cobben (1968), detailed knowledge on the behaviour of chromosomes and ways of recognizing them are needed to apply chromosome studies to the solution of major taxonomical disputes. Unless this is done, the application of the knowledge of cytology in taxonomy would be a sheer guess work. However, to date, chromosome cytology has made major contribution to insect systematics in several different ways, especially in distinguishing the sibling or cryptic species. Notwithstanding these limitations, it is hoped that, with the collection of adequate chromosome data on various insect groups and the application of modern staining methods like C-, G- and Q- banding

techniques in the identification and characterization of the chromosomes, detection of chromosome rearrangements etc., the actual advantage of cytotaxonomy would be realised and accepted. Keeping these facts in view, the present work has been carried out by the author.

The main body of this thesis is subdivided into two chapters :

In the first chapter, the chromosome behaviour during meiosis in 44 species of Heteroptera belonging to seven families has been described.

The second chapter deals with the study of the banding patterns of the chromosomes in 18 species of Heteroptera belonging to seven families.