RESULTS

I - Subfamily: Pentatominae

I. Aeliomorpha sheanensis  Linnavuori (Plates:1-2)

Spermatocyte first metaphase shows six autosomal bivalents and two sex chromosomes (X and Y). This implies that A. sheanensis has a male diploid chromosome number of 14 = (12A + XY). The autosomal bivalents show size gradation which is seen in metaphase I plates. These can be put roughly into three size groups: two large, three medium-sized and one small. The Y chromosome is the smallest member of the complement while the X is nearly equal to the smallest autosome (Fig. 4).

At diffuse stage, the sex chromosomes, X and Y are fused together and form a very darkly stained heteropycnotic body located on one side of the nucleus while the autosomes are moderately decondensed (Fig. 1). At diplotene, six autosomal bivalents become distinct due to condensation. The sex chromosomes get separated, appear bipartite and are isopycnotic to the autosomes. Two of the autosomal bivalents show two chiasmata while four show only one chiasma each. In few plates, there is only one ring bivalent. Almost in all of the diplotene plates, the Y-chromosome lies close to one of the medium sized autosomal bivalent (Fig. 2). During diakinesis, the sex chromosomes lie near to each other and their bipartite nature is clear (Fig. 3).

At metaphase I, two types of arrangements are most commonly observed. In the first type, a ring of six chromosomes is formed which includes five autosomal bivalents and the Y chromosome while one autosomal bivalent and X chromosome lie outside the ring (Fig. 4). In the second type, one of the autosomal bivalents lies inside the ring formed by rest of the autosomal bivalents and the sex chromosomes (Fig. 5).
Results

Metaphase II, in this species, has the typical petatomid arrangement by which six autosomal univalents form a ring in the center of which lies an end-to-end associated sex chromosomal pseudobivalent (Fig. 6). Sex chromosomes divide reductionally during the second division so that the X goes to one pole and the Y to the other forming two types of nuclei at telophase II (Fig. 7).

**C-banding**

The sex chromosome mass is positively heterochromatic at diffuse stage (Fig. 8). At diplotene, two ring shaped autosomal bivalents show both terminal and interstitial C-bands, while rest of the autosomal bivalents have terminal C-bands either on one end or both the ends. One autosomal bivalent is C-negative. Closely placed X and Y show conspicuous C-band region on one side (Fig. 9).

**Fluorescent banding**

At diffuse stage XY sex chromatin body appears both DAPI/CMA$_3$ positive. Besides, a few DAPI/CMA$_3$ positive signals are observed on the autosomes (Fig. 10, 11). During diplotene, two autosomal bivalents show DAPI positive/CMA$_3$ negative signals while one autosomal bivalent has a DAPI negative but CMA$_3$ positive signal. Three autosomal bivalents show overlapping terminal/interstitial DAPI and CMA$_3$ signals (Figs. 12, 13). The fused XY body is bright to both DAPI/CMA$_3$. However, subsequently at metaphase-I, the X-chromosome is weakly positive to DAPI/CMA$_3$ while the Y-chromosome is both DAPI/CMA$_3$ negative (Figs. 14, 15).
2. *Apodiphus pilipes* (Horvath) (Plates: 3-4)

Spermatogonial metaphase shows a diploid chromosome number of 2n=14=12A+XY. One pair of large, three pairs of medium and two pairs of small autosomes are seen. Sex chromosomes, X and Y are smaller than autosomes, the Y-chromosome being the smallest member of the complement (Fig. 16).

During the diffuse stage, the sex chromosomes remain associated and form a single heteropycnotic body while the autosomes are partially decondensed (Fig. 17). At diplotene, three to four of the autosomal bivalents are seen as ring bivalents. Sex chromosomes appear bipartite and lie side by side (Fig. 18). During diakinesis, autosomal bivalents become more condensed and the sex chromosomes lie close to each other (Fig. 19).

At metaphase I, six autosomal bivalents and the X chromosome form a ring inside which lies the Y-chromosome (Fig. 20). During metaphase II, six autosomal univalents form a ring and the sex chromosome pseudobivalent is seen in the center of the ring (Fig. 21). The sex chromosomes divide reductionally during the second meiotic division as a result of which the X and the Y move to opposite poles and two types of nuclei are formed at telophase II, one with six autosomes and the X-chromosome and the other with six autosomes and the Y-chromosome (Fig. 22).

**C-banding**

At diffuse stage, the X and the Y chromosomes are associated and are positively heterochromatic (Fig. 23). During pachytene, conspicuous C-bands are seen on the autosomes while the sex chromosome mass is positively heterochromatic (Fig. 24). At diplotene, two of the autosomal bivalents show terminal C-bands at both ends, two others have terminal C-bands at one end while the rest two are negatively heterochromatic. Both X and Y-chromosomes are fully heterochromatic (Fig. 25).
Ag-NOR banding

Three to six nucleolar bodies are observed at interphase (Fig. 26). At early prophase-I, a single large nucleolar body is seen (Fig. 27). Nucleolar organizer regions are seen to be associated with one autosomal bivalent (Fig. 28).
3. Bagrada picta Fabricius (Plates: 5-6)

Metaphase I plate shows six autosomal bivalents and two sex chromosomes (X and Y). Thus B. picta has a male diploid number of $14 = (12A + XY)$. It is possible to note size gradation in autosomal bivalents. Two of them are large, three are medium-sized and one small. Y chromosome is the smallest element of the complement while X is slightly shorter than the smallest autosome (Fig. 33).

During diffuse stage, the degree of decondensation of the autosomes is very high and only a slight sign is seen for their presence in most of the plates. The sex chromosomes, X and Y are associated to form a darkly stained heteropycnotic body located on one side of the nucleus (Fig. 29). At diplotene, the X and Y separate and appear isopycnotic with the autosomes. The autosomal bivalents show single terminal chiasma per bivalent except one which is a ring bivalent possessing two chiasmata (Fig. 30). Diakinesis is marked by six rod shaped autosomal bivalents and two sex chromosomes (Fig. 31).

Metaphase I and Metaphase II show the common chromosomal arrangement of the family. In the former, six autosomal bivalents form a ring and two sex chromosomes (X and Y) lie in the center of the ring (Figs. 32, 33). In the latter, six autosomal univalents form a ring in the center of which lies the pseudobivalent formed by the sex chromosomes, X and Y (Fig. 34). The sex chromosomes undergo reductional division during second meiotic division as a result of which the X and Y chromosomes migrate to opposite poles forming two types of nuclei at telophase II, one with the X and the other with the Y (Fig. 35).

C-bandng

At diffuse stage, XY sex chromatin body shows a prominent C-positive region. Besides, a few C-positive regions are observed on the partially decondensed
Results

Autosomes (Fig. 36). Heavy terminal blocks of C-heterochromatin are observed on three autosomal bivalents while one autosomal bivalent shows very small C-bands on both ends. The Y-chromosome is fully heterochromatic while the X-chromosome shows terminal C-block (Fig. 37).

Ag-NOR banding

In interphase cells, two to four nucleolar bodies are observed (Fig. 38) which subsequently fuse to form two large nucleoli (Fig. 39). Finally a single large nucleolus located at the periphery of the nucleus is seen (Fig. 40). During diplotene/diakinesis, silver impregnations are seen to be associated with 1 to 3 autosomal bivalents (Figs. 41, 42). In most of the elongated spermatids also, there are three nucleolar bodies located in middle and posterior region of the head (Fig. 43).
4. *Carbula scutellata* Distant (Plates: 7-8)  

The first meiotic metaphase plate shows six autosomal bivalents and two sex chromosomes. This implies that this species has a male diploid chromosome number of \(2n=14=12A + XY\). One large, four medium-sized and one small autosomal pairs are distinguished, the X chromosome is similar in size to the smallest autosome and the Y chromosome is the smallest member of the complement (Figs. 47, 48).

During the diffuse stage, the autosomes show moderate decondensation while the sex chromosomes are fused together to form a positively heteropycnotic body lying on one side of the nucleus (Fig.44). At diplotene, the largest pair of autosomes is seen as a ring bivalent (Fig. 45). At diakinesis, all the autosomes appear as rod bivalents with single terminal chiasma in each (Fig.46). Sex chromosomes remain fused (Figs. 45, 46).

At metaphase I, sex chromosomes get separated. Six autosomal bivalents and the X chromosome arrange in a circle inside which lies the Y chromosome (Fig. 47). Telophase I shows two newly formed nuclei with six autosomes and two sex chromosomes each which indicates reductional division of autosomes and the equational division of the sex chromosomes during meiosis I (Fig. 49). Metaphase II shows the typical pattern of chromosome arrangement of the family by which autosomal univalents arrange in a ring in the center of which lies the pseudobivalent XY (Figs. 50, 51).

**C-banding**

The sex chromosome mass is positively heterochromatic during the diffuse and diplotene stages. Scattered C-bands are seen in all the autosomes (Figs. 52, 53, 54).
5. Dolycoris baccarum (Linnaeus) (Plates: 9-10)

*D. baccarum* has a male diploid chromosome number of 2n = 14=12A + XY as is observed in spermatogonial metaphase plate (Fig. 55). One pair of autosomes is distinctly large while the rest show gradation of size. The X chromosome is equal in size to the smallest autosome and Y chromosome is the smallest and very lightly stained member of the complement.

During diffuse stage, the bivalents get decondensed but do not lose their identity and appear as chromatin strands while the sex chromosomes are fused together forming a darkly stained heteropycnotic body (Fig. 56). During diplotene, five of the autosomal bivalents show single terminal chiasma and are rod-shaped while the largest bivalent shows two terminal chiasmata and exists as a ring bivalent (Fig. 57). At diakinesis also, one of the autosomal bivalents is a ring bivalent with two terminal chiasmata and the rest of the bivalents have single terminal chiasma each (Figs. 58, 59).

At metaphase I, the autosomal bivalents and the X chromosome form a ring while the Y chromosome lies in the center of the ring (Fig. 60). During metaphase II, the X and Y chromosomes associate end-to-end forming a pseudobivalent that lies in the center of a ring formed by autosomal univalents. At this stage, the difference in size between the X and Y chromosomes is very clear (Fig. 61). At anaphase-II, the sex chromosomes segregate reductionally (Fig. 62).

**C-band**ing

The sex chromosome mass is positively heterochromatic during diffuse stage (Fig. 63). Two autosomal bivalents show terminal C-bands on one side of the chromosome, one autosomal bivalent has both terminal and interstitial C-bands and another autosomal bivalent shows small interstitial C-bands. Two autosomal bivalents are negatively heterochromatic Sex chromosomes appear C-positive (Fig. 64).

Spermatogonial metaphase plate shows fourteen chromosomes which include twelve autosomes and two sex chromosomes i.e., 2n=14=12A + XY. Two large, two medium-sized and two small autosomal pairs are distinguished, X chromosome is similar in size to the smallest autosome and Y-chromosome is the smallest member of the complement (Fig. 65).

In most of the diffuse stage plates, the X and Y chromosomes are seen as two unassociated, far placed, positively heteropycnotic bodies while autosomes are completely decondensed (Fig. 66). At diplotene, all the six bivalents show single terminal chiasma each. Sex chromosomes are very lightly stained and appear distinctly bipartite (Fig. 67).

During metaphase I, polar view shows a ring of six autosomal bivalents inside which lie the sex chromosomes, X and Y (Fig. 68). Metaphase II shows the typical pattern of chromosome arrangement of the family by which autosomal univalents arrange in a ring in the center of which lies the pseudobivalent XY (Fig. 70).

**C-banding**

The X and Y chromosomes appear as heterochromatic bodies at diffuse stage (Fig. 71). Three autosomal bivalents show small C-positive regions while three others and the sex chromosomes, X and Y are negatively heterochromatic (Fig. 72).
7. Eurydema pulchrum (Westwood) (Plates: 12-13)

Spermatogonial metaphase plates show fourteen chromosomes which include twelve autosomes and two sex chromosomes. So *E. pulchrum* has a male diploid chromosome number of \(2n=14=12A + XY\). Autosomes show gradation in size. The X chromosome is as equal as the smallest pair of autosomes while the Y chromosome is the smallest member of the complement (Fig. 73).

During diffuse stage, the sex chromosomes are associated to form a single darkly stained heteropycnotic body lying on one side of the nucleus while the autosomes are moderately decondensed appearing as chromatin threads (Fig. 74). At diplotene, the sex chromosomes remain fused and positively heteropycnotic. Three of the autosomes are ring bivalents with two terminal chiasmata each. The rest of the autosomal bivalents show single terminal or sub terminal chiasma (Fig. 75). At diakinesis, the sex chromosomes get separated and become isopycnotic (Fig. 76).

At metaphase I, all the chromosomes arrange in a circle and the center of the circle is hollow (Fig. 77). At anaphase-I, the autosomes divide reductionally and the sex chromosomes equationally (Fig. 78). At metaphase II, the autosomes arrange in a ring configuration with the XY pseudobivalent located at its center (Fig. 79).

**C-banding**

At diffuse stage the sex chromatin mass is positively heterochromatic (Fig. 80). During diplotene, C-bands are clearly seen on terminal and interstitial regions of the autosomal bivalents while the sex chromosomes are observed as a fused or closely associated positively heterochromatic body (Figs. 82, 83). In closely associated XY, it is possible to observe a C-positive band on the X-chromosome while the Y-chromosome is homogenously stained.
Fluorescent banding

Localized signals overlapping for DAPI and CMA$_3$ staining are seen scattered on the autosomal bivalents. The X-chromosome is both DAPI and CMA$_3$ bright while Y is negative for both the stains (Figs. 84, 85, 86, 87).
8. *Eysarcoris guttiger* (Thunberg) (Plate: 14)

First meiotic metaphase shows six autosomal bivalents and two sex chromosomes (Fig. 91). This implies that this species has a diploid chromosome number of 2n=14=12A+XY. One autosomal pair is distinctly large, four pairs are medium-sized and one pair is small. There is a distinct size difference between the sex chromosomes. X is as equal in size as the smaller autosome while Y is the smallest member of the complement.

At diffuse stage, the sex chromosomes, X and Y are associated and form a single heteropycnotic body while the autosomes are partially decondensed (Fig. 88). During diplotene, one autosomal bivalent exists as a ring bivalent with two terminal chiasmata. The sex chromosomes maintain their association and appear as a single dark body (Fig. 89). During diakinesis, the autosomal bivalents become distinct all showing single terminal chiasma. The sex chromosomes are distinctly separated but lie close to each other and their bipartite appearance is clear (Fig. 90).

At metaphase I, five autosomal bivalents and the two sex chromosomes form a ring inside which lies the largest autosomal bivalent (Fig. 91). During metaphase II, six autosomal univalents form a ring while the sex chromosome pseudobivalent is positioned in center (Fig. 92). During the second meiotic division, the sex chromosomes divide reductionally by which the X and Y move to opposite poles and form two types of nuclei at telophase: one with six autosomes and the X-chromosome and the other with six autosomes and the Y-chromosome. The size difference between the two sex chromosomes is clear at this stage II (Fig. 93).

**C-banding**

During the diffuse stage, the sex chromosome mass is observed as a single heterochromatic body. Scattered heterochromatic regions are also observed on the
diffused autosomes (Fig. 94). The largest autosomal bivalent shows terminal and interstitial bands. One autosomal bivalent shows terminal C-bands on both ends. The rest of the autosomal bivalents show terminal C-bands only on one end. The sex chromosomes are associated and exist as a single C-positive body (Fig. 95).
9. *Eysarcoris inconspicuous* (Herrich-Schaffer) (Plates: 15-17)

There are six autosomal bivalents and two sex chromosomes at metaphase-I of this species. This shows that *E. inconspicuous* possesses a male diploid number of $2n=14=12A + XY$. The autosomes show gradation of size as is clear from diplotenes and diakinesis by which one is clearly larger than the rest, two medium sized autosomes, two small and one distinctly very small. The Y chromosome is the smallest and lightest unit of the complement and X chromosome is equal in size to the smallest autosome (Fig. 100, 101).

At pachytene, all the chromosomes appear as entangled heteropycnotic threads. The sex chromosomes, X and Y appear as densely compact single heteropycnotic body (Fig.96). At diffuse stage, the autosomes are completely decondensed while the X and Y chromosomes are associated and form a positively heteropycnotic body located interiorly (Fig. 97). During diplotene, two autosomal pairs are ring bivalents while four autosomal bivalents present single terminal chiasma each. Sex chromosomes remain fused (Fig.98). At diakinesis, the X and the Y chromosomes get separated. The Y chromosome appears negatively heteropycnotic (Fig. 99).

During metaphase I, a definite polar arrangement of chromosomes is not observed. Usually a ring is formed and its interior is occupied by one or more of the chromosomes in different plates (Fig.100). At metaphase II, the X and Y chromosomes come close to form a pseudobivalent which lies in the center of the ring formed by autosomal univalents (Fig.102). At anaphase II, autosomes divide equationally while the sex chromosomes divide reductionally to form two types of nuclei at telophase II, one with 6A+X and the other with 6A+Y (Fig.103).
C-banding

The sex chromosome body is positively heterochromatic during the diffuse stage (Fig. 104). The largest autosomal bivalent shows a thick terminal C-band towards the chiasmatic end and an interstitial band. Five autosomal bivalents have terminal C-bands. In the closely associated X and Y chromosomes, X is C-negative while Y is C-positive (Fig. 105).

Fluorescent banding

At diffuse stage, sex chromatin body is all over CMA$_3$ bright with a small central DAPI bright region. In addition, CMA$_3$ signals are seen on the diffused autosomes which are negative to DAPI (Figs. 106, 107). During diplotene, all the autosomal bivalents and XY body stain homogenously dull for DAPI (Fig. 108). With CMA$_3$, the largest autosomal bivalent shows conspicuous terminal and interstitial signals while the rest of the autosomal bivalents appear CMA$_3$ positive (Fig. 109). Metaphase II plates show the largest autosomal bivalent with a bright CMA$_3$ signal. Rest of the autosomal bivalents and sex chromosomes appear bright with CMA3 and dull with DAPI (Figs. 110, 111).

Ag-NOR banding

Interphase nuclei show two to four nucleolar bodies (Fig. 112). Cells at initial meiotic prophase are seen with varying number (1-3) and size of nucleoli (Fig. 113). At diakinesis and metaphase I, conspicuous silver impregnations have been observed to be associated with the largest autosomal bivalent (Figs. 114, 115). Nucleolar bodies are also observed in different phases of spermeiogenesis with varying size and position. These are present at the anterior and posterior regions of the head of partially elongated spermatids (Fig. 116) while more matured elongated spermatids show thick silver impregnation at the anterior and medial region of the head (Fig. 117).
10. *Eysarcoris rosaceous* Distant (Plate: 18)

Spermatocyte metaphase-I shows six autosomal bivalents and two sex chromosomes. This implies that *E. rosaceous* has a male diploid chromosome number of 2n=14=12A + XY. As evident from metaphase I, autosomes do not show significant gradation of size. However, they can be assigned to three size groups: one pair large, four pairs medium-sized and one pair small. The sex chromosomes are smaller than the autosomes with Y being the smallest component of the complement (Figs. 121, 122).

At diffuse stage, the autosomes are moderately decondensed while the sex chromosomes, X and Y are condensed and are seen as heteropycnotic bodies. Two types of plates have been observed with respect to the association between the sex chromosomes. In one, the sex chromosomes are separated but lie side by side (Fig. 118). In the second, they are associated to form a single body. The former is more frequent than the later. At diplotene, the sex chromosomes remain associated. All autosomal bivalents show only one chiasma (Fig. 119). During diakinesis, the sex chromosomes get separated and each appears bipartite. All the autosomal bivalents show single terminal chiasma (Fig. 120).

Chromosome arrangement at metaphase I is not definite and is different from the common type of the family. In some plates, seven chromosomes (five autosomal bivalents and the X and the Y chromosome) form roughly a ring while a medium-sized autosomal bivalent lies inside the ring (Fig. 121). In another type of arrangement, chromosomes form a ring enclosing a hollow center and two or three chromosomes lie outside the ring (Fig. 122). During metaphase II, six autosomal univalents form ring and the sex chromosomes associate end-to-end to form a pseudobivalent occupying the center of the ring (Fig. 123).
**C-banding**

The sex chromosome mass appears positively heterochromatic during the diffuse stage (Fig. 124). Two autosomal bivalents show terminal/subterminal C-bands on both ends, one autosomal bivalent shows thin terminal and interstitial C-bands, two autosomal bivalents show terminal C-bands on one end and one autosomal bivalent is negatively heterochromatic. The closely associated sex chromosomes are positively heterochromatic (Fig. 125).
11. *Halys seregera* (Westwood) (Plates:19-21)

Metaphase I plate shows the presence of six autosomal bivalents and two sex chromosomes. This shows that the male diploid chromosome number of *Halys seregera* is \(2n=14=12A + XY\). The autosomes show gradation of size which can be roughly put into three groups: two pairs of large, three pairs of medium-size and one pair of small autosomes. Y chromosome is the smallest element of the complement and X chromosome is equal in size to the smallest autosome (Figs.130, 131).

At the diffuse stage, the sex chromosomes are fused together to form a darkly stained heteropycnotic body located in the center of the nucleus while the autosomes are highly decondensed losing their identity (Fig.126). During diplotene, the sex chromosomes are separated but lie near to each other. The bivalents become well defined and one or two chiasmata per bivalent are conspicuous. At least one ring bivalent is observed in all the plates. Occasionally, plates with two to three ring bivalents are also observed (Fig.127). At diakinesis, the sex chromosomes become negatively heteropycnotic and their bipartite nature is clear. Four or five of the autosomes are rod bivalents while two or three are ring bivalents (Figs. 128, 129).

During metaphase I, two types of plates are commonly observed. In one, a ring of five autosomal bivalents and X-chromosome is formed inside which lie the Y chromosome and one of the autosomal bivalents (usually the medium-sized) (Fig.130). In the second type, all of the chromosomes form a ring with an empty center (Fig.131). The former type is more frequent (84.85% of the 33 cells analysed) than the later (15.15% of the 33 cells analysed). At metaphase II, the sex chromosomes, X and Y associate to form a pseudobivalent that lies at the center of the ring formed by autosomal univalents (Fig.132).
Fluorescent banding

During the diffuse stage, sex chromatin body is homogenously bright to both DAPI and CMA3 with no specific signals. In addition, CMA3/DAPI positive signals are seen on the diffused autosomes (Figs. 133, 134). At diplotene, all the autosomal bivalents show scattered but localized terminal and interstitial signals which overlap for both DAPI and CMA3 (Figs. 135, 136). During metaphase I, all the autosomal bivalents and the X-chromosome are DAPI/CMA3 positive while Y-chromosome shows DAPI bright signal which is CMA3 dull (Figs 137, 138).

Ag-NOR banding

Interphase cells show darkly stained nucleolus along with three to several nucleolar bodies (Fig. 139). During early prophase I, cells with 2 to 3 nucleoli with varying size are seen (Figs. 140, 141). During metaphase I, nucleolar organizer regions are seen associated with four of the autosomal bivalents (Fig. 142). Elongated spermatids are also observed with nucleolar bodies at both anterior (rounded) and posterior (elongated) regions of the head (Fig.143).

Spermatocyte metaphase-I shows six autosomal bivalents and two sex chromosomes. This implies that *H. sulcata* has a male diploid chromosome number of 2n=14=12A + XY. The autosomes show gradation of size. X chromosome is similar in size to the smallest autosome and Y is the smallest element of the complement (Figs. 146, 147).

At diffuse stage, the autosomes are decondensed while the sex chromosomes are associated to form a single heteropycnotic body (Fig. 144). At diakinesis, the sex chromosomes become isopycnotic and their bipartite appearance is clear. All the autosomal bivalents are rod shaped with single terminal chiasma each (Fig.145).

At metaphase I, five autosomal bivalents and the X chromosomes form a ring inside which lie the Y chromosome and one autosomal bivalent (Fig. 146). During anaphase I, the sex chromosomes divide equationally and one X and one Y migrate to each pole (Fig. 148). At metaphase II, the autosomal univalents arrange in a circle while the XY pseudobivalent lies in the center (Fig. 149). At anaphase II, autosomes divide equationally while the sex chromosomes divide reductionally to form two types of nuclei at telophase II, one with 6A+X and the other with 6A+Y (Fig. 151).

**C-banding**

During the diffuse stage, the sex chromosome mass is positively heterochromatic (Fig. 152). Scattered, thin C-positive bands are observed on the autosomal bivalents. The X-chromosome is fully heterochromatic while the Y is negatively heterochromatic (Fig. 153).

**Fluorescent banding**

Diffuse stage shows DAPI/CMA$_3$ bright sex chromatin body with a small conspicuous terminal CMA$_3$ signal (Figs. 154, 155). During early diplotene, all the
autosomal bivalents show overlapping DAPI and CMA3 positive regions. Here also, the sex chromatin body shows a bright terminal signal for CMA3 (Fig. 157) which is negative to DAPI (Fig. 156).

**Ag-NOR staining**

Silver stains have been seen starting to appear at initial meiotic prophase cells which are observed with two nucleoli (Fig. 158). During metaphase I, the silver impregnation is seen to be associated with one autosomal bivalent (Fig. 159). The spermatids show nucleolar bodies at the posterior region of the head (Fig. 160).
**13. Halyomorpha murrea Distant (Plates: 25-27)**

Spermagonial metaphase I shows sixteen chromosomes which include fourteen autosomes and two sex chromosomes. Thus the male diploid chromosome complement of *H. murrea* is 2n=16=14A +XY. The autosomes show gradation of size by which two large, four medium-sized and one small autosomal pairs are observed. The Y chromosome is the smallest element in the complement while X chromosome is as equal as the smallest autosome (Fig. 161).

During the diffuse stage, the sex chromosomes, X and Y are associated to form a single heteropycnotic body while the autosomes are moderately decondensed (Fig. 162). At diplotene, most of the autosomal pairs exist as ring-shaped bivalents while the sex chromosomes are seen separated, and appear heteropycnotic and bipartite (Figs. 163, 164).

During metaphase I, six autosomal bivalents and the Y chromosome form a ring and X and one of the autosomal bivalents lie in the center of the ring (Fig. 165). At metaphase II, the autosomal univalents form a ring inside which lie closely placed X and Y. Pseudobivalent formation is not observed at this stage (Fig. 166). During anaphase II, the sex chromosomes divide reductionally and the X and Y are seen moving to the opposite poles ahead of the autosomes (Fig. 168).

**C-banding**

The sex chromosome mass is positively heterochromatic while a few prominent heterochromatic regions are observed to be scattered on the partially decondensed autosomes during diffuse and pachytene stages (Figs. 169, 170). During early diplotene, the autosomal bivalents show prominent terminal C-bands (Fig. 171). Besides, a few interstitial C-bands are also observed. The sex chromosomes are positively heterochromatic during diplotene stage (Fig. 172).
Fluorescent banding

Diffuse stage shows DAPI and CMA₃ bright sex chromatin body and signals on the diffused autosomes (Figs. 173,174). The autosomal bivalents show predominantly terminal and interstitial conspicuous localized signals which mostly overlap for DAPI and CMA₃ dyes (Figs. 175,176).

Ag-NOR banding

Silver stains start to appear in the interphase nuclei where one to five nucleolar bodies are observed (Fig. 177). The cells in early prophase I (leptotene to pachytene) show prominent nucleoli which are varying in number (1-3), size and location (Fig. 178, 179, 180). During late prophase I (diplotene), one nucleolus is seen to be associated with one autosomal bivalent (Fig. 181). At metaphase I, silver impregnation is seen to be associated with one autosomal bivalent (Fig. 182). At anaphase I also, silver impregnation has been seen to be associated with one autosomal bivalent (Fig. 183). Throughout meiotic division, sex chromosomes remain negative to silver nitrate staining. They are undifferentiated in early prophase I and appear negative at diplotene, metaphase I and anaphase I (Figs. 178, 179, 180). In round-shaped spermatids, one nucleolar body is observed at the base of the head (Fig. 184).
14. Nezara graminea (Fabricius) (Plates: 28-30)

Spermatogonial metaphase shows fourteen chromosomes that include twelve autosomes and two sex chromosomes. The chromosomal complement of *N. graminea* can be represented as $2n=14=12A + XY$. The autosomes show size gradation into three groups: one pair large, four pairs medium and one pair small. The largest autosomal pair shows a constriction close to the middle. There is slight size difference between the sex chromosomes with the Y chromosome appearing slightly smaller than the X (Fig. 185).

At diffuse stage, the autosomes show high degree of decondensation while the sex chromosomes are associated together to form a moderately stained heteropycnotic body (Fig. 186). During diplotene, the sex chromosomes remain associated and the autosomal bivalents become well condensed. Two or three of the autosomal bivalents appear as ring bivalents (Figs. 187, 188).

At metaphase I, a ring of five autosomal bivalents and two sex chromosomes is formed while one of the medium sized autosomal bivalents lies slightly outside the ring (Fig. 189, 190). Metaphase II shows the typical arrangement of chromosomes of the family by which six autosomal univalents form a ring in the center of which lies the pseudobivalent of the sex chromosomes. At this stage, the very slight size difference between X and Y chromosomes is clear (Fig. 191). At anaphase II, the autosomal univalents divide equationally while the sex chromosome pseudobivalent divides reductionally so that at telophase II, two types of nuclei are formed (Fig. 192). One is with 6 autosomes and the X chromosome and the other with 6 autosomes and Y chromosome which indicates post-reductional division of the sex chromosomes.
C-banding

The sex chromosome mass is seen as a partially heterochromatic body during the diffuse stage (Fig. 193). Scattered heterochromatic regions are seen on the partially condensed autosomes during pachytene (Fig. 194). During diplotene, all the autosomal bivalents show distinct terminal and interstitial C-bands. The sex chromosome mass is positively heterochromatic (Figs. 195, 196).

Fluorescent banding

During diplotene, all the autosomal bivalents show DAPI/ CMA$_3$ positive regions distributed at terminal and interstitial positions. The sex chromatin body is bright to both DAPI and CMA$_3$ with no specific signals (Figs. 197, 198). At metaphase I four autosomal bivalents appear brightly stained with both DAPI/ CMA$_3$ while two are dull for both. However, one of the dull autosomal bivalents shows a localized DAPI bright/ CMA$_3$ negative signal. The sex chromosomes, X and Y are both DAPI and CMA3 negative (Fig. 199, 200).

Ag-NOR banding

During interphase, two to four nucleolar bodies are observed (Fig. 201). During leptotene to zygotene, nuclei are observed with one or two nucleoli (Fig. 202, 203). During dipolotene to diakinesis, nucleolar organizer regions are observed to be associated with autosomal bivalents (Figs. 204, 205). During metaphase I, nucleolar bodies are seen to be associated with all the autosomal bivalents (Fig. 206).
15. *Nezara viridula* (Linnaeus) (Plates: 31-33)

*N. viridula* possesses a male diploid chromosome number of \(2n=14=12A + XY\) as is clear from metaphase I. One of the autosomal pair is distinctly large while the rest of the autosomal pairs show gradation of size. The X chromosome is slightly bigger than the smaller autosome and the Y chromosome is the smallest element of the complement (Figs. 210, 211).

At the diffuse stage, the autosomes decondense partially while the sex chromosomes are associated to form a single heteropycnotic body (Fig. 207). At diplotene, the sex chromosomes remain associated and heteropycnotic. The largest bivalent exists as a ring with two sub-terminal chiasmata (Fig. 208). At diakinesis, the autosomal bivalents become distinct and five of them show single terminal chiasma each while one shows sub terminal chiasma. Sex chromosomes remain closely associated (Fig. 209).

Two types of plates have been observed during metaphase I. In the first type, five autosomal bivalents and sex chromosomes form a circle inside which lies the largest autosomal bivalent (Fig. 210). In the second type, a ring is formed by six autosomal bivalents and the X chromosome inside which lies the Y chromosome (Fig. 211). The latter type is more frequent than the former. At metaphase II, the autosomal univalents arrange in a ring with the sex chromosome pseudobivalent lying in the center (Fig. 213).

**C-banding**

The sex chromosome mass is positively heterochromatic during the diffuse stage (Fig. 214). Four autosomal bivalents show terminal C-bands either on one or both ends. One autosomal bivalent shows both terminal and interstitial C-bands while one autosomal bivalent is negatively heterochromatic. The X and the Y chromosomes
show C-band which is terminal in the X-chromosome and interstitial in the Y-chromosome (Figs. 215, 216).

**Fluorescent banding**

At diplotene, one autosomal bivalent is DAPI negative and CMA$_3$ dull while a part of the largest autosomal bivalent is both DAPI and CMA$_3$ positive but major portion is DAPI positive and CMA$_3$ negative. One autosomal bivalent is DAPI dull but shows CMA$_3$ bright signals. The ring autosomal bivalent shows both DAPI and CMA$_3$ positive signals along with few localized CMA$_3$ positive signals and two other autosomal bivalents are weakly positive to DAPI and CMA$_3$ (Figs. 217, 218). The X-chromosome is DAPI dull and CMA$_3$ positive while the Y-chromosome is negative to both DAPI and CMA$_3$ (Figs. 219, 220).

**Ag-NOR banding**

During interphase, three to six nucleolar bodies are observed (Fig. 221). During early prophase I, single dark nucleolus is seen (Fig. 222). During metaphase I, silver impregnation is observed to be associated with only one autosomal bivalent (Fig. 223). Nucleolar bodies are also seen in matured spermatids usually located in the posterior region of the head (Fig. 224).
Results

16. Piezodorus rubrofasciatus (Fabricius) (Plates: 34-36)

First spermatocyte metaphase shows six autosomal bivalents and two sex chromosomes. This shows that *P. rubrofasciatus* has a male diploid chromosome number of $2n=14=12A + XY$. The autosomes show very little gradation of size. The Y chromosome is the smallest element of the complement while the X chromosome is almost equal to the smallest autosome (Figs. 228, 229).

At diffuse stage, the autosomes are partially decondensed. The X and Y chromosomes are closely placed and appear as two darkly stained heteropycnotic bodies (Fig. 226). At diplotene, at least two of the autosomal pairs exist as ring bivalents. The sex chromosomes remain fused (Fig. 227).

At metaphase I, the autosomal bivalents arrange in a circle while the sex chromosomes lie inside the circle (Figs. 228, 229). In most of metaphase I plates, the sex chromosomes lie closely associated. During metaphase II, the sex chromosomes, X and Y join end-to-end to form the pseudobivalent which is seen inside the ring of autosomal univalents (Fig. 230). At telophase II, two types of plates are formed, the one with six autosomes and the X-chromosome and the other with six autosomes and the Y-chromosome (Fig. 231).

C-bandung

During diffuse stage, the X and the Y-chromosomes are seen as positively heterochromatic bodies while nucleolus appears to be partially heterochromatic (Fig. 232). All the autosomal bivalents and the X-chromosome are negatively heterochromatic. The Y-chromosome shows terminal C-bands (Fig. 233).

Fluorescent banding

At diffuse stage, the sex chromatin bodies (X and Y) are distinct but not very bright to both DAPI and CMA$_3$ (Figs. 234, 235). All autosomal bivalents stain
homogenously to both DAPI and CMA₃ with no specific signals while the sex chromosomes (X and Y) are relatively dull to DAPI and CMA₃ (Figs. 236, 237).

**Ag-NOR banding**

Silver stains start appearing in interphase nuclei where two to four nucleolar bodies are observed (Fig. 238). During early prophase I, nuclei show two different sized nucleoli, one strongly stained and one lightly stained (Figs. 239, 240). During late prophase I, the darkly stained nucleolus disintegrates into two smaller nucleoli which are seen associated with two autosomal bivalents (Figs. 241, 242). Silver impregnations have also been observed during spermiogenesis in the elongated spermatids (Fig. 243).
17. Priassus exemptus (Walker) (Plate: 37)

Spermatocyte first metaphase shows six autosomal bivalents and two sex chromosomes, X and Y. This implies that *P. exemptus* has a male diploid chromosome number of 2n=14=12A + XY. The autosomal bivalents show size gradation which is clear in metaphase I plate. One autosomal bivalent is distinctly larger, four medium sized and one small. The Y chromosome is the smallest element of the complement while the X chromosome is nearly equal to the smallest autosome (Fig. 247).

At diffuse stage, the sex chromosomes, X and Y are seen as two darkly stained heteopycnotic bodies while the autosomes are highly decondensed (Fig. 244). At diplotene, all the autosomal bivalents are distinct and all of them show single chiasma per bivalent. The sex chromosomes remain associated (Fig. 245). During diakinesis, the sex chromosomes lie near to each other and their bipartite nature is clear (Fig. 246).

At metaphase-I, the common arrangement of chromosomes in Pentatomidae is not observed. Rather, all the chromosomes form a ring with a hollow center (Fig. 247). Telophase I shows two newly formed nuclei with six autosomes and two sex chromosomes each which indicates reductinal division of autosomes and equational division of the sex chromosomes during meiosis I (Fig. 248). Metaphase II, in this species, has the typical pentatomid arrangement by which six autosomal univalents form a ring in the center of which lies an end-to-end associated sex chromosomal pseudobivalent (Fig. 249). Sex chromosomes divide reductionally during the second division so that the X goes to one pole and the Y to the other forming two types of nuclei at telophase II (Fig. 250).
18. *Plautia fimbriata* (Fabricius) (Plates: 38-39)

First meiotic metaphase I plate shows six autosomal bivalents and two sex chromosomes (Fig. 254). This shows that the diploid chromosome complement of this species is $2n=14=12A+XY$.

During diffuse stage, the sex chromosomes form a darkly stained heteropycnotic body while the autosomes are almost completely decondensed (Fig. 251). During diplotene, one of the autosomal pairs appears as a ring bivalent. The sex chromosomes remain associated and heteropycnotic (Fig. 252). During diakinesis, the sex chromosomes get separated, each appearing bipartite. Bipartite X and Y lie close to each other and Y chromosome is very lightly stained (Fig. 253).

At metaphase I, all the chromosomes form a ring with an empty center (Fig. 254). Metaphase II shows the typical arrangement of the family by which six autosomal univalents form a ring inside which lies the sex chromosome pseudobivalent (Fig. 255).

**C-banding**

At diffuse stage, the sex chromosome mass is seen as a positively heterochromatic body (Fig. 256). At early prophase, distinct terminal and interstitial C-bands are observed though it is difficult to differentiate individual chromosomes (Fig. 257). At diplotene, all the autosomal bivalents show terminal and interstitial C-bands while the sex chromosomes are seen as a single heterochromatic (Fig. 258).

**Fluorescent banding**

Sex chromatin body is DAPI and CMA$_3$ bright. In addition, a few DAPI and CMA$_3$ signals are seen on the decondensed autosomes during the diffuse stage (Figs. 259, 260). During spermatogonial stage, one autosomal pair has heavy terminal signal which overlaps for both DAPI and CMA$_3$. Three pairs of autosomes show interstitial
Results

DAPI/CMA<sub>3</sub> signals while two pairs of autosomes and the sex chromosomes (X and Y) are negative to both DAPI and CMA<sub>3</sub> (Figs. 261, 262). Autosomal bivalents also show overlapping terminal and interstitial DAPI/CMA<sub>3</sub> regions while the sex chromosomes are seen as a single sex chromosome body which is positive to both DAPI and CMA<sub>3</sub> (Figs. 263, 264).
**19. Tropicoris punctipes (Stal) (Plate: 40)**

Spermatocyte first metaphase shows six autosomal bivalents and two sex chromosomes. This indicates that this species has a male diploid chromosome number of 2n=14=12A + XY. One autosomal bivalent is distinctly large while the rest of the bivalents decrease gradually in size. X is smaller than the autosomes while Y chromosome is the smallest element of the complement (Figs. 268, 269).

At the diffuse stage, the sex chromosomes are associated end-to-end and form a darkly stained heteropycnotic body while the autosomes are completely decondensed (Fig. 265). At diplotene, the sex chromosomes get separated and appear darkly stained bodies. All the autosomal bivalents show single terminal chiasma (Fig. 266). At diakinesis, the sex chromosomes become separated and their bipartite nature is clear (Fig. 267).

At metaphase I, six autosomal bivalents and the X chromosome arrange in a ring with the Y univalent lying inside (Fig. 268). Very rarely, a second type of arrangement is observed by which five autosomal bivalents and Y form a ring inside which lies one autosomal bivalent while X lies outside the ring (Fig. 269). Each nuclei formed at telophase I comprises two sex chromosomes (X and Y) and six autosomes (Fig. 270). At metaphase II, autosomal univalents form a ring inside which lies an end-to-end associated XY pseudobivalent (Fig. 271). During anaphase II, sex chromosomes divide reductionally so that the X goes to one pole while the Y to the other (Fig. 272).
II - Subfamily: Asopinae

1. *Andrallus spinidens* (Fabricius) (Plates: 41-42)

Metaphase-I shows six autosomal bivalents and two sex chromosomes which implies that *Andrallus spinidens* has a male diploid number of \(2n=14=12A + XY\). One of the autosomal bivalents is distinctly larger, four are medium and one is distinctly smaller. The X chromosome appears only slightly bigger than the Y chromosome. (Figs. 276, 277).

During diffuse stage, the sex chromosomes are fused together and form a darkly stained heteropycnotic body lying against highly decondensed autosomes (Fig. 273). At diplotene, the sex chromosomes are yet associated. One of the autosomal bivalents forms a ring bivalent. (Fig. 274). During diakinesis, the sex chromosomes are separated but lie side by side. The ring nature of one of the autosomal bivalent persists showing two terminal chiasmata while the rest of the autosomal bivalents show single terminal chiasma (Fig. 275).

At first metaphase, the arrangement of chromosomes is typically pentatomid wherein the autosomal bivalents form a ring in the center of which lie the sex chromosomes, X and Y (Fig. 276,277). At metaphase II, X and Y join to form a pseudobivalent which lies in the center of a ring formed by six autosomal univalents (Fig. 278). At telophase II, the sex chromosomes divide reductionally by which the X and Y move to opposite poles and form two types of nuclei, one with six autosomes and the X chromosome and the other with six autosomes and the Y chromosome (Fig. 279).

**C-bANDING**

During the diffuse stage, the sex chromosome mass is seen as a single heterochromatin body. Scattered C-heterochromatin is observed on the diffused
autosomes (Fig. 280). During diakinesis, all autosomal bivalents appear C-positive while the sex chromosomes, X and Y are negatively heterochromatic (Fig. 281).

**Ag-NOR staining**

Silver stains start appearing in the interphase nuclei where three to six nucleolar bodies are observed (Fig. 282). Early prophase nuclei show 2-3 small nucleoli or a single large nucleolus (Figs. 283, 284). During early diplotene, single large nucleolus is seen to be associated with an autosomal bivalent (Fig. 285). At metaphase I, silver impregnations have been observed to be associated with one autosomal bivalent (Fig. 286). Elongated spermatids show nucleolar bodies distributed throughout the head region (Fig. 287).
2. *Canthecona furcellata* Wolff (Plates: 43-44)

Spermatocyte first metaphase shows six autosomal bivalents and two sex chromosomes. Thus *C. furcellata* has a male diploid number of 2n=14=12A + XY. Autosomal bivalents show a gradation in size, the Y chromosome is the smallest element of the complement and the X chromosome is almost equal to the smallest autosome (Figs. 291, 292).

At diffuse stage, X and Y are fused and form a darkly stained heteropycnotic body located on one side of the nucleus while the autosomal bivalents are completely decondensed (Fig. 288). At diplotene, six autosomal bivalents become distinct due to condensation and two or three of them are seen as ring bivalents. The sex chromosomes, X and Y remain closely associated (Fig. 289). Diakinesis is characterized by terminalization of chiasma in the bivalents and separation of the sex chromosomes, X and Y which appear bipartite. At least three autosomal bivalents are ring bivalents with two terminal chiasmata (Fig. 290).

Metaphase I shows two types of arrangements. In one, six autosomal bivalents form a ring inside which lie the sex chromosomes. Y lies exactly in the center while X lies close to the inner border of the ring (Fig. 291). In the second, all the eight chromosomes arrange in a ring with an empty center (Fig. 292). The former is more frequent (10 out of 13 metaphase I counts) than the latter (3 out of 13 metaphase I counts). During meiosis I, the sex chromosomes divide equationally and X and Y move to each pole forming nuclei with eight chromosomes at telophase I (Fig. 293). At metaphase II, X and Y chromosomes are joined end–to-end forming a pseudobivalent that lies in the center of a ring formed by autosomal univalents (Fig. 294).
Fluorescent banding

At diffuse stage, the sex chromatin body is both DAPI and CMA$_3$ bright. In addition, DAPI/CMA$_3$ signals are seen on the diffused autosomes (Figs. 295, 296). During diplotene, five autosomal bivalents show localized signals overlapping for both DAPI and CMA$_3$. However, all the signals are brighter to CMA$_3$ as compared to DAPI. One autosomal bivalent is DAPI dull and CMA$_3$ bright. The X and Y appear as a single bright sex chromatin body to both DAPI and CMA$_3$ (Figs. 297, 298). At metaphase I, five autosomal bivalents are positive to DAPI and CMA$_3$ and one autosomal bivalent is dull to DAPI and slightly bright to CMA$_3$. X-chromosome shows positive signals for both DAPI and CMA$_3$ while Y-chromosome is DAPI positive and CMA$_3$ dull (figs. 299, 300).
3. *Perillus bioculatus* (Fabricius) (Plates: 45-46)

First meiotic metaphase plate shows six autosomal bivalents and two sex chromosomes. Thus, the male diploid chromosome number of *Perillus bioculatus* is 2n = 14=12A+XY. Two pairs of autosomes are large, three pairs medium-sized and one pair small, X chromosome is similar in size to the smaller autosome while the Y chromosome is only slightly smaller than the X chromosome (Fig. 304, 305).

At diffuse stage, the X and the Y form a darkly stained heteropycnotic body located against partially decondensed autosomes (Fig. 301). During diplotene, the sex chromosomes get separated and lie side by side. Two autosomal bivalents appear as ring bivalents (Fig. 302). Diakinesis is marked by the presence of two ring bivalents which are more densely stained than rest of the four bivalents. The sex chromosomes are well separated, isopycnotic to the autosomal bivalents and appear bipartite (Fig. 303).

Two types of metaphase-I plates have been observed. In one, the typical pattern of the family is observed wherein a ring of six autosomal bivalents is formed in the center of which lie the sex chromosomes (Fig. 304). In the second, all the chromosomes (autosomal bivalents and sex chromosomes) form a ring with a hollow center (Fig. 305). The former pattern is more frequent (16 out of 23 metaphase I counts) than the latter (7 out of 23 metaphase I counts). In both of the patterns, the sex chromosomes lie close to each other. At metaphase II, six autosomal univalents form a ring and the sex chromosomes join to form a pseudobivalent which lies in the center of the ring (Fig. 306). During second meiotic division, sex chromosomes divide reductionally by which, X goes to one pole while Y to the other (Fig. 307).

**C-banding**

During the diffuse stage, the sex chromomome mass is positively
Results

heterochromatic (Fig. 308). During diplotene, three autosomal bivalents have terminal and interstitial C-bands, one has only single interstitial band while two autosomal bivalents are negatively heterochromatic (Fig. 309). The fused XY is C-positive. However, during diakinesis, X-chromosome appears positively heterochromatic while Y-chromosome is negatively heterochromatic (Fig. 310).

Fluorescent banding

Diffuse stage shows DAPI/CMA$_3$ bright sex chromatin body with localized CMA$_3$ positive signals (Figs. 311, 312). At metaphase I, all the autosomal bivalents are homogeneously positive to both DAPI and CMA$_3$ while X and Y are negative to DAPI but positive to CMA$_3$. One autosomal bivalent and X-chromosome show CMA$_3$ positive localized signals (Figs. 313, 314).
III - Subfamily: Podopinae

*1. Podops inuncta* Fabricius (Plates: 47-48)

Spermatogonial metaphase shows 14 chromosomes which include 12 autosomes and 2 sex chromosomes. So the chromosome complement of *P. inuncta* is $2n=14=12A + XY$. One large, four medium-sized and one small autosomal pairs are distinguished. The X chromosome is similar in size to the smallest autosome and the Y chromosome is the smallest element of the complement (Fig. 315).

At the diffuse stage, the autosomes are highly decondensed while X and Y remain condensed forming two closely associated but distinct heteropycnotic bodies (Fig. 316). During diplotene, the sex chromosomes are well separated. At least two autosomal bivalents exist as ring bivalents with two terminal chiasmata each (Fig. 317). During diakinesis, the bipartite nature of the sex chromosomes becomes clear. All the autosomal bivalents show single terminal chiasma (Fig. 318).

At metaphase I, the common arrangement of the family is not observed. Rather five autosomal bivalents and the sex chromosomes (X and Y) form a ring and one autosomal bivalent lies inside the ring (Fig. 319). At anaphase II, the sex chromosomes divide reductionally and the autosomes divide equationally (Fig. 321). During telophase II, two types of plates are formed because of reductional division of the sex chromosomes. In one, six autosomal univalents and X chromosome are observed and in the second six autosomal univalents and Y chromosome are observed (Fig. 322).

**C-banding**

During the diffuse stage, the sex chromosome body is positively heterochromatic (Fig. 323). During late diplotene, terminal and interstitial C-bands are observed on five autosomal bivalents. However, one autosomal bivalent is
negatively heterochromatic. The X and the Y-chromosomes are C-positive (Fig. 324).

**Fluorescent banding**

At diffuse stage, the sex chromosome body is bright for both DAPI and CMA₃ (Figs. 225, 226). During early diplotene, DAPI/CMA₃ signals overlap for four autosomal bivalents and the X-chromosome while one autosomal bivalent shows DAPI dull/CMA₃ bright signal. One autosomal bivalent and the Y-chromosome are both DAPI and CMA₃ negative (Figs. 327, 328).
DISCUSSION

The importance of Heteroptera as material for cytological studies was emphasized more than a century ago by Henking (1891), Montgomery (1901a, b, 1906) and Wilson (1907a, 1909a). Since then Heteroptera has been a group of continuing interest and several cytologists have been providing important cytological data on different groups of Heteroptera. The major reason for such an interest is the nature of heteropteran chromosomes and their peculiar behavior during cell division.

The integral part of chromosome structure is its kinetic organization. As a rule, in the monokinetic system, both mitotic and meiotic chromosomes show similar kinds of kinetic organization. However, typical of holokinetic chromosomes is the restriction of kinetic activity to telomeres in meiotic cells, indicated by the axial co-orientation of chromosomes during the first meiotic division and the movement of chromosomes with telomeres foremost during the first and second anaphases (Hughes-Schrader and Schrader, 1961). In Heteroptera, chromosomes are holocentric (without a localized centromere) which was first reported by Schrader (1935) in his study on chromosomes of Protenor belfragei (Alydidae) and he coined the term ‘diffused kinetochore’. Later on, Schrader (1941a, b, 1945a, b, 1946a, b, 1947, 1960a, b) and Hughes-Schrader (1940, 1942) provided significant contribution to a better knowledge on the organization and function of heteropteran chromosomes and their behavior during cell division. In radiation experiments of Euschistus servus, Euschistus tristigmus and Solubea pugnax, Hughes-Schrader and Schrader (1961) reported that each of the resulting fragments of chromosomes after radiation retained their kinetic activity and survived during division. On the contrary, Piza (1953, 1956, 1957) suggested dicentric nature for the Heteropteran chromosomes while Dutt (1955), Rao (1955, 1958), Parshad (1958), Ruthmann and Permantier (1973)
suggested the presence of a localized centromere in heteropteran chromosomes. However, holokinetic nature of chromosomes of Heteroptera was strengthened by electron microscopic observations by Buck (1967) in *Rhodnius prolixus* and by Comings and Okada (1972) in *Oncopeltus fasciatus*, and by C-banding pattern studies by Muramoto (1980). The holokinetic nature of heteropteran chromosomes has led to the hypothesis that fusions and fragmentations have played the key role in karyotype evolution as with diffused kinetic activity, each fragment is mitotically stable in contrast to the constraints imposed by a localized centromere in species with monocentric chromosomes (Schrader and Hughes-Schrader, 1956; Hughes-Schrader and Schrader, 1956, 1957).

Owing to their holokinetic nature, chromosomes of heteropteran insects show meiotic behavior different from monocentric chromosomes. Meiosis in Heteroptera is pre-reductional for the autosomes and post-reductional for the sex chromosomes i.e. the autosomes segregate reductionally while the sex chromosomes equationally during the first meiotic division and the reverse happens during the second meiotic division (Ueshima, 1963; Papeschi, 1994; Grozeva and Nokkala, 2001; Papeschi *et al.*, 2003). In addition Ueshima (1979), Nokkala (1985), Perez *et al.* (1997) and Cattani *et al.* (2004), in their study of different groups of Heteroptera, showed autosomal bivalents to be chiasmatic whereas sex chromosomes to be achiasmatic during meiosis.

Pentatomidae is one of the largest families of Heteroptera which includes a diverse assemblage of insects. Karyologically, a diploid number of 2n=14=12A+XY possessed by about 83% (243 from 294) species has been considered as the modal number of this family (Ueshima, 1979; Muramoto, 1981; Dey and Wangdi, 1985; Satapathy and Patnaik, 1988). In the rest of the 17% species, the diploid number
varies from only 6 in *Rhytidolomia senilis* (Wilson, 1913; Schrader, 1940a) to 28 in *Thyanta calceata* (Wilson, 1911; Hughes-Schrader and Schrader, 1956).

In the present study, twenty three species belonging to three subfamilies of Pentatomidae (Pentatominae, Asopinae and Podopinae) have been cytogenetically investigated. Out of these, twenty two species have a diploid chromosome number of $2n=14$ while one has $2n=16$ and all the twenty three species have XX/XY (female/male) sex chromosome determining system.

**i) Pentatominae**

Pentatominae is the largest subfamily of Pentatomidae which comprises about 75% (228 of the 294 species) of the species reported for chromosome studies. Within this subfamily, diploid numbers range from 6 in *Rhytidolomia senilis* (Wilson, 1913; Schrader, 1940a) to 27 in *Thyanta calceata* (Wilson, 1911; Schrader and Hughes-Schrader, 1956).

In the present study, nineteen species of Pentatominae have been cytogenetically investigated. Out of these ten species (*Aeliomorpha sheanensis*, *Apodiphus pilipes*, *Eysarcoris rosaceous*, *Halys seregera*, *Halys sulcata*, *Halyomorpha murrea*, *Nezara graminea*, *Piezodorus rubrofasciatus*, *Plautia fimbriata* and *Tropicoris punctipes*) have been investigated for the first time. Chromosome number and sex mechanism of nine species (*Bagrada picta*, *Carbula scutellata*, *Dolycoris baccarum*, *Erthesina fullo*, *Eurydema pulchrum*, *Eysarcoris inconspicuous*, *Nezara viridula* and *Priassus exemptus*) have been reported earlier by different authors (Table 2).
### Table 2- Chromosome details of Pentatominae species reported earlier

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All the presently studied species except *Halyomorpha murrea* possess a diploid chromosome number of $2n=14=12A+XY$ and lack m-chromosomes. This chromosome number is the most common number and possessed by about 82% (186 out of 228) of the species of Pentatominae studied so far confirming high karyotypic conservation during the evolution of this group as suggested by Ueshima (1979). *Halyomorpha murrea* has a diploid chromosome number of $2n=16=14+XY$, the second most frequent diploid number of the subfamily Pentatominae (observed in 19
out of 228 species) reported earlier in *Cosmopepla carnifex* (Montgomery, 1901), *Banasa dimidiata*, *Banasa rolstoni* (Wilson, 1907b; Thomas and Yonke, 1981), *Thyanta pallidovirens* (Wilson, 1911), *Eysarcoris aeneus*, *Eysarcoris fabricii*, *Palomena prasina*, *Palomena uridissima* (Schachow, 1932a, b), *Eysarcoris melanocephalus* (Xavier and Da, 1945), *Palomena angulosa* (Yosida, 1946), *Spermatodes sp.* (Manna, 1951), *Thyanta custator* and *Banasa lenticularis* (Schrader and Hughes-Schrader, 1956, 1958), *Caystrus pallipes*, *Palomena reuteri* and *Niphe sp.* (Parshad, 1957b), *Dunnis sp.* (Dey and Wangadi, 1988), *Gynenica affinis* (Satapathy and Patnaik, 1989) and *Thyanta sp.* (Rebagliati et al., 2005). In addition, 13 species are reported with a diploid number of 2n=24=22A+XY, 8 species with 2n=12=10A+XY, 1 species with 2n=6=4A+neo-X-neo-Y and 1 species with 2n=27=24+X1X2Y (Rebagliati et al., 2005). In Heteroptera, the commonest number present in a group is considered to be ancestral (Ueshima, 1979) and a decrease or an increase from the modal number is thought to be the result of fusion or fragmentation of chromosomes respectively as is true for most of the holokinetic systems (Bressa et al., 2005). Within Pentatomidae, 13% of the species studied so far (39 from 294) show an increase from the modal number while only 4% of the species (12 from 294) have a decreased diploid number suggesting fragmentation of autosomes and/or sex chromosomes to be more frequent than fusions in Pentatomidae (Rebagliati et al., 2005).

It has been commonly assumed that taxa whose chromosomes possess only a single centromere (monocentric chromosomes) have more restrained diploid counts than taxa with holokinetic chromosomes (chromosomes with multiple attachment sites for spindle fibers) (Suomalainen, 1965). However, this does not always seem to be the case. Some of the most chromosomally diverse animal taxa such as the
common shrew *Sorex araneus* (Hausser *et al*., 1985; Wojcik, 1986; Searle, 1986; Halkka *et al*., 1987), the house mouse *Mus domesticus* (Nachman and Searle, 1995; Britton-Davidian *et al*., 2000), grasshoppers (White, 1978) and ants (Crosland and Crozier, 1986; Imai *et al*., 1990) have monocentric chromosomes. There are also many examples of taxa that possess holokinetic chromosomes and show modest chromosomal variations such as rhabditine nematodes (Blaxter, 2000), bugs of the family Pentatomidae (Mikolajski, 1968; Rebagliati *et al*., 2005; Lanzone and Souza, 2006a) and the family Reduviidae (Panzera *et al*., 1996), and the scale insect families, such as Eriococcidae (Cook, 2000; Gavrilov, 2007). Thus, there does not appear to be a direct link between holocentric chromosomes and high karyotypic variation.

In all the nineteen species studied, the sex determining mechanism is XX/XY (female/male). This type of sex determining system is the commonest mechanism in Pentatominae present in 226 species out of 228 species studied so far. Deviations are seen in *Rhytidolomia senilis* with 2n=6 and NeoX-NeoY as the sex mechanism (Wilson, 1913; Schrader, 1940a) and *Thyanta calceata* with 2n=27 and X1X2Y as the sex mechanism (Wilson, 1911; Schrader and Hughes-Schrader, 1956).

The general course of meiosis in all the presently studied species is fairly uniform and behavior of chromosomes is typical of the Heteroptera. In all of them, the autosomes divide reductionally while the sex chromosomes divide equationally during the first meiotic division and just the reverse happens during the second meiotic division. However, there are certain variations which are discussed here. One important variation is in the diffuse stage. The diffuse stage has been a common meiotic feature in heteropteran species during which autosomes are decondensed, sex chromosomes are condensed and the cell size increases (Ueshima, 1979). Among
different species of Heteroptera, the degree of decondensation of the autosomes during the diffuse stage varies from those with high degree of decondensation to species whose chromosomes do not decondense at all and diffuse stage is absent (Lanzone and Souza, 2006a). In the present study, eleven species *viz.*, *Carbula scutellata, Eurydema pulchrum, Eysarcoris inconspicuous, Halys seregera, Halys sulcata, Halyomorpha murrea, Nezara viridula, Piezodorus rubrofasciatus, Eysarcoris guttiger, Priassus exemptus* and *Tropicoris punctipes* show high degree of decondensation of the autosomes. In *Plautia fimbriata, Ertesina fullo* and *Bagrada picta*, decondensation is almost complete as autosomes are seen to lose their identity. Similar results have been recorded in *Nezara viridula* of the subfamily Pentatominae by Camacho *et al.* (1985) and *Antiteuchus mixtus, Antiteuchus sepulcralis* and *Antiteuchus macraspis* of the subfamily Discocephalinae by Lanzone and Souza (2006a). In other families of Heteroptera also, this behavior has been recorded by Solari (1979) and Rebagliati *et al.* (1998) in Reduviidae, by Nokkala and Nokkala (1984) in Tingidae and by Nokkala (1986) in Coreidae. In *Aeliomorpha sheanensis, Apodiphus pilipes, Dolycoris baccarum, Eysarcoris rosaceous* and *Nezara graminea*, however, the autosomes show partial decondensation and it is recorded for the first time in the family Pentatomidae though it is earlier reported in Coreidae (Papeschi and Mola, 1990) and Aradidae (Jacobs and Liebenberg, 2001). The reasons for variations in the degree of decondensation and its significance have not yet been established. Lanzone and Souza (2006a) suggested that differences in the duration of the diffuse stage and levels of autosomes’ decondensation correspond to variations in the interval of disintegration between the meiotic and mitotic chromosome structure among different organisms.

In Pentatomidae, sex chromosomes usually associate during the diffuse stage
although there is much variation with respect to degree of association between X and Y among different species (Rebagliati et al., 2001; Lanzone and Souza, 2006a). In the present study, X and Y chromosomes remain associated to form a single heteropycnotic body throughout the diffuse stage in seventeen species viz., *Aeliomorpha sheanensis*, *Apodiphus pilipes*, *Bagrada picta*, *Carbula scutelata*, *Dolycoris baccarum*, *Eurydema pulchrum*, *Eysarcoris guttiger*, *Eysarcoris inconspicuous*, *Eysarcoris rosaceus*, *Halys seregera*, *Halys sulcata*, *Halyomorpha murrea*, *Nezara graminea*, *Nezara viridula*, *Piezodorus rubrofasciatus*, *Plautia fimbriata* and *Priassus exemptus*. This behavior has earlier been observed in other species of Pentatominae which include *Piezodorus hybnerri* and *Spermatdes sp.* (Manna, 1951), *Gynenica affinis*, *Acrosternum graminea* and *Agonoscelis nubile* (Satapathy and Patnaik, 1988, 1991), *Proxy albopunctulatus* and *Dichelops furactus* (Rebagliati et al., 2001) and *Paracritheus trimaculatus* and *Eurydema pulchrum* (Kaur and Semahagn, 2010a). On the other hand, in *Erthesina fullo* and *Tropicoris punctipes*, the two sex chromosomes are seen to remain separated in most of the diffuse stage plates. This behavior is less common and has been recorded in *Piezodorus guildini* and *Loxa deducta* (Pentatominae) by Rebagliati et al. (2001) and in *Antiteuchus mixtus*, *A. sepulcralis* and *A. macraspis* (Discocephalinae) by Lanzone and Souza (2006a).

In Heteroptera, in general and in Pentatomidae, in particular, the general trend is the predominance of one chiasma per bivalent during diplotene/diakinesis (Satapathy and Patnaik 1988; Gonzalez-Garcia et al., 1996; Grozeva and Nokkala, 1996; Bressa et al., 1999; Nokkala and Nokkala, 1999; Lanzone and Souza 2006a). However, in the present study, fourteen species are found to have more than one chiasma per bivalent. Out of these, eleven species (*Aeliomorpha sheanensis*, *Bagrada*
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picta, Carbula scutelata, Dolycoris baccarum, Eysarcoris guttiger, Halys seregera, Nezara graminea, Nezara viridula, Piezodorus rubrofasciatus and Plautia fimbriata) show 1 to 2 ring bivalents with two terminal chiasmata each and three species (Apodiphus pilipes, Eurydema pulchrum and Halyomorpha murrea) show 3 to 4 ring bivalents with two terminal/sub-terminal chiasmata each during diplotene/diakinesis. Only five species (Erthesina fullo, Eysarcoris rosaceous, Halys sulcata, Priassus exemptus and Tropicoris punctipes) lack any ring bivalent and possess only single chiasma per bivalent. The presence of more than one chiasma per bivalent is of rare occurrence in Pentatomidae. In Pentatominae, it has been reported only in one species which is Nezara viridula by Camacho et al. (1985) and Papeschi et al. (2003). In other subfamilies of Pentatomidae, it has been recorded in Macropygium reticulare (Discocephalinae) and Edessa meditabunda (Edessinae) by Rebagliati et al. (2001, 2003). Through the present study, thirteen more species have been added to the existing three species and it suggests that chiasma frequency in Pentatomidae might be more than what has been suggested earlier.

In most of the Pentatomidae species, metaphase I is characterized by a ring of autosomal bivalents in the centre of which lie the X and Y univalents (Manna, 1951; Satapathy and Patnaik, 1988; Rebagliati et al., 2001; Lanzone and Souza, 2006a). However, in the presently studied Pentatominae species, this trend has been observed only in four species (Bagrada picta, Erthesina fullo, Piezodorus rubrofasciatus and Tropicoris punctipes) and in the rest of the species (Aelionomorpha sheanensis, Apodiphus pilipes, Carbula scutellata, Dolycoris baccarum, Eurydemia pulchrum, Eysarcoris guttiger, Eysarcoris rosaceous, Eysarcoris inconspicuous, Halys seregera, Halys sulcata, Halyomorpha murrea, Nezara graminea, Nezara viridula, Plautia fimbriata and Priassus exemptus), deviations from this trend have been observed. The
most common type of arrangement observed for this subfamily in the present study is placement of six autosomal bivalents and the X-chromosome in a ring inside which lies the Y-chromosome which has been observed in five species (*Apodiphus pilipes*, *Carbula scutellata*, *Dolycoris baccarum*, *Nezara viridula* and *Tropicoris punctipes*).

Two other types of arrangements are also frequently observed in few species. In one, five autosomal bivalents and the sex chromosomes (X and Y) form a ring inside which lies one autosomal bivalent (*Aeliomorpha sheanensis*, *Eysarcoris rosaceous*, *Nezara viridula* and *Eysarcoris guttiger*) and in the second, all chromosomes form a ring with a hollow center (*Eurydema pulchrum*, *Eysarcoris rosaceous*, *Halys seregera*, *Plautia fimbriata* and *Priassus exemptus*). Deviations from the typical metaphase I arrangement have also been reported earlier in two species of subfamily Pentatominae viz., *Carbula socia* (Satapathy and Patnaik, 1988) and *Eurydema pulchrum* (Kaur *et al.*, 2006; Kaur and Semahagn, 2010a) where all the chromosomes are randomly arranged on the metaphase plate.

In Pentatomidae, Metaphase II is radial where autosomal univalents form a ring in the centre of which lies the end-to-end associated XY pseudobivalent (Manna, 1951; Parshad, 1957b; Satapathy and Patnaik, 1988; Rebagliati *et al.*, 2001). Same results were observed in all the pentatominae species analysed in this work.

ii) **Asopinae**

The Asopinae is a cosmopolitan subfamily of predatory bugs of the family Pentatomidae comprising 63 genera and 357 species (Schuh and Slater, 1995) and some of them are important agents of biological control (Schaefer and Panizzi, 2000). However, only twenty two species have been cytogenetically investigated with a diploid chromosome number of 12, 14, 16 or 18 and XY sex determining mechanism.

In the present investigation, three species of Asopinae have been
cytogenetically studied which are *Andrallus spinidens*, *Canthecona furcellata* and *Perillus bioculatus*. The diploid number of *Perillus bioculatus* agrees with the prescription given by Wilson (1906) as $2n = 14 = 12A + XY$. *Andrallus spinidens* and *Canthecona furcellata*, investigated for the first time, also show the same number which is the modal number for the family Pentatomidae. Similar diploid number has been reported so far in fourteen species of Asopinae which are *Apoecilus bracteatus*, *Perillus bioculatus* and *Stiretrus anchorago* (Wilson, 1906, 1909b), *Afrius yolofus* and *Macrorhaphis acuta* (Nuamah, 1982), *Arma custos* (Schachow, 1932b; Muramoto, 1973b), *Oechalia pacifica* and *Oechalia grisea* (Heizer, 1950, 1951), *Perillus confluous* (Montgomery, 1901a, 1906), *Picromerus bidens* (Geitler, 1939b), *Piceromerus nigrigens* (Xavier and Da, 1945; Miyamoto, 1957), *Piceromerus sp.* (Dey and Wangdi, 1985, 1988), *Troilus luridus* (Miyamoto, 1957; Parshad, 1957c) and *Zicrona caerulea* (Muramoto, 1973a). The second most common diploid number in the subfamily is $2n=16=14A+XY$ which is reported in four species of *Podisus*: *Podisus maculiventris* and *Podisus placidus* (Montgomery, 1901a, 1906; Wilson, 1906, 1909b), *Podisus distinctus* and *Podisus nigrispinus* (Rebagliati et al., 2002). A decrease from the modal diploid chromosome number ($2n=12=10A+XY$) has been reported in *Oechalia patruelis* (Heizer, 1950) and *Piceromerus bidens* (Yosida, 1946, 1956) and an increase ($2n=18=16A+XY$) has been observed in *Dynorhynchus dybowskii* (Muramoto, 1981). Comparing the chromosome complements of *Oechalia patruelis* ($2n=12$) and *Oechalia pacifica* ($2n=14$), Heizer (1950) suggested the extremely large autosome present in *O. patruelis* to have originated as a result of fusion of two autosomes of the ancestor as other autosomes and the X and the Y are almost similar in size in both species.

In the present study, all the three species show XY male sex determining
mechanism. This mechanism is the only sex system in all the species studied from the subfamily Asopinae (Rebagliati et al., 2005). In the three predator species, X and Y chromosomes associate closely to form a single heteropycnotic body during the diffuse stage as has been observed in other species of Asopinae which includes *Perillus confluens* (Montgomery, 1901a, 1906), *Oechalia pacifica* and *Oechalia grisea* (Heizer, 1950, 1951). X and Y get separated during diplotene in *Perillus bioculatus* and *Canthecona furcellata*. In *Andrallus spinidens*, however, XY association has been seen extended even up to the diplotene stage as is also recorded in another predator pentatomid, *Oechalia grisea* (Heizer, 1951).

The three species show variations in the degree of decondensation of autosomes during the diffuse stage. *Andrallus spinidens* and *Canthecona furcellata* show high degree of decondensation as has been recorded in eleven species of the subfamily Pentatominae during the present study and *Antiteuchus mixtus*, *A. sepalcralis* and *A. macraspis* of the subfamily Discocephalinae by Lanzone and Souza (2006a). In *Perillus bioculatus*, however, the autosomes show a partial decondensation as has been seen in five species of Pentatominae during the present study and some species of Coreidae (Papeschi and Mola, 1990) and Aradidae (Jacobs and Liebenberg, 2001).

In *Canthecona furcellata* and *Perillus bioculatus*, two to three ring bivalents have been observed while in *Andrallus spinidens*, a single ring bivalent has been commonly seen in diplotene and diakinesis plates. In all the cases, the chiasma frequency is more than one as the ring bivalents bear two chiasmata each. The presence of more than one chiasma per bivalent has not been reported in any of the species of Asopinae studied so far, and in Pentatomidae, in general, one chiasma per bivalent is the predominant condition. However, during the present study, in
Pentatomininae, fourteen species out of nineteen species investigated show more than one chiasma pre bivalent while in Asopinae, all the species possess ring bivalents. This indicates that in Pentatomidae species from India, the chiasma frequency is more than one per bivalent as against species from other countries which show predominantly one chiasma per bivalent.

All the three species show the regular arrangement of chromosomes at metaphase I plate typical of the family Pentatomidae by which autosomal bivalents form a ring inside which lie the sex chromosomes. However, in *Canthecona furcellata* and *Perillus bioculatus*, additional arrangement pattern of chromosomes has also been observed, though less frequently, in which all the chromosomes form a ring with an empty centre. Deviations from the typical arrangement have also been reported by Heizer (1951) in *Oechalia grisea* and *Oechalia pacifica* in which two arrangement patterns occur with equal frequency. One is exactly similar to the present study (formation of a ring with an empty center) and the second is a ring of six or seven chromosomes encircling any one of the other chromosomes. All the three presently studied species show the regular arrangement of chromosomes during metaphase II wherein autosomal univalents form a ring in the centre of which lies the end-to-end associated XY pseudobivalent. It is a common feature of majority of Pentatomidae species (Lanzone and Souza, 2006a).

iii) **Podopinae**

Regardless of the presence of 255 described species (Schuh and Slater, 1995), cytogenetic report on Podopinae is restricted only to ten species. In the present study, one species belonging to this subfamily (*Podops inuncta*) has been cytogenetically investigated. *Podops inuncta* has a diploid chromosome number of 2n=14=12A+XY. Southwood and Leston (1959) reported the same chromosome number in this species.
collected from British Island Isles without a mention of the sex chromosome system. Similar diploid chromosome number has also been reported in seven other species of this subfamily viz., *Ancyrosoma leucogrammes* (Schachow, 1932a; Xavier and Da, 1945), *Graphosoma italicum* (Schachow, 1932b; Geitler, 1939; Xavier and Da, 1945), *Graphosoma semipunctatum* (Schachow, 1932b), *Scotinophara horvathi* (Toshioka, 1934), *Graphosoma rubrolineatum* (Yosida, 1950; Takenouchi and Muramoto, 1968, 1970a), *Stortheoris nigricepes* (Mittal and Joseph, 1981) and *Scotinophara fibulata* (Nuamah, 1982). On the other hand, *Scotinophara coarctata* (Satapathy et al., 1990) and *Scotinophara sp.* (Jande, 1959b, 1960a) are reported with a reduced diploid chromosome number of 2n=12=10A+XY.

The sex determining mechanism in *Podops inuncta* is XY (♂). Similar type of mechanism is reported in all the Podopinae species studied so far indicating that this sex mechanism is well stable within the subfamily.

In *Podops inuncta*, the X and the Y-chromosomes, during the diffuse stage, exist as closely associated but distinct heteropycnotic bodies. The autosomes are highly decondensed during this stage as is common in most of the Pentatominae and Asopinae species discussed above in the present study. At least two ring bivalents with two chiasmata per bivalent each have been observed during the diplotene stage revealing that the feature of one chiasma per bivalent described to be common in Pentatomidae by Satapathy and Patnaik (1988) and Lanzone and Souza (2006a) is not followed in *Podops inuncta* also as in most of the species belonging to Pentatominae and Asopinae analysed during the present study.

A definite arrangement of chromosomes at metaphase-I is observed in *Podops inuncta* by which, five autosomal bivalents and the sex chromosomes (X and Y) form a ring and one autosomal bivalent lies inside the ring. Similar result has also been
observed in four presently studied species of Pentatominae (*Aeliomorpha sheanensis, Eysarcoris guttiger, Eysarcoris rosaceous* and *Nezara viridula*) but this does not correspond to the typical pattern described for Pentatomidae. Deviation from the regular arrangement of chromosomes during metaphase I is also reported in *Scotinophara fibulata* by Nuamah (1982) wherein all the chromosomes are irregularly arranged without a definite pattern.

**C-Banding**

The genetic system of a species is the way of organization and transmission of the genetic material which determines the balance between coherence and recombination of genes and controls the amount and type of gene combinations. Evolution of genetic systems means evolution of those mechanisms effecting and affecting genetic variability (Darlington, 1939). One of the factors that characterize the genetic system of a species is the mode of chromosome organization. Repeated DNA sequences in insect genomes are organized according to different patterns. They occur either as families of repeated elements interspersed throughout the genome or as large arrays usually representing satellite DNA sequences which is usually called heterochromatin (Brutlag, 1980; Blanchelot, 1991). Despite the general presumption that constitutive heterochromatin is inert material, there is abundant and increasing evidence that constitutive heterochromatin can have important functions in chromosome pairing and segregation, position effect variegation and can even contain genes and other functional DNA sequences (Sumner, 1972). It is commonly supposed that holokinetic chromosomes contain only a small amount of constitutive heterochromatin (Blackman, 1985). However, in Heteroptera, it has been observed that there are species with a good amount of constitutive heterochromatin (Perez et al., 1997). C-banding can thus be used to distinguish the karyotypes of species which
are known to have the same chromosome number, as is observed in most of the pentatomid species.

In the present study, nineteen species have been subjected to C-banding investigation: sixteen species of Pentatomaiae, two species of Asopinae and one species of Podopinae. The results show a heterogeneous C-banding pattern with respect to the location, amount and the number of chromosomes having C-bands. In general, terminal, sub-terminal and/or interstitial C-bands have been observed. The amount of constitutive heterochromatin has been seen to vary from a very thin array to thick blocks in different species. Similarly, the number of chromosomes showing C-bands ranges from species with no C-banded chromosome to those species which have C-bands in all the chromosomes.

Autosomal chromosomes of eleven species investigated in the present study are seen to show both terminal and interstitial C-positive regions. These are Aeliomorpha sheanensis, Dolycoris baccarum, Eurydema pulchrum, Eysarcoris inconspicuous, Halyomorpha murrea, Nezara graminea, Nezara viridula, Plautia fimbriata, Eysarcoris guttiger (Pentatomaiae), Perillus bioculatus (Asopinae) and Podops inuncta (Podopinae). Similar C-banding pattern has been reported in four species of Pentatomaiae by Muramoto (1978a) viz., Carpocoris purpureipennis, Eurydema rugosa, Graphosoma rubrolineatum and Palomena angulosa. In Nezara viridula, one autosomal bivalent shows both terminal and interstitial bands which does not agree with earlier observation of Camacho et al. (1985) who reported that the chromosome with interstitial band always lacks terminal band. The presence of terminal and interstitial C-bands on autosomes has also been reported in other families of Heteroptera by Dey and Wangdi (1990) in Petillia patullicolis (Coriedae), by Panzera et al. (1997) in Triatoma patagonica (Reduvidae), by Grozeva and Nokkala
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Terminal C-bands have been observed in the autosomes of Apodiphus pilipes, Bagrada picta, Erthesina fullo (Pentatominae) and Andrallus spinidens (Asopinae). Similar results have been reported by Lanzone and Souza (2006b) in Antiteuchus mixtus, Antiteuchus sepuclaris and Antiteuchus macraspis (Pentatomidae), by Solari and Agopian (1987) in Triatoma infestans (Reduviidae), by Papeschi (1988, 1991) in Belostoma dentatum and Belostoma elegans (Belostomatidae), by Dey and Wangdi (1990) in Anolocenemis phasiana, Leptoglossus impictus and Phthia picta (Coreidae), by Dey and Wangdi (1990) and Bressa et al. (2005) in Iphita limbata and Largus rufipennis (Largidae) and by Grozeva et al. (2004) in Acalypta carinata and Physatocelia smrecznskii (Tingidae).

In the present study, terminal, sub-terminal and interstitial C-banding pattern is observed only in the autosomes of Eysarcoris rosaceus. In this species, two autosomal bivalents show terminal C-bands, two autosomal bivalents show terminal and sub-terminal C-bands, one autosomal bivalent shows terminal and interstitial C-bands and one autosomal bivalent is negatively heterochromatic. This type of C-banding pattern has never been reported in the family Pentatomidae so far. However, in other families of Heteroptera, similar results have been reported by Maudlin (1974) in Triatoma infestans (Reduviidae), by Grozeva and Nokkala (2001) in Corythucha ciliate (Tingidae), by Ituarte and Papeschi (2004) in Tenagobia fuscata (Micronectidae), by Angus et al. (2004) in Notonecta oblique (Notonectidae), by Waller and Angus (2005) in Corixa affinis and Corixa panzer (Corixidae), by Kuznetsova et al. (2007) in Arachnocoris trinitatus (Nabidae) and by Bressa et al.
In the present study, *Carbula scutelata* and *Halys sulcata* (Pentatominae) have shown C-bands scattered throughout the length of the autosomes. This type of pattern has been seen in *Dysdercus koenigii* (Pyrrhocoridae) by Kaur and Singh (2010).

In *Piezodorus rubrofasciatus* (Pentatominae), all chromosomes have been seen to be C-negative as is reported in *Carbula humerigera* (Pentatominae) by Muramoto (1978a). In other families of Heteroptera, the same result has been reported in *Acalypta carinata* and *Lasiacantha capucina* (Tingidae) by Grozeva and Nokkala (2001), in *Athaumastus haematicus* (Coreidae) by Bressa et al. (2005), in *Prostemma gutala* (Nabidae), in *Corixa dentipes*, *Corixa iberica* and *Corixa punctata* (Corixidae), in *Macrolophus geranii* and *Macrolophus pygmaeus* (Miridae) by Grozeva et al. (2005, 2007) and in *Neophysopelta schlubushi* by Kaur and Singh (2010).

In Heteroptera, in general and in Pentatomidae in particular, the most common pattern is considered to be the terminal location of C-bands (Solari and Agopian, 1987; Papeschi, 1991; Panzera et al., 1995; Cattani et al., 2004; Bressa et al., 2005). Results of the present study on nineteen species, however, fail to corroborate this suggestion. Out of nineteen studied species, this pattern is shown by only four species while the most common pattern comes out to be terminal and interstitial C-bands being shown by eleven species.

With respect to the number of autosomes showing C-bands, the present study shows heterogeneity. C-bands are observed in all the autosomes in *Aeliomorpha sheanensis*, *Carbula scutellata*, *Eurydema pulchrum*, *Eysarcoris inconspicuous*, *Halys sulcata*, *Halyomorpha murrea*, *Nezara graminea*, *Plautia fimbriata* and *Eysarcoris guttiger* (Pentatominae) and *Andrallus spinidens* (Asopinae). This has
been observed in most of the heteropteran species studied so far (Maudlin, 1974; Muramoto, 1978a, 1980; Camacho et al., 1985; Dey and Wangdi, 1990; Papeschi, 1995; Grozeva and Nokkala, 2001; Angus et al., 2004; Grozeva et al., 2004; Bressa et al., 2005; Lanzone and Souza, 2006b). The rest of the studied species have 1 to 3 C-negative autosomes. The presence of a few C-negative autosomes in the complement is reported in Belostoma micantulum (Belostomatidae) by Papeschi (1988), in Nezara icteria (Pentatominae) by Dey and Wangdi (1990), in Metatropis rufescens (Berytidae) by Nokkala and Nokkala (1997), in Triatoma infestans (Reduviidae) by Panzera et al. (1992), in Acalypta nigrim, Elasmotropis testacea, Tingis sideritis and Corythucha ciliata (Tingidae) by Grozeva and Nokkala (2001), in Notonecta glauca and Notonecta maculata (Notonectidae) by Angus et al. (2004), in Holhymenia rubiginosa (Coreidae) by Bressa et al. 2008) and in Dieuches coloratus (Lygaeidae) by Kaur et al. (2010).

The C-banding pattern in the sex chromosomes of heteropteran species is found to be extremely diverse. Moreover, the C-banding pattern of X differs from that of Y chromosome. Sex chromosomes may either be completely C-positive or completely C-negative or may have localized C-bands. In the present study, X chromosome shows terminal C-bands in Aeliomorpha sheanensis, Bagrada picta, Eurydema pulchrum, Eysarcoris inconspicuous, Nezara viridula (Pentatominae) and Podops inuncta (Podopinae). This is so far the most common condition in Heteroptera and has been reported in Belostoma oxyurum and Belostoma elegans (Belostomatidae) by Papeschi (1988), in Ochrochira granulipes, Leptoglossus impictus and Phthia picta (Coreidae) By Dey and Wangdi (1990) and Bressa et al. (2005), in Leptocorisa acuta (Alydidae) by Dey and Wangdi (1990), in Acalypta carinata, Acalypta pavula, Capium clavicorne, Dictyla echii, Elasmotropis testacea,
Kalama tricorins, Lasiacantha capucina capucina, Physatocheila smreczynskii and Stephanitis oberti (Tingidae) by Grozeva and Nokkala (2001), in Notonecta obliqua (Notonectidae) by Angus et al. (2004), in Tenagobia fuscata (Micronectidae) by Ituarte and Papeschi (2004), in Corixa punctata, Corixa panzeri and Corixa iberica (Corixidae) by Waller and Angus (2005), in Largus ruhipennis (Largidae) by Bressa et al. (2005), in Arachnocoris trinatatus (Nabidae) by Kuznetsova et al. (2007), in Rhodnius pallescens (Reduviidae) by Palacio et al. (2008) and in Dieuches insignis (Lygaeidae) by Kaur et al. (2010). Camacho et al. (1985), however, reported X chromosome to be completely C-positive in Nezara viridula.

The X-chromosome is completely heterochromatic in Apodiphus pilipes, Halys sulcata (Pentatominae) and Perillus bioculatus (Asopinae) as is also reported in Corythucha ciliate and Elasmotropis testacea (Tingidae) by Grozeva and Nokkala (2001), in Himacerus mirmicoides, Nabis indicus, Nabis indicus and Nabis viridulus (Nabidae) by Grozeva et al. (2004) and in Dieuches coloratus (Lygaeidae) by Kaur et al. (2010).

In Andrallus spinidens (Asopinae), Erthesina fullo and Piezodorus rubrofasciatus (Pentatominae), the X-chromosome is completely C-negative which is also reported earlier in three species of Pentatomidae (Carbula humerigera, Dolycoris baccarum and Nezara icterica) by Muramoto (1980); in three species of Coreidae (Molipteryx fuliginosa, Anopolocnemis phasiana, Petillia patullicolis and Athaumastus haematicus) by Muramoto (1980), Dey and Wangdi (1990) and Bressa et al. (2005); one species each of Largidae (Iphita limbata) by Dey and Wangdi (1990) and Reduviidae (Triatoma infestans) by Panzera et al. (1992).

The Y-chromosome has been mentioned to contain large amount of heterochromatin if not fully heterochromatic in most of the Heteropteran species
(Grozeva and Nokkala, 2001). In the present study, Y chromosome has been seen to be C-positive in eight species and C-negative in four species. It has terminal C-positive regions in *Aeliomorpha sheanensis*, *Eurydema pulchrum*, *Eysarcoris inconspicuous*, *Nezara viridula*, *Piezodorus rubrofasciatus* (Pentatominae) and *Podops inuncta* (Podopinae) while it is completely C-heterochromatic in *Apodiphus pilipes* and *Bagrada picta* (Pentatominae). The result for *Nezara viridula* in the present study matches with the description given earlier by Camacho *et al.* (1985).

Three other species of Pentatomidae (*Antitieuchus mixtus*, *Antitieuchus macraspis* and *Antitieuchus sepulcralis*) have also been reported to have the same pattern by Lanzone and Souza (2006b). C-positive Y-chromosome is the most common pattern in Heteroptera and is reported in *Triatoma infestans* by Solari (1979) and *Triatoma maculata* and *Triatoma pseudomaculata* (Reduviidae) by Pires (2008), in *Belostoma martini*, *Belostoma micantulum* and *Belostoma oxyurum* (Belostomatidae) by Papeschi (1988, 1991, 1995), in *Tingis caucasica* and *Tings sideritis* (Tingidae) by Grozeva and Nokkala (2001), in *Himacerus mirmicoides*, *Nabis indicus*, *Nabis viridulus* and *Prostemma guttala* (Nabidae) by Grozeva *et al.* (2004), in *Notonecta glauca*, *Notonecta maculate* and *Notonecta oblique* (Notonectidae) by Angus *et al.* (2004), in *Tenagobia fuscata* (Micronectidae) by Ituarte and Papeschi (2004) and in *Dieuches uniguttataus* (Lygaeidae) by Kaur *et al.* (2010).

*Andrallus spinidens*, *Perillus bioculatus* (Asopinae), *Erthesina fullo* and *Halys sulcata* (Pentatominae) are seen to have C-negative Y chromosome. Similar result is reported in *Carbula humerigera*, *Dolycoris baccarum* and *Nezara icterica* (Pentatomidae) by Muramoto (1980) and Dey and Wangdi (1990), in *Belostoma elegans*, *Belostoma bifoveolatum* and *Belostoma dentatum* (Belostomatidae) by Papeschi (1988, 1991), in *Capium clapicorine*, *Coritucha ciliata*, *Dictyla echii*,
Elasmotropis testacea, Physatocheila smreczynskii, Stephanitis oberti (Tingidae) by Grozeva and Nokkala (2001), in Notonecta viridis (Notonectidae) by Angus et al. (2004), in Corixa iberica (Corixidae) by Waller and Angus (2005) and in Dieuches coloratus and Dieuches insignis (Lygaeidae) by Kaur et al. (2010).

In six species (Dolycoris baccarum, Eysarcoris guttiger, Eysarcoris rosaceous, Halyomorpha murrea, Nezara graminea and Plautia fimbriata), X and Y chromosomes remain associated during diplotene and appear as a single dark heterochromatic body, and it is not possible to observe the C-banding pattern of individual sex chromosomes while in Carbula scutellata, the sex chromosomes are not differentiated from autosomes.

**Sequence specific-banding**

There is still little information about base composition of the heterochromatin in Heteroptera, i.e. whether the heterochromatin is rich in AT or GC bases as revealed by fluorescent dyes (DAPI and CMA₃ respectively). Most reports referring to heterochromatin characterization in Heteroptera describe C-bands as DAPI-bright/CMA₃-dull (Papeschi and Bressa, 2002; Papeschi et al., 2003, Rebagliati et al., 2003; Bressa et al., 2005). On the other hand, CMA₃ positive signals have been reported to correspond to NORs (Gonzalez-Garcia et al., 1996; Papeschi et al., 2003; Rebagliati et al., 2003) though it has been suggested that NORs may not always be GC rich (Fossey and Liebenberg, 1995).

In the present study, thirteen species belonging to the subfamilies Pentatominae (ten species), Asopinae (two species) and Podopinae (one species) have been investigated for sequence specific banding. In almost all of the species investigated, one or more of the chromosomes show homogeneous staining which overlaps for both DAPI/CMA₃. In Piezodorus rubrofasciatus, all the autosomal
bivalents stain homogeneously without any specific signal. Uniform fluorescence of autosomes overlapping for DAPI/CMA$_3$ are reported in *Edessa meditabunda* and *Edessa rufarmarginata* (Pentatomidae) by Rebagliati et al. (2003), *Prostemma guttala* (Nabidae) by Grozeva et al. (2004), *Triatoma vitticeps* (Reduviidae) by Severi-Aguiar et al. (2006) and *Macrolophus pygmaeus* and *Macrolophus geranii* (Miridae) by Grozeva et al. (2007).

Localized signals overlapping for both DAPI and CMA$_3$ for one or more autosomes have been observed in *Aeliomorpha sheanensis*, *Eurydema pulchrum*, *Halyomorpha murea*, *Halys seregera*, *Nezara viridula* and *Plautia fimbriata* (Pentatomidae), *Canthecona furcellata* (Asopinae) and *Podops inuncta* (Podopinae). In *Halyomorpha murea* and *Eurydema pulchrum*, all the C-bands are similar with overlapping DAPI/CMA$_3$ signals showing that the C-heterochromatic regions are rich in interspersed AT and GC blocks. Such results have been reported earlier in *Tenagobia fuscata* (Micronectidae) by Ituarte and Papeschi (2004), in *Nabis indicus* (Nabidae) by Grozeva et al. (2004), in *Athaumastus haematicus* and *Jadera sanguinolenata* (Coreidae) by Bressa et al. (2005), in *Macrolophus pygmaeus* and *Macrolophus costalis* (Miridae) by Grozeva et al. (2006, 2007).

In *Aeliomorpha sheanensis*, *Eurydema pulchrum*, *Halys seregera*, *Halys sulcata*, *Halyomorpha murea*, *Nezara graminea*, *Nezara viridula*, *Plautia fimbriata* (Pentatominae), *Canthecona furcellata* (Asopinae) and *Podops inuncta* (Podopinae), localized DAPI signals are observed in one or more of the autosomes. Similar results have been reported in *Dysdercus albofasciatus* (Pyrrhocoridae) by Bressa et al. (1999), in *Triatoma infestans* (Reduviidae) by Perez et al. (2000), in *Nabis indicus*, *Himacerus mirmicoides* and *Nabis viridulus* (Nabidae) by Grozeva et al. (2004), in *Largus rufipennis* (Largidae) by Bressa et al. (2005), in *Antiteuchus sepulcralis*

In general, fluorescent banding results of sex chromosomes (X and Y) in Heteroptera show that they are positive to both DAPI and CMA$_3$ in most of the species (Grozeva and Nokkala, 2002). In the present study, the sex chromatin body has been observed to be bright to both DAPI and CMA$_3$ in all the species until diplotene. Rebagliati *et al*. (2003) recorded similar results in *Edessa meditabunda* and *Edessa ruformarginata* (Pentatomidae) and suggested that DAPI/CMA$_3$ positivity probably reflects differences in degree of chromatin condensation rather than differences in base composition. This suggestion seems plausible because from early prophase until diplotene/diakinesis, X and Y chromosomes remain more condensed than the autosomes and appear heteropycnotic even for conventional preparations in all the species investigated in the present study. However, the fluorescent banding pattern becomes diverse for X and Y chromosomes after diplotene/diakinesis in different species which is discussed here.

(Pentatominae) and *Podops inuncta* (Podopinae), X chromosome is positive to both DAPI and CMA. This pattern is widely prevalent in Heteroptera and is reported in *Cimex sp.* (Cimicidae) by Grozeva and Nokkala (2002), *Himacerus mirmicoides, Nabis indicus* and *Nabis viridulis* (Nabidae) by Grozeva et al. (2004), in *Athaumastus haematicus, Leptoglossus impictus, Phthia picta* (Coreidae) by Bressa et al. (2005), in *Antiteuchus macrasis, Antiteuchus mixtus* and *Antiteuchus sepulcralis* (Pentatomidae) by Lanzone and Souza (2006b) and in *Dieuches uniguttatus* (Lygaeidae) by Kaur et al. (2010). In *Eysarcoris inconspicuous, Nezara viridula, Piezodorus rubrufasciatus* (Pentatominae) and *Perillus bioculatus* (Asopinae), X chromosome is only DAPI positive, a less common condition reported so far only in three species: *Dysdercus albofasciatus* and *Dysdercus chaquensis* (Pyrrhocoridae) by Bressa et al. (1999, 2002) and *Tenagobia fuscata* (Micronectidae) by Ituarte and Papeschi (2004). In contrast, X chromosome in *Plautia fimbriata* and *Nezara graminea* (Pentatominae) is seen to be negative to both DAPI and CMA as is observed so far only in one species i.e. *Macrolophus costalis* (Miridae) by Grozeva et al. (2006).

In Heteroptera, Y chromosome is reported to be positive to both DAPI and CMA in most of the species studied so far. It has been observed in Pentatomidae (*Edessa ruformarginata, Antiteuchus macrasis, Antiteuchus mixtus* and *Antiteuchus sepulcralis*) by Rebagliati et al. (2003) and Lanzone and Souza (2006b), in Miridae (*Macrolophus costalis*) by Grozeva et al. (2006), in Nabidae (*Arachnocoris trinitatus*) by Kuznetsova et al. (2007), in Lygaeidae (*Dieuches insignis* and *Dieuches uniguttatus*) by Kaur et al. (2010). However, in the present study, only *Eysarcoris inconspicuous* (Pentatominae) shows this result. Rather, Y chromosome is observed to be negative to both DAPI and CMA in seven species viz. *Aeliomorpha sheanensis,
Eurydema pulchrum, Nezara graminea, Nezara viridula, Plautia fimbriata, Piezodorus rubrofasciatus (Pentatominae) and Podops inuncta (Podopinae). This result could be related to the small size of the Y chromosome in the aforementioned species investigated in the present study as has been suggested by Rebagliati et al. (2003) in their study of Edessa meditabunda (Pentatomidae) that the Y chromosome becomes dull to both DAPI and CMA$_3$ due to its small size and its strong stretching between the poles by the spindle fibers.

Y chromosome is positive to only DAPI in Halys seregera (Pentatominae) and Perillus bioculatus (Asopinae). This pattern is not common and is observed only in Triatoma vitticeps (Reduviidae) by Severi-Aguiar et al. (2006). Y chromosome is positive to only CMA$_3$ in Perillus bioculatus. This result has not been reported in Heteroptera so far.

**Ag-NOR banding**

The number and size of nucleoli are supposedly related to the biosynthetic activity of the cell (Nanya and Bicudo, 1995; Tavares and Azeredo-Oliveira, 1997; Abdo-Banhos et al., 2004). This indicates that differences in the size and number of nucleoli reflect differences in metabolic activities of the cells. The nucleolus and pre-nucleolar bodies persist in meiosis due to strong demand for rRNA synthesis during spermatogenesis (Bressa et al., 2003). Proteins necessary for rRNA transcription and pre-ribosome processing are able to reduce silver nitrate, acquiring a dark brown color. Nucleolar proteins continue to be associated with the NORs found at the edge of chromosomes during prophase until the beginning of telophase (Fischer et al., 1991; Wachtler and Stahl, 1993; Schwarzacher and Wachtler, 1993; González-Garcia et al., 1995; Dunder et al., 1997).

In the present study, ten species have been subjected to silver nitrate staining to
investigate the nucleolar organizer regions (NORs) viz. *Apodiphus pilipes, Bagrada picta, Eysarcoris inconspicuous, Halys sulcata, Halys seregera, Halyomorpha murrea, Nezara graminea, Nezara viridula, Piezodorus rubrofasciatus* (Pentatominae) and *Andrallus spinidens* (Asopinae). In most of these species, nucleolar bodies start appearing in early interphase cells. The number and size of these bodies have been found to vary even within the same species. In the later stages, these nucleolar bodies associate to form one or more nucleoli. In general, the nucleoli disintegrate during diplotene or diakinesis in Heteroptera (Cattani and Papeschi, 2004). In the present study, such an observation is recorded in *Andrallus spinidens* (Asopinae), *Apodiphus pilipes, Bagrada picta, Eysarcoris inconspicuous, Halys sulcata, Halys seregera* and *Nezara viridula* (Pentatominae). However, in *Halyomorpha murrea, Nezara graminea* and *Piezodorus rubrofasciatus* (Pentatominae), the nucleoli persist as intact bodies even during diakinesis. Such behavior has been reported in *Carlisis wahlbergi, Acanthocoris sordidus, Eubule sculpta, Spartocera fusca* (Coreidae) and *Coptosoma punctissimum* (Plataspidae) (Yosida, 1947, 1950; Colombo and Bidau, 1985; Fossey and Liebenberg, 1995; Cattani and Papeschi, 2004).

In *Bagrada picta, Eysarcoris inconspicuous, Halys sulcata, Halys seregera, Halyomorpha murrea, Nezara viridula* and *Piezodorus rubrofasciatus* (Pentatominae), the presence of nucleolar bodies have been observed from the interphase cells to the completely differentiated spermatozoa, suggesting the occurrence of protein synthesis throughout spermeiogenesis. During this process, however, variations in their size, shape and location have been recorded, indicating the dynamic functional involvement of nucleolar material during different stages of the process as has been suggested by Souza et al. (2007b). Similar results have been
reported in *Nysius californicus* (Lygaeidae), *Niesthrea sidae* (Rhopalidae), *Hyalymenus sp.* and *Neomegalotomus pallescens* (Alydidae) by Souza et al. (2007b, 2009), in *Triatoma klugi* (Reduviidae) by Costa da et al. (2008) and Souza et al. (2009), in *Euschistus heros* (Pentatomidae) by Souza and Itoyama (2010) and in *Chariesterus armatus* (Coreidae) by Arakaki et al. (2010).

In *Heteroptera*, nucleolar organizer regions have been seen to be associated with the autosomes or the sex chromosomes or both (Papeschi, 1995; Severi-Aguiar et al., 2006). In the present study, silver impregnations have been seen associated only with autosomal bivalents. Similar results are reported in *Belostoma elegans* and *Belostoma dentatum* (Belostomatidae) by Papeschi and Bidau (1985), in *Edessa meditabunda, Antiteuchus mixtus, Antiteuchus sepulcralis* and *Antiteuchus macraspis* (Pentatomidae) by Rebagliati et al. (2003) and Lanzone and Souza (2006b), in *Dysdercus imitator* (Pyrrhocoridae) by Bressa et al. (2003), in *Spartocera fusca* (Coreidae) by Cattani and Papeschi (2004), in *Arachnocoris trinitatis* (Nabidae) by Kuznetsova et al. (2007) and in *Limnogonus aduncus* (Gerridae) by Castanhole et al. (2008). In *Nezara viridula*, however, Camacho et al. (1985) reported NORs to be associated with both the autosomes and the sex chromosomes. This result disagrees with the present observation in *Nezara viridula* where NORs are seen associated only with autosomes.

It has been suggested that CMA3 bright signals correspond to nucleolar organizer regions (Gonzalez-Garcia et al., 1996). In *Eysarcoris inconspicuous*, the largest autosomal bivalent shows silver impregnated region which corresponds to CMA3 bright signal. Similarly, in *Halys sulcata*, silver impregnation on the sex chromosome mass during diffuse stage corresponds to the CMA3 bright signal. Correspondence between CMA3 bright signals and nucleolar organizer regions on the
CYTOLOGICAL MARKERS

Chromosome number and morphology are important parameters to differentiate related species. However, in Pentatomidae, most of the species show constant chromosome number and the chromosomes have no longitudinal differentiation (holocentric chromosomes) by which one chromosome could be distinguished from the other. As a result, it is very difficult to compare their chromosome complements. In such cases, characterization of meiotic behavior of chromosomes provides useful information for species differentiation as the meiotic behavior of different groups of chromosomes (autosomal bivalents, autosomal univalents and sex chromosomes) is differential. Similarly, holokinetic chromosomes provide no morphological markers and in case of symmetrical karyotypes with the same chromosome number, as in most pentatomid species, it is nearly impossible to individualize chromosomes using only non-specific techniques of staining. Differential staining of chromosomes using various techniques thus becomes a necessity to overcome this challenge.

In the present study, differences in cytogenetic features with respect to meiotic behavior of chromosomes, constitutive heterochromatin organization, base sequence specificity of heterochromatic regions and nucleolar behavior during meiosis have been described for three species of *Eysarcoris*, two species of *Halys* and two species of *Nezara* and a few species-specific cytogenetic markers have been identified (Table 1). Such differences have been used as cytogenetic markers to distinguish meiotic behavior of individual chromosomes and to differentiate related species with similar chromosome complements in earlier studies. Perez *et al.* (1997) have used a C-band block in one of the autosomes in *Triatoma infesta* (Reduviidae) to analyze the
behavior of this chromosome during meiosis. On the other hand, Grozeva and Nokkala (2001) distinguished some Tingidae species which are known to have the same number of autosomes (2n=12A+XY/X0) based on the C-banding pattern of chromosomes. Similarly, Rebagliati et al. (2003) described differences between two species of *Edessa* (Pentatomidae) which have similar chromosome complements (2n=12A+XY) based on chiasma frequency, metaphase I arrangement of chromosomes, fluorescent signals and nucleolar behavior. Angus et al. (2004) reported three species of the genus *Notonecta* (Notonectidae) with constant chromosome complement of 2n=22+XY and similar chromosome sizes to have characteristic C-banding pattern of four long autosomes and the X-chromosome. By using C-banding, base specific fluorochrome and silver nitrate staining, Lanzone and Souza (2006a) compared the karyotypes in three species of *Antiteuchus* (Pentatomidae) with similar chromosome complement (2n=12A+XY) and observed differences in size and location of C-bands, fluorescent signals and nature of nucleolar organizer regions. Similarly, Kaur et al. (2010) reported differences in the C-banding pattern of chromosomes in two species of *Dieuches* (Lygaeidae) having similar chromosome complement (2n=8A+2m+XY).
### Table 3: Differences in cytogenetic features of three species of *Eysarcoris*

<table>
<thead>
<tr>
<th>Species</th>
<th>Chromosome Complement</th>
<th>Meiotic behavior</th>
<th>C-banding</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><strong>Diffuse</strong></td>
<td><strong>Dipotene/Diakinesis</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td>High decondensation of autosomes</td>
<td>1 ring bivalent with two chiasmata</td>
</tr>
<tr>
<td><em>Eysarcoris guttiger</em></td>
<td>2n=14=12A+X Y</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eysarcoris inconspicuous</em></td>
<td>2n=14=12A+X Y</td>
<td>High decondensation of autosomes</td>
<td>2 ring bivalents with two chiasmata</td>
</tr>
<tr>
<td><em>Eysarcoris rosaceus</em></td>
<td>2n=14=12A+X Y</td>
<td>Partial decondensation of autosomes</td>
<td>No ring bivalent</td>
</tr>
</tbody>
</table>
### Table 4: Differences in cytogenetic features of two species of *Halys*

<table>
<thead>
<tr>
<th>Species</th>
<th>Chromosome Complement</th>
<th>Meiotic behavior</th>
<th>Fluorescent banding</th>
<th>Ag-NOR banding</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Halys seregera</em></td>
<td>2n=14=12A+XY</td>
<td>High decondensation of autosomes</td>
<td>Autosomes: localized signals overlapping to DAPI/CMA&lt;sub&gt;3&lt;/sub&gt;</td>
<td>2-3 nucleoli</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1-2 ring bivalents with two chiasmata</td>
<td>Sex chromosome mass : with no localized signals</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>All the chromosomes form a ring with an empty center</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Halys Sulcata</em></td>
<td>2n=14=12A+XY</td>
<td>Partial decondensation of autosomes</td>
<td>Autosomes: No localized signals</td>
<td>2 nucleoli</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No ring bivalent</td>
<td>Sex chromosome mass: with localized CMA&lt;sub&gt;3&lt;/sub&gt; positive DAPI negative signal</td>
<td></td>
</tr>
</tbody>
</table>
### Table 5: Differences in cytogenetic features of two species of *Nezara*

<table>
<thead>
<tr>
<th>Species</th>
<th>Chromosome Complement</th>
<th>Meiotic behavior</th>
<th>C-banding</th>
<th>Fluorescent banding</th>
<th>Ag-NOR banding</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nezara</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>graminea</em></td>
<td>2n=14=12A+XY</td>
<td>Partial decondensation of autosomes</td>
<td>Terminal and interstitial C-bands</td>
<td>Autosomes: localized DAPI signals</td>
<td>2-4 nucleolar bodies</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 ring bivalents with two chiasmata</td>
<td></td>
<td>X: DAPI/CMA&lt;sub&gt;3&lt;/sub&gt; negative</td>
<td>Nucleolar bodies associated with all autosomal bivalents</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5 autosomal bivalents, X and Y form a ring, 1 autosomal bivalent outside the ring</td>
<td></td>
<td></td>
<td>Silver impregnations have not been observed beyond metaphase I.</td>
</tr>
<tr>
<td><em>viridula</em></td>
<td>2n=14=12A+XY</td>
<td>High decondensation of autosomes</td>
<td>Terminal C-bands</td>
<td>Autosomes: localized DAPI/CMA&lt;sub&gt;3&lt;/sub&gt; signals</td>
<td>3-6 nucleolar bodies</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1 ring bivalents</td>
<td></td>
<td>X: DAPI negative, CMA&lt;sub&gt;3&lt;/sub&gt; positive</td>
<td>Nucleolar bodies associated with only 1 autosomal bivalent</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6 autosomal bivalents and X form a ring, Y inside the ring</td>
<td></td>
<td></td>
<td>Silver impregnations seen associated with spermatids at posterior region</td>
</tr>
</tbody>
</table>
The order Hemiptera comprises about 80,000 species which are distributed in two suborders: Homoptera and Heteroptera. Approximately 37,000 species distributed in 77 families belong to Heteroptera. Some of the major subfamilies of Heteroptera are Pentatomidae, Reduviidae, Coreidae, Lygaeidae, Miridae, Alydidae and Pyrrhocoridae. Members of the suborder Heteroptera have very distinctive front wings called hemelytra in which the basal half is leathery and the apical half is membranous, and the name Heteroptera comes from this feature. The Heteroptera includes a diverse assemblage of insects that have become adapted to a broad range of habitats: terrestrial, aquatic and semi-aquatic. Terrestrial species are often associated with plants and they feed on vascular tissues or nutrients stored within seeds. Some species are predators on a variety of small arthropods while a few species even feed on the blood of vertebrates. Economically, plant feeding heteropterans are important pests of many crop plants. Predatory species are generally regarded as beneficial as they attack primarily lepidopteran and coleopteran larvae which are important pests in agro systems. Some heteropteran species received attention as potential biological control agents for agricultural pests.

Cytogenetically, members of the suborder Heteroptera form an interesting group due to the presence of unique features. Heteropteran insects possess holocentric chromosomes (chromosomes with diffused centromere) that allow fragments resulting due to fusion and fission to survive during cell division. This has been mentioned as a means of chromosome complement evolution in this group. Heteropterans are also characterized by the presence of a special stage of prophase called the diffuse stage where autosomes decondense while the sex chromosomes remain condensed. Another characteristic feature is the presence of an “inverted meiosis” (Post-reductional
meiosis for sex chromosomes) wherein the autosomes segregate reductionally during anaphase I and equationally during anaphase II while sex chromosomes follow the reverse. In addition, the presence of minute chromosomal bodies called microchromosomes (m-chromosomes) which behave differently from both autosomes and sex chromosomes is also one of the major cytogenetic features of Heteroptera. Chromosome studies in Heteroptera have been limited only to reporting chromosome number and sex determining mechanisms as it is difficult to characterize chromosomes due to their small size and lack of primary constriction. In the last 30 years, differential staining techniques have developed and individual chromosome variations have been used for species differentiation in different groups of Heteroptera. C-banding, fluorescent banding and silver nitrate staining techniques are used to characterize constitutive heterochromatin, sequence specificity of the heterochromatin and nucleolar organizer regions respectively and these techniques reveal species specific cytogenetic markers.

The Pentatomidae is one of the largest families of Heteroptera comprising about 642 genera and 4112 species distributed in eight subfamilies (Pentatominae, Asopinae, Podopinae, Edessinae, Phyllococephalinae, Discocephalinae, Cyrtocorinae and Serbaninae). Regardless of this rich biodiversity, cytogenetic work on Pentatomidae is meager with cytogenetic reports of only less than 400 species. Keeping in mind the economic importance of Pentatomidae and very meager knowledge on its cytogenetic aspects, this group has been selected for the present study in which a comprehensive work has been carried out on the cytogenetics of some representative species of the family by the use of both conventional and modern cytogenetic techniques.

Collection-cum-survey tours were conducted in different localities of Punjab,
Haryana, Himachal Pradesh and Uttarakhand states extending from April 2008 to October 2010 and as many as 23 species belonging to the family Pentatomidae have been collected referable to 3 subfamilies and 19 genera. A few specimens of each species were killed using ethyl-acetate and were stretched, dried and pinned. For cytogenetic investigations, testes were extracted from live male insects in 0.67% saline solution, fixed in Carnoy’s fixative (3:1, Ethyl alcohol: acetic acid) and stored in refrigerator. The fixed material was teased on cleaned slides and the slides were air dried. Air-dried slides were stained with Carbol-fuchsin to study normal chromosomal complement, with Giemsa stain to study C-banding patterns, with fluorescent dyes DAPI and CMA$_3$ to study sequence specificity of the heterochromatic regions and with Silver Nitrate for the study of nucleolar organizer regions (NORs). Prepared slides were scanned and well spread stages were photographed under the microscope (Nikon-Optiphot-2). Slides stained with fluorescent dyes were studied and photographed under Nikon fluorescent microscope using UV filter for DAPI and BV for CMA$_3$. Out of twenty three species investigated, nineteen belong to Pentatominae, three to Asopinae and one to Podopinae. Twelve species have been cytogenetically investigated for the first time. The significant results pertaining to each subfamily are summarized as follows:

**Subfamily: Pentatominae**

Pentatominae is the largest subfamily of Pentatomidae which comprises about 75% (228 of the 294 species) of the species reported for chromosome studies. In the present study, 19 species of Pentatominae have been cytogenetically investigated. Out of these, 10 species (*Aeliomorpha sheanensis*, *Apodiphus pilipes*, *Eysarcoris rosaceous*, *Halys seregera*, *Halys sulcata*, *Halyomorpha murrea*, *Nezara graminea*, *Piezodorus rubrofasciatus*, *Plautia fimbriata* and *Tropicoris punctipes*) are new to the
cytogenetic world. For the rest of the 9 species (Bagrada picta, Carbula scutellata, Dollocoris baccarum, Erthesina fullo, Eurydema pulchrum, Eysarcoris inconspicuous, Nezara viridula and Priassus exemptus), chromosome number and sex mechanism have been reported earlier by different authors, but C-banding pattern, sequence specificity and nucleolar organizer regions have been described for the first time.

Eighteen species out of nineteen have a diploid number of 2n=14=12A+XY while Halyomorpha murrea shows a diploid number of 2n=16=14A+XY. All the presently studied nineteen species of Pentatominae have a sex determining mechanism of XY. However, the size differences between X and Y chromosomes are highly variable among the different species.

The general course of meiosis in all the presently studied species is fairly uniform. In all of them, the autosomes divide reductionally while the sex chromosomes divide equationally during the first meiotic division and just the reverse happens during the second division. However, significant differences in the meiotic behavior of chromosomes with regard to degree of decondensation of autosomes and association between X and Y during diffuse stage, presence or absence of ring bivalents during diplotene/diakinesis and arrangement of chromosomes during metaphase I.

The diffuse stage has been a common meiotic feature in Heteroptera during which autosomes are decondensed, sex chromosomes are condensed and cell size increases. Degree of decondensation of autosomes is variable in different species of Heteroptera. During the present investigation, 11 species viz., Carbula scutellata, Eurydema pulchrum, Eysarcoris inconspicuous, Halys seregera, Halys sulcata, Halyomorpha murrea, Nezara viridula, Piezodorus rubrofasciatus, Eysarcoris
guttiger, Priassus exemptus and Tropicoris punctipes show high degree of
decondensation of the autosomes during diffuse stage. In Plautia fimbriata, Erthesina
fullo and Bagrada picta, decondensation is almost complete while in Aeliomorpha
sheanensis, Apodiphus pilipes, Doliocoris baccarum, Eysarcoris rosaceous and
Nezara graminea, the autosomes show partial decondensation.

In Pentatomidae, sex chromosomes usually associate during the diffuse stage.
Variations with respect to degree of association between X and Y have been recorded.
In 14 species (Aeliomorpha sheanensis, Apodiphus pilipes, Bagrada picta, Carbula
scutellata, Dolicoris baccarum, Eurydema pulchrum, Eysarcoris guttiger, Eysarcoris
inconspicuous, Halys seregera, Halys sulcata, Halyomorpha murrea, Nezara
graminea, Nezara viridula and Plautia fimbriata), X and Y fuse to form a single
heteropycnotic body while in 5 species (Erthesina fullo, Eysarcoris rosaceous,
Piezodorus rubrofasciatus, Priassus exemptus and Tropicoris punctipes), X and Y
remain separated at the diffuse stage.

In Heteroptera, in general and in Pentatomidae, in particular, the general trend
is the predominance of one chiasma per bivalent during diplotene/diakinesis.
However, in the present study, 14 species (Aeliomorpha sheanensis, Bagrada picta,
Carbula scutelata, Dolicoris baccarum, Eysarcoris guttiger, Halys seregera, Nezara
graminea, Nezara viridula, Piezodorus rubrofasciatus, Plautia fimbriata, Apodiphus
pilipes, Eurydema pulchrum and Halyomorpha murrea) show more than one chiasma
per bivalent and only five species (Erthesina fullo, Eysarcoris rosaceous, Halys
sulcata, Priassus exemptus and Tropicoris punctipes) lack any ring bivalent and
possess only single chiasma per bivalent.

In most of the Pentatomidae species, metaphase-I is characterized by a ring of
autosomal bivalents in the centre of which lie the X and Y univalents. However, in the
presently studied Pentatominae species, this trend has been observed only in four species (*Bagrada picta, Erthesina fullo, Piezodorus rubrofasciatus* and *Tropicoris punctipes*) and in the rest of the species (*Aeliomorpha sheanensis, Apodiphus pilipes, Carbula scutellata, Dolocoris baccarum, Eurypedema pulchrum, Eysarcoris guttiger, Eysarcoris rosaceous, Eysarcoris inconspicuous, Halys seregera, Halys sulcata, Halyomorpha murrea, Nezara graminea, Nezara viridula, Plautia fimbriata and Priassus exemptus*), deviations from this trend have been observed.

Similarly, major differences in differential staining patterns have been observed. Sixteen species of Pentatominae (*Apodiphus pilipes, Bagreda picta, Erthesina fullo, Aeliomorpha sheanensis, Dolocoris baccarum, Eurypedema pulchrum, Eysarcoris inconspicuous, Halyomorpha murrea, Nezara graminea, Nezara viridula, Plautia fimbriata, Eysarcoris guttiger, Eysarcoris rosaceous, Carbula scutelata, Halys sulcata, Piezodorus rubrofasciatus*) have been subjected to C-banding. Autosomal bivalents of all the species except *Piezodorus rubrofasciatus* show C-bands. The results show a heterogeneous C-banding pattern with respect to the location, amount and the number of chromosomes having C-bands. In general, terminal, sub-terminal or interstitial C-bands have been observed. The amount of constitutive heterochromatin has been seen to vary from very thin arrays to thick blocks in different species studied. Similarly, the number of chromosomes showing C-bands ranges from species with no C-banded chromosome to those species which have C-bands in all the chromosomes. Sex chromosomes (X and Y) also show heterogeneous C-banding pattern, being C-positive in some species and C-negative in others.

Ten species of Pentatominae (*Aeliomorpha sheanensis, Eysarcoris inconspicuous, Eurypedema pulchrum, Halys seregera, Halys sulcata, Halyomorpha...*)
murrea, Nezara graminea, Nezara viridula, Piezodorus rubrofasciatus and Plautia fimbriata) have been subjected to fluorescent banding. In almost all of the species investigated, one or more of the chromosomes show homogenous staining which overlaps for both DAPI/CMA3. Besides, a few localized DAPI signals are observed in one or more of the autosomal bivalents in some species while in others, a few localized CMA3 signals have been seen, and in some species, overlapping DAPI/CMA3 signals which correspond to C-positive regions are observed. Similar type of heterogeneity to fluorescent banding has also been observed for the sex chromosomes.

Nine species of Pentatominae (Apodiphus pilipes, Bagrada picta, Eysarcoris inconspicuous, Halys sulcata, Halys seregera, Halyomorpha murrea, Nezara graminea, Nezara viridula, Piezodorus rubrofasciatus) have been subjected to Silver Nitrate staining. In most of these species, nucleolar bodies start appearing since interphase cells. The number and size of these bodies have been found to vary, sometimes even within the same species. In the later stages, these nucleolar bodies associate to form one or more nucleoli. During diplotene/metaphase I, silver impregnations have been seen associated only with autosomal bivalents in all the species studied. Sex chromosomes are conspicuously free of nucleolar bodies in Pentatominae. In some species, nucleolar bodies have been observed in completely differentiated spermatozoa also and their size, shape and location within the sperm head are variable.

Subfamily: Asopinae

The Asopinae is a subfamily of predatory bugs comprising 63 genera and 357 species and some of them are important agents of biological control. However, only 22 species have been cytogenetically investigated so far.
Three species of Asopinae (*Andrallus spinidens*, *Canthecona furcellata* and *Perillus bioculatus*) have been investigated all possessing a diploid chromosome number of 14 and XY male sex mechanism. Cytogenetic results of *Andrallus spinidens* and *Canthecona furcellata* are reported for the first time.

The three species show variations in degree of decondensation of autosomes during the diffuse stage. *Andrallus spinidens* and *Canthecona furcellata* show high degree of decondensation while *Perillus bioculatus* shows partial decondensation of autosomes. Similarly, differences in the number of ring bivalents have been observed. In *Canthecona furcellata* and *Perillus bioculatus*, two to three ring bivalents have been observed while in *Andrallus spinidens*, a single ring bivalent has been commonly seen. All the three species show the regular arrangement of chromosomes typical of the family Pentatomidae at metaphase I plate. However, in *Canthecona furcellata* and *Perillus bioculatus*, additional arrangement patterns of chromosomes have also been observed.

Two species (*Andrallus spinidens* and *Perillus bioculatus*) have been subjected to C-banding. In *Andrallus spinidens*, only terminal C-bands have been observed while both terminal and interstitial C-bands are seen in *Perillus bioculatus*. A complete contrast has been seen on the C-banding pattern of X-chromosome in the two species. X is completely heterochromatic in *Perillus bioculatus* while it is completely C-negative in *Andrallus spinidens*. Y-chromosome is observed to be C-negative for both the species.

In *Canthecona furcellata*, autosomal bivalents show both DAPI/CMA<sub>3</sub> localized signals while in *Perillus bioculatus*, all autosomal bivalents are homogeneously positive to both DAPI/ CMA<sub>3</sub> except one autosomal bivalent which shows a CMA<sub>3</sub> localized signal. X and Y are both DAPI/ CMA<sub>3</sub> positive in
Summary

*Canthecona furcellata* but DAPI-negative/ CMA$_3$ positive in *Perillus bioculatus*.

**Subfamily: Podopinae**

Regardless of the presence of 255 described species, cytogenetic report on Podopinae is restricted only to 10 species so far. One species (*Podops inuncta*) is investigated cytogenetically which shows a diploid number of 14 and XY male sex system. Autosomes are decondensed highly while the sex chromosomes exist as two condensed heteropycnotic bodies during the diffuse stage. Two ring bivalents with two chiasmata each are present at diplotene. A definite arrangement at metaphase I has been observed which, however, differs from the typical arrangement described for Pentatomidae.

Five autosomal bivalents show terminal and interstitial C-bands while one autosomal bivalent is C-negative. Both X and Y chromosomes are C-positive. All the C-positive regions of the autosomal bivalents have been seen to be overlapping for DAPI/CMA$_3$ while one autosomal bivalent is negative to both the stains. X-chromosome is DAPI/CMA$_3$ positive and Y chromosome is negative to both DAPI and CMA$_3$.

In this study, chromosome number, sex mechanism and behavior of chromosomes during meiosis in 12 species have been described for the first time and thus are new to the cytogenetic world. Besides, through differential banding, the present study has added C-banding pattern of 17 species, sequence specificity of heterochromatin in 12 species and localization of nucleolar organizer regions in 9 species for the first time. Based on all these results, some previous suggestions regarding heteropteran meiosis have been confirmed and some new suggestions have been forwarded. Besides, some species specific cytogenetic markers have been identified for two species of *Halys*, two species of *Nezara* and three species of *Eysarcoris*. 

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