*Journal of Biological Research-Thessaloniki* **18**: 235–248, 2012
*J. Biol. Res.-Thessalon.* is available online at http://www.jbr.gr
Indexed in: WoS (Web of Science, ISI Thomson), SCOPUS, CAS (Chemical Abstracts Service) and DOAJ (Directory of Open Access Journals)

# First cytogenetic report on seven species of Coreidae (Heteroptera) with a bibliographic review of chromosomal data

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Received: 12 October 2011 Accepted after revision: 6 February 2012

Seven species of Coreidae from North India have been described for their chromosome number and course of meiosis in males for the first time. These include six species of Coreinae *viz. Acanthocoris anticus* Walker (Acanthocorini)*, Anhomoeus sulcatus* (Distant) (Anhomoeini)*, Cletomorpha raja* Distant*, Cletus pallescens* Walker (Gonocerini)*, Anoplocnemis compressa* Dallas*, Ochrochira aberrans* (Distant) (Mictini) and one of Pseudophloeinae – *Clavigralla scutellaris* (Westwood) (Clavigrallini). In six Coreinae species, diploid chromosome number ranged from 16 to 24, microchromosomes were present in four and absent in two, while sex mechanism was X0 and $X_1X_20$ (in three each). $X_1$ and $X_2$, wherever present, remained closely associated during meiosis. In one species of Pseudophloeinae, diploid number was $13 = 10A + 2m + X0$. In all species, arrangement of chromosomes at metaphase I and II was typical of coreid type. In *A. anticus*, however, a few metaphase I plates were observed with an alternate arrangement. During anaphase II, sex chromosomes moved to one of the poles as laggard in all species. With seven more species added in the present study, the total number of cytogenetically known species becomes 123. Also, this is the first ever cytogenetic report on any species of the tribe Anhomoeini.

**Key words**: Heteroptera, Coreidae, India, chromosomes.

## INTRODUCTION

The suborder Heteroptera comprises 73 families with more than 50000 described species (Meyer, 2005). It is one of the most important insect groups because most of its species are pests and disease transmitters, inflicting damage on crops, forests and orchards (Schuh & Slater, 1995; Schaefer & Panizzi, 2000). Pentatomidae, Coreidae, Lygaeidae, Reduviidae and Miridae are some of its major families. The family Coreidae includes 2200 species belonging to 500 genera distributed throughout the world (Dursun & Fent, 2009). Coreidae is divided into 4 subfamilies: Coreinae, Pseudophloeinae, Meropachydinae and Agriopocorinae. Coreinae are distributed worldwide and are the most abundant in tropics. Pseudophloeinae is distributed predominantly in the Old World while Meropachydinae and Agriopocorinae are rarely found and only a few genera for each subfamily are known (Schuh & Slater, 1995). Coreids are phytophagous and the majority of them live on plants above the ground feeding on the plant vascular system.

Cytogenetically, Coreidae is characterized by the presence of a pair of microchromosomes and absence of Y-chromosome [besides having holocentric chromosomes and post-reductional behavior of sex chromosomes (heteropteran features)]. However, some members lack a pair of microchromosomes, while a few have Y-chromosome (three species of genus *Metapodius*). Autosomal fusions and both autosomal and sex chromosome fragmentations have been considered to be the key mechanisms for karyotype evolution in this group while other chromosome rearrangements, such as inversions and reciprocal translocations have rarely been reported (Ueshima, 1979; Manna, 1984; Thomas, 1987; Papeschi & Mola, 1990).

The previous cytogenetic data on Coreidae reveals 116 species to be cytogenetically known worldwide (see online supplementary material, Table S1). These include 112 species belonging to 50 genera falling in 17 tribes of the subfamily Coreinae and four species belonging to three genera falling in two tribes

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of the subfamily Pseudophloeinae. Due to limited availability, cytogenetic data for Agriopocorinae and Meropachydinae is not available. From India, 33 species of family Coreidae have been cytogenetically analyzed previously (Manna, 1951; Dutt, 1957; Parshad, 1957a, b, 1958; Banerjee, 1958; Das, 1958; Jande, 1959; Manna & Deb Mallick, 1981; Dey & Wangdi, 1985, 1988, 1990; Satapathy & Patnaik, 1989; Satapathy *et al*., 1990; Kaur *et al*., 2006; Kaur, 2007). In the present paper, chromosomes and their meiotic behavior in seven Coreidae species from India has been described for the first time. These include six species of Coreinae and one species of Pseudophloeinae. Also, the entire chromosomal data until today has been tabulated and trends in coreid cytogenetics have been outlined.

## MATERIALS AND METHODS

Coreids are known for their host specificity (Schaefer & Mitchell, 1983). Adults of *Cletomorpha raja* Distant were collected from wild *Achyranthes* plants growing in Forest Research Institute, Dehradun (Uttarakhand). Adults of *Acanthocoris anticus* Walker were found voraciously feeding on *Calotropis* plants. *Anhomoeus sulcatus* (Distant) was collected from *Dalbergia* plants growing extensively in the regions of Punjab. *Clavigralla scutellaris* (Westwood) was found feeding on legumes in Punjab while *Anoplocnemis compressa* Dallas, *Ochrochira aberrans* (Distant) and *Cletus pallescens* Walker were found feeding on wild plants in the regions of Uttarakhand and Punjab. Male specimens (Table 1) of the collected species were dissected live in 0.67% saline and gonads were fixed in Carnoy's fixative. Slides were prepared by air-dried technique and stained in carbol fuchsin (Carr & Walker, 1961).

## RESULTS

### *Coreinae*

a) Acanthocorini

*Acanthocoris anticus* Walker (Fig. 1)

The diploid complement of *Acanthocoris anticus* Walker was $2n = 24 = 22A + X_1X_20$. Diffuse stage reveals two darkly stained X-chromosomes ($X_1$ and $X_2$) of unequal size against highly decondensed chromatin (Fig. 1A). At diplotene, 11 autosomal bivalents and fused sex chromosomes were observed (Fig. 1B). Each autosomal bivalent showed one chiasma. At diakinesis, $X_1$ and $X_2$ became distinct but remained closely associated (Fig. 1C). At metaphase I, two types of plates were observed. In one, all the autosomal bivalents form a ring and $X_1X_2$ lie outside the ring while in the other, one or two autosomal bivalents lie within the ring formed by rest of the bivalents and $X_1X_2$ lie outside the ring (Fig. 1D, E). At metaphase II, $X_1X_2$ lie away from autosomes (Fig. 1F). At anaphase II, $X_1X_2$ were seen moving laggardly towards one of the poles (Fig. 1G).

TABLE 1. Chromosome complements of species investigated

| Species | Number of insects studied | 2n | Chromosome Complement |
|---|---|---|---|
| COREINAE | | | |
| **Acanthocorini** | | | |
| *Acanthocoris anticus* Walker | 7 | 24 | $22A + X_1X_20$ |
| **Anhomoeini** | | | |
| *Anhomoeus sulcatus* (Distant) | 7 | 21 | 18A + 2m + X0 |
| **Gonocerini** | | | |
| *Cletomorpha raja* Distant | 6 | 20 | $16A + 2m + X_1X_20$ |
| *Cletus pallescens* Walker | 7 | 18 | $14A + 2m + X_1X_20$ |
| **Mictini** | | | |
| *Anoplocnemis compressa* Dallas | 6 | 16 | $14A + X_1X_20$ |
| *Ochrochira aberrans* (Distant) | 2 | 21 | 18A + 2m + X0 |
| PSEUDOPHLOEINAE | | | |
| **Clavigrallini** | | | |
| *Clavigralla scutellaris* (Westwood) | 4 | 13 | 10A + 2m + X0 |

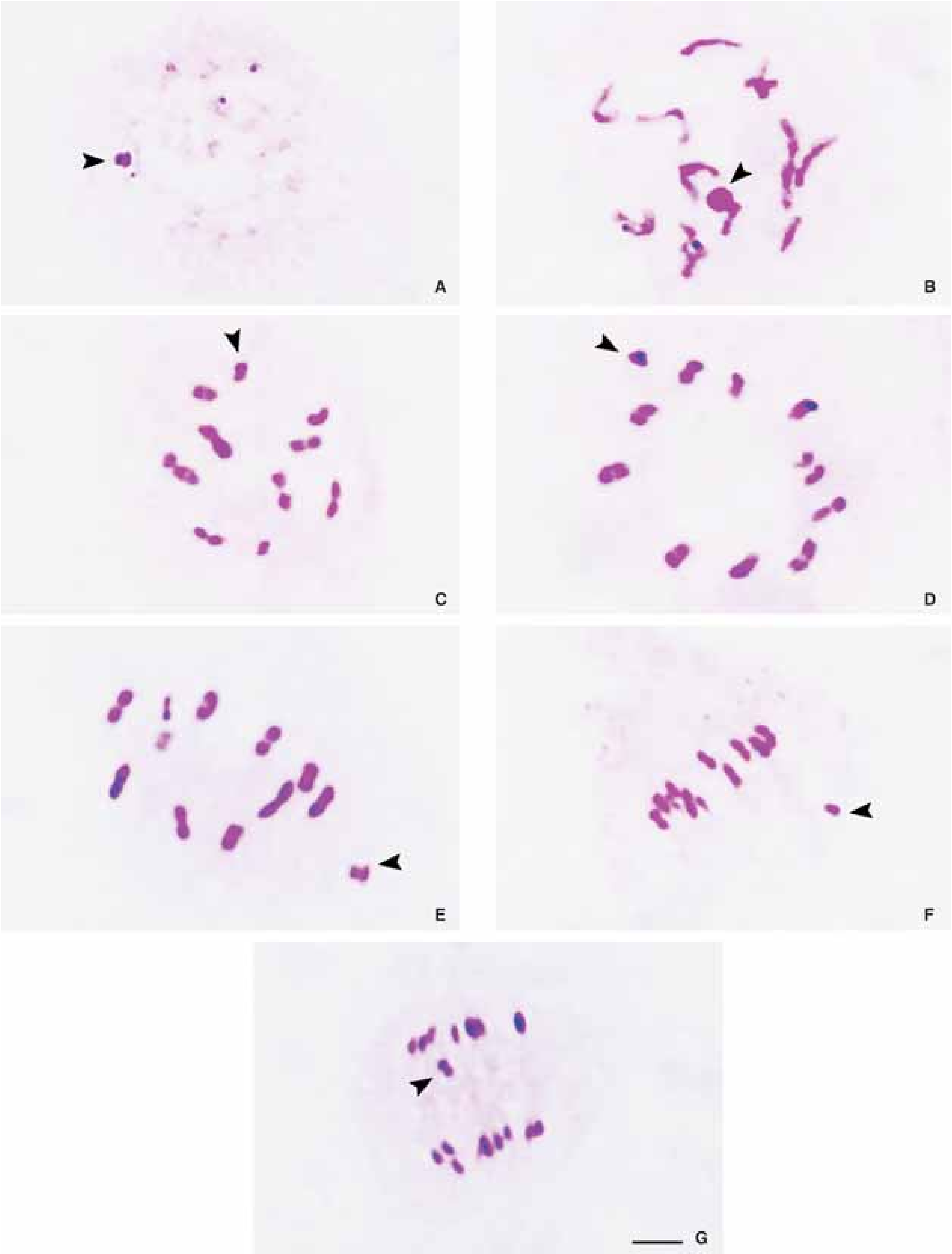

FIG. 1. *Acanthocoris anticus* ($2n = 24 = 22A + X_1X_2 0$): (A) Diffuse stage showing unequal $X_1$ and $X_2$; (B) Diplotene showing 11 autosomal bivalents and fused $X_1X_2$; (C) Diakinesis showing closely associated but distinct $X_1X_2$; (D) Metaphase I showing all the autosomal bivalents forming a ring; (E) Metaphase I showing two autosomal bivalents within the ring; (F) Metaphase II showing $X_1X_2$ lying away from autosomes; (G) Anaphase II showing $X_1X_2$ as a laggard.
Arrowheads indicate $X_1X_2$. Bar = 10 μm.

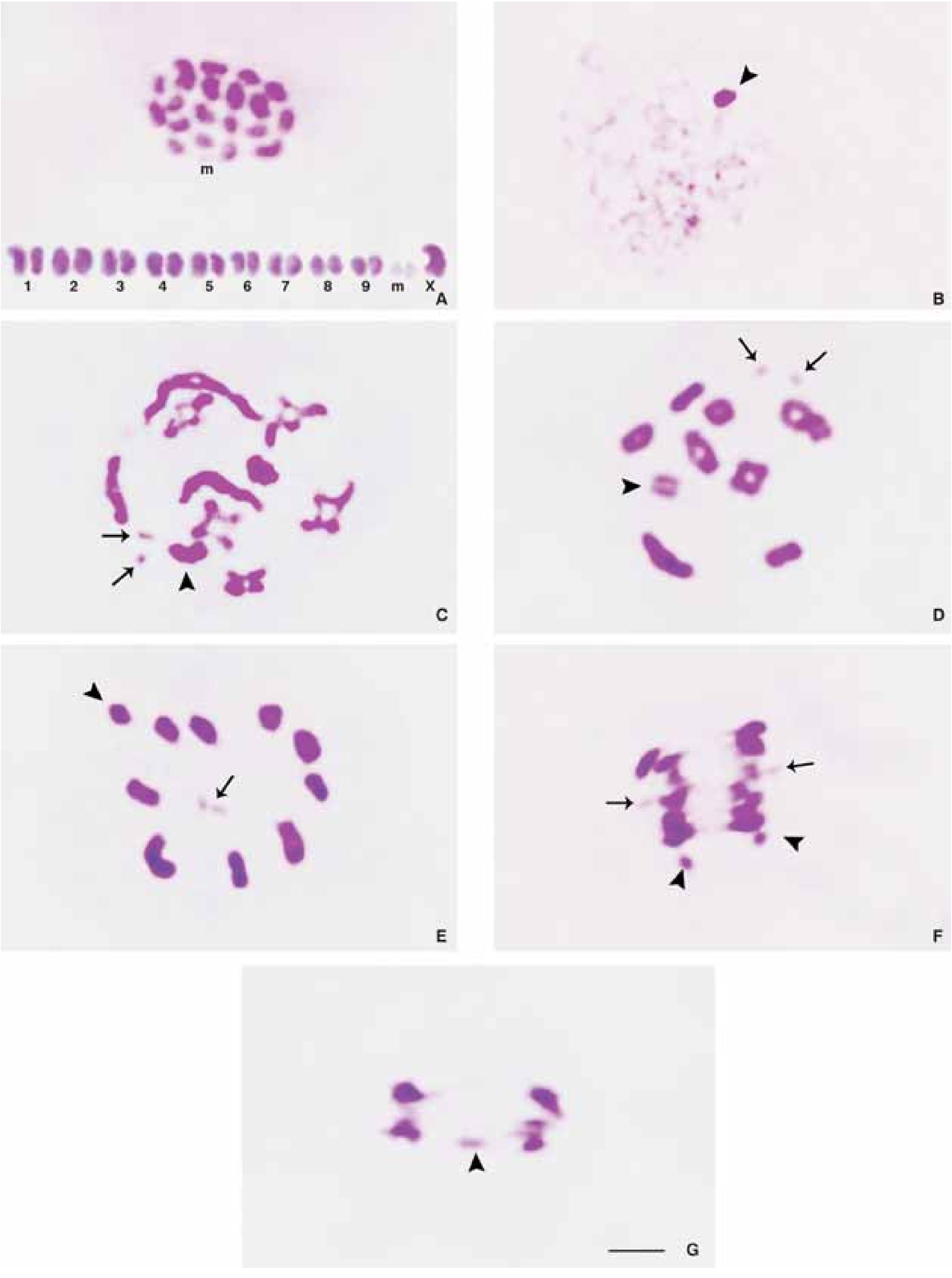

FIG. 2. *Anhomoeus sulcatus* (2n = 21 = 18A + 2m + X0): (A) Spermatogonial metaphase with karyotype; (B) Diffuse stage; (C) Diplotene showing one chiasma per autosomal bivalent and closely placed microchromosomes; (D) Diakinesis showing distinctly bipartite X; (E) Metaphase I showing m-pseudobivalent in the centre and X outside the ring formed by autosomal bivalents; (F) Anaphase I showing equational division of X chromosome; (G) Anaphase II showing X as a laggard. Arrows point to microchromosomes. Arrowheads indicate X chromosome. Bar = 10 μm.

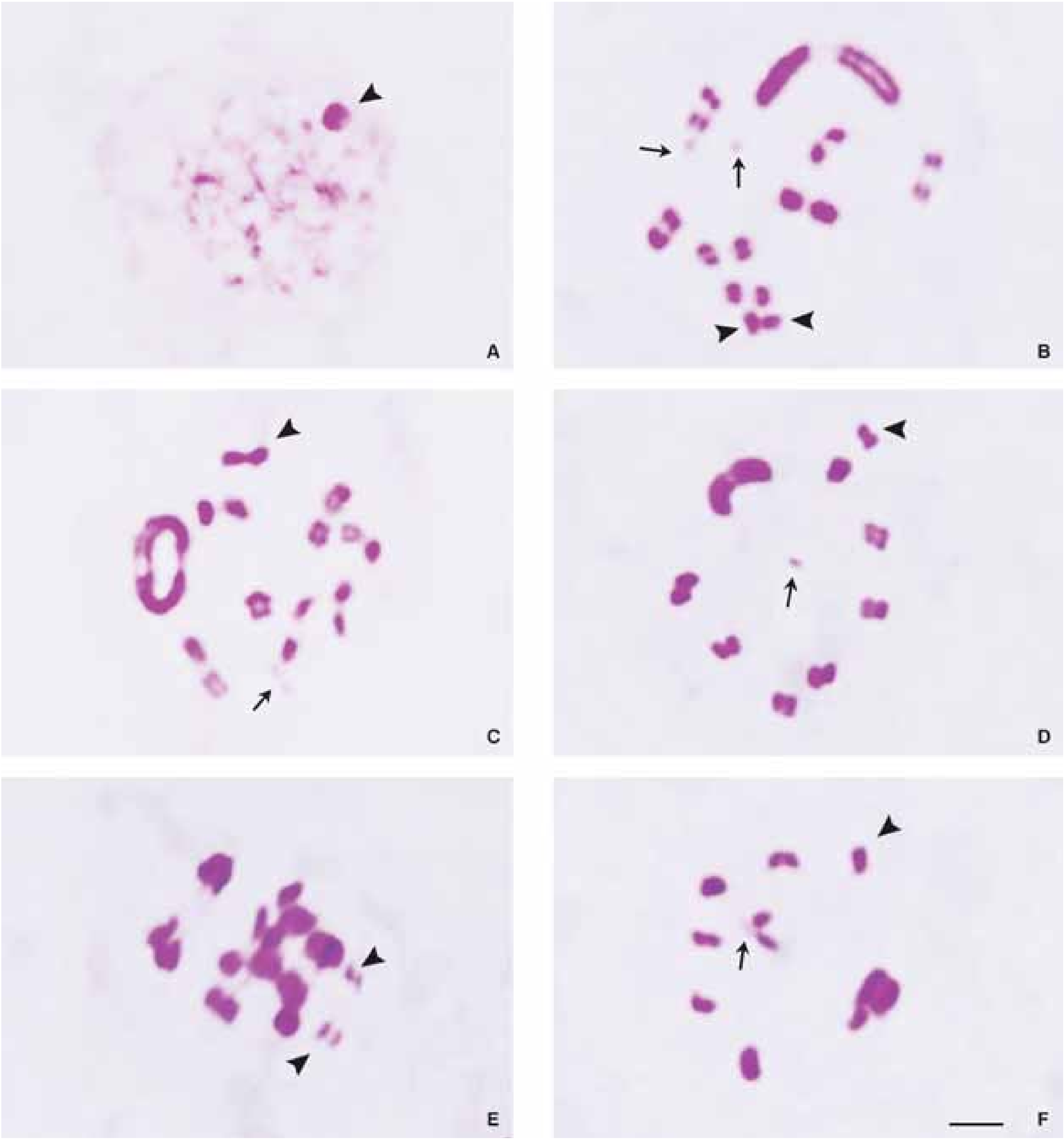

FIG. 3. *Cletomorpha raja* (2n = 20 = 16A + 2m + $X_1X_2$0): (A) Diffuse stage; (B) Diplotene showing all bivalents with single terminal chiasma each; (C) Diplotene showing largest bivalent with 2 terminal chiasmata; (D) Metaphase I showing m-pseudobivalent in the centre and $X_1X_2$ outside the ring formed by autosomal bivalents; (E) Anaphase I showing equational division of $X_1$ and $X_2$; (F) Metaphase II showing 7 autosomes forming a ring with 1 autosome and microchromosome lying in the centre and $X_1X_2$ lying outside the ring. Arrows point to microchromosomes. Arrowheads indicate $X_1X_2$. Bar = 10 µm.

### b) Anhomoeini

#### *Anhomoeus sulcatus* (Distant) (Fig. 2)

Spermatogonial metaphase of *Anhomoeus sulcatus* (Distant) revealed 18 autosomes, 2 microchromosomes and X chromosome (Fig. 2A). At diffuse stage, X chromosome lies at the periphery of highly condensed chromatin (Fig. 2B). During diplotene, one chiasma per autosomal bivalent is present which was terminal, sub-terminal or interstitial. Microchromosomes lie closely placed (Fig. 2C). During diakinesis, X appeared distinctly bipartite (Fig. 2D). During metaphase I, autosomal bivalents formed a ring with terminally associated m-pseudobivalent lying in the centre and X outside the ring (Fig. 2E). During anaphase I, X-chromosome divided equationally (Fig. 2F). During anaphase II, X-chromosome was observed moving towards one of the poles as a laggard (Fig. 2G).

c) Gonocerini

*Cletomorpha raja* Distant (Fig. 3)

The diploid complement of *Cletomorpha raja* Distant is $2n = 20 = 16A + 2m + X_1X_2 0$. At the diffuse stage, darkly stained X-chromosome was observed lying at the periphery of highly decondensed chromatin (Fig. 3A). At diplotene, in some plates, all autosomal bivalents showed single terminal chiasma each, whereas in others, the largest bivalent formed a ring with two terminal chiasmata (Fig. 3B, C). At metaphase I, all autosomal bivalents formed a ring with microchromosomes lying in the centre and $X_1X_2$ lying outside the ring (Fig. 3D). Two equationally dividing sex chromosomes can be seen moving towards two poles during anaphase I (Fig. 3E). At metaphase II, seven autosomes formed a ring with one autosome and microchromosome lying in the centre and $X_1X_2$ lying outside the ring (Fig. 3F).

*Cletus pallescens* Walker (Fig. 4)

The diploid chromosome complement of *Cletus pallescens* Walker is $2n = 14A + 2m + X_1X_2 0$. At the diffuse stage, closely associated $X_1$ and $X_2$ were observed lying at the periphery of highly decondensed autosomes (Fig. 4A). At diplotene, 2-3 ring bivalents were observed (Fig. 4B). Two pairs of autosomal bivalents were seen to be distinctly larger than the rest. During diakinesis, microchromosomes tend to move closer to each other (Fig. 4C). At metaphase I and metaphase II, the autosomal bivalents were arranged in a ring with microchromosomes lying within the ring and closely associated $X_1$ and $X_2$ lying outside the ring (Fig. 4D, E). During anaphase II, fused $X_1$ and $X_2$ move towards one of the poles as a laggard (Fig. 4F). X-chromosome is seen being added to one of the poles at telophase II (Fig. 4G).

d) Mictini

*Anoplocnemis compressa* Dallas (Fig. 5)

Prometaphase stage reveals 14 autosomes and 2 sex chromosomes ($X_1$ and $X_2$) (Fig. 5A). At diplotene, two pairs of autosomes appear distinctly larger than the rest. $X_1$ and $X_2$ are unequal in size and remain closely associated. Each autosomal bivalent shows single chiasma which is terminal, sub-terminal or interstitial (Fig. 5B, C). At metaphase I and II, autosomes form a ring with fused $X_1X_2$ lying outside the ring (Fig. 5D, F). Anaphase I (Fig. 5E) reveals reductional division of autosomes and equational division of X chromosomes while during telophase II, fused $X_1X_2$ body acts as laggard and is seen moving towards one of the poles (Fig. 5G).

*Ochrochira aberrans* (Distant) (Fig. 6)

The diploid chromosome complement of *Ochrochira aberrans* (Distant) is $2n = 18A + 2m + X0$. Diffuse stage revealed darkly stained X-chromosome lying against decondensed chromatin (Fig. 6A). At diplotene, single chiasma per bivalent is present. Microchromosomes appear constricted and lie well apart (Fig. 6B). They are comparatively larger than observed in other coreids and can be visualized throughout the course of meiosis. At metaphase I, autosomal bivalents form a ring with microchromosomes lying in the centre and X lying outside the ring (Fig. 6C). During anaphase I, X divides equationally while during anaphase II, X divides reductionally and moves as a laggard towards one of the poles (Fig. 6D, E).

*Pseudophloeinae*

a) Clavigrallini

*Clavigralla scutellaris* (Westwood) (Fig. 7)

The diploid chromosome complement of *Clavigralla scutellaris* (Westwood) is $2n = 13 = 10A + 2m + X0$. Diffuse stage reveals darkly stained X-chromosome lying against decondensed chromatin (Fig. 7A). During diplotene, each autosomal bivalent shows single chiasma, X appears distinctly bipartite and microchromosomes are faintly stained (mostly untraceable) (Fig. 7B). Autosomal bivalents form a ring during metaphase I with microchromosomes (just a speck) lying within and X chromosome lying outside the ring (Fig. 7C). During metaphase II, X chromosome lies far away from the autosomal group and is seen moving towards one of the poles as a laggard during anaphase II (Fig. 7D, E).

## DISCUSSION

In the presently studied six species of Coreinae, diploid number varies from 16 to 24. Variations are

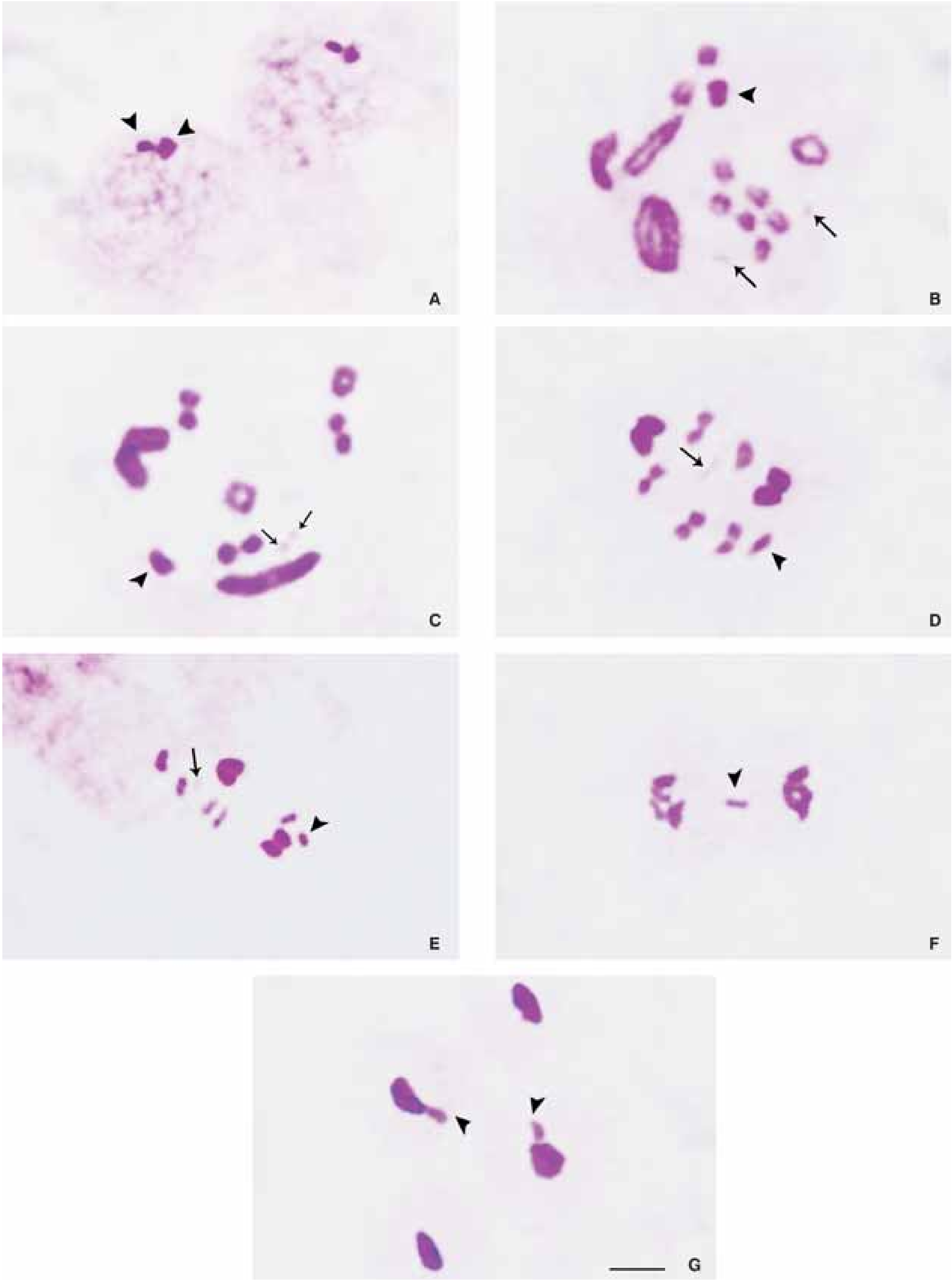

FIG. 4. *Cletus pallescens* (2n = 18 = 14A + 2m + $X_1X_2$0): (A) Diffuse stage; (B) Diplotene showing two ring bivalents; (C) Diakinesis showing closely placed microchromosomes; (D) Metaphase I showing m-pseudobivalent in the centre and $X_1X_2$ outside the ring formed by autosomal bivalents; (E) Metaphase II; (F) Anaphase II showing $X_1X_2$ as laggard; (G) Telophase II. Arrows point to microchromosomes. Arrowheads indicate $X_1X_2$. Bar = 10 μm.

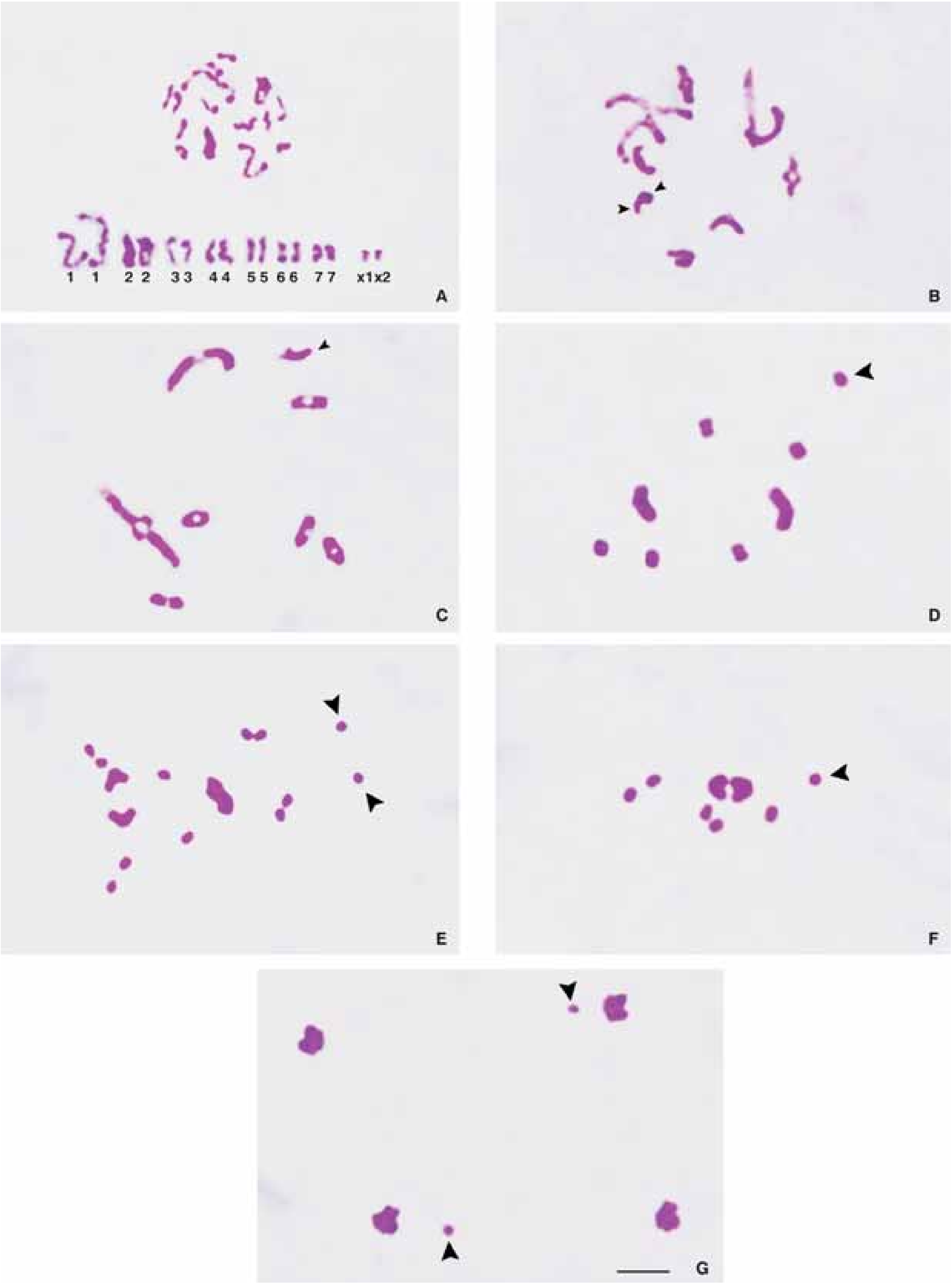

FIG. 5. *Anoplocnemis compressa* ($2n = 16 = 14A + X_1X_20$): (A) Prometaphase with karyotype; (B, C) Diplotene showing each autosomal bivalent with single chiasma and fused $X_1X_2$; (D) Metaphase I showing fused $X_1X_2$ lying outside the ring of autosomal bivalents; (E) Anaphase I showing reductional division of autosomes and equational division of sex chromosomes; (F) Metaphase II showing fused $X_1X_2$ lying outside the ring of autosomal bivalents; (G) Telophase II showing X as a laggard. Arrowheads indicate $X_1X_2$. Bar = 10 μm.

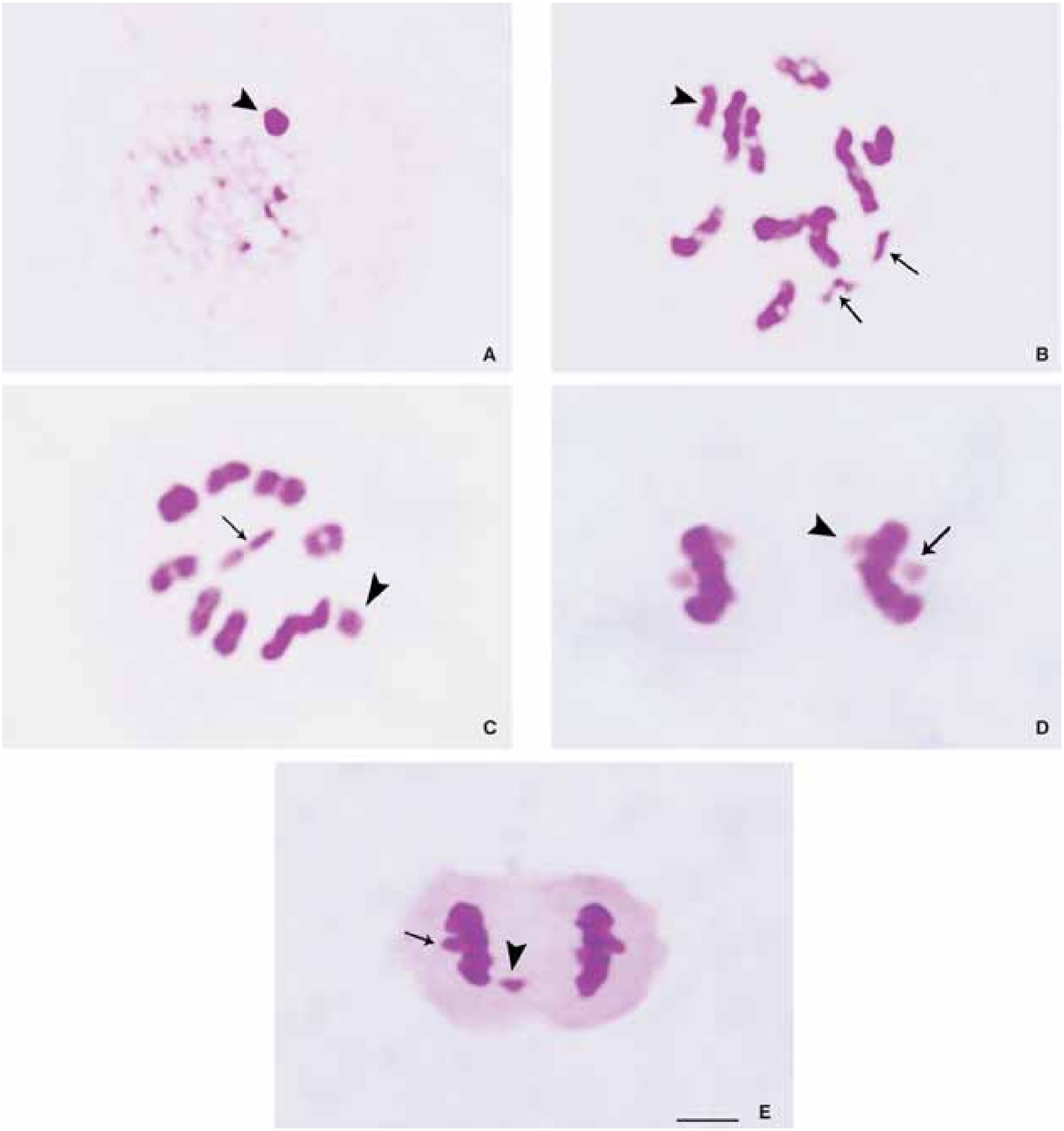

FIG. 6. *Ochrochira aberrans* (2n = 21 = 18A + 2m + X0): (A) Diffuse stage; (B) Diplotene showing autosomal bivalents with single chiasma each and constricted microchromosomes; (C) Metaphase I showing m-pseudobivalent lying in the centre and X outside the ring formed by autosomal bivalents; (D) Anaphase I showing reductional division of autosomes and microchromosomes and equational division of X chromosome; (E) Anaphase II showing X as a laggard. Arrows point to microchromosomes. Arrowheads indicate X chromosome. Bar = 10 μm.

with respect to number of autosomes and X chromosome, and presence or absence of microchromosomes. Y chromosome is absent in all studied species. In species with nine pairs of autosomes [*Ochrochira aberrans* (Distant) of Mictini and *Anhomoeus sulcatus* (Distant) of Anhomoeini], there are gradual size variations in autosomes. In species with eight pairs of autosomes (*Cletomorpha raja* Distant), one pair of autosomes is distinctly large while in species with seven pairs of autosomes (*Anoplocnemis compressa* Dallas and *Cletus pallescens* Walker), two pairs of autosomes are distinctly large. Presence of extremely large pair of autosomes in species with reduced number of autosomes suggested that their origin is due to autoso-

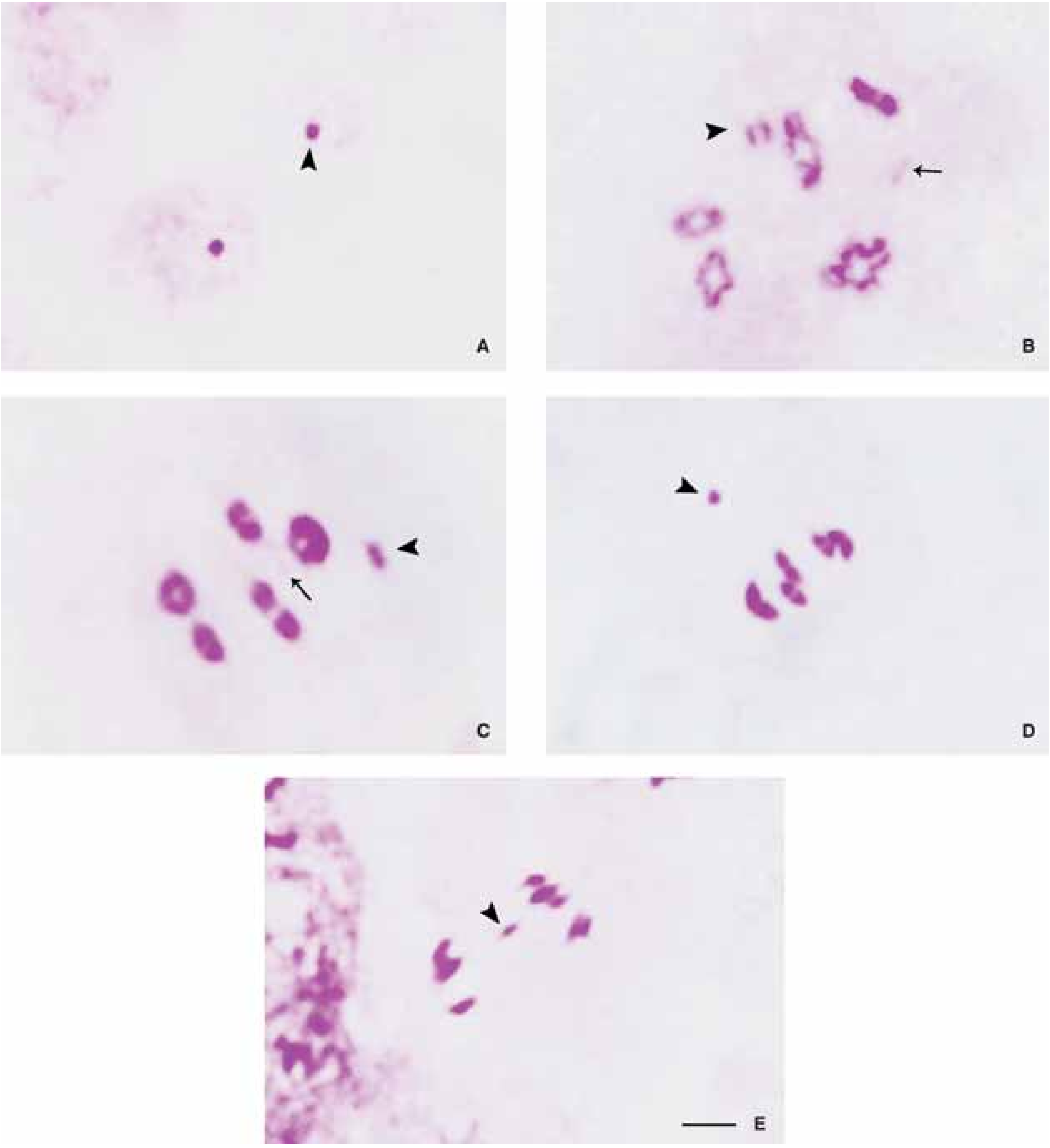

FIG. 7. *Clavigralla scutellaris* (2n = 13 = 10A + 2m + X0): (A) Diffuse stage; (B) Diplotene showing autosomal bivalents with single chiasma each and distinctly bipartite X; (C) Metaphase I showing faintly stained m-pseudobivalent lying in the centre and X outside the ring formed by autosomal bivalents; (D) Metaphase II showing X chromosome lying far away from autosomes; (E) Anaphase II showing X as a laggard. Arrows point to microchromosomes. Arrowheads indicate X chromosome. Bar = 10 µm.

mal fusion/s as 2n = 21 (with nine pairs of autosomes, two microchromosomes and X0 sex mechanism) is considered to be the modal number of Coreidae; other numbers are thought to have deviated from this number by fragmentations and fusions (Leston, 1956; Ueshima, 1979; Sands, 1982). In *Acanthocoris anticus* Walker, autosome number is increased to 11 pairs, all with minor variations in size, suggesting fragmentation of autosomes.

Four species *viz. Acanthocoris anticus* Walker*, Anoplocnemis compressa* Dallas, *Cletomorpha raja* Distant and *Cletus pallescens* Walker show $X_1X_2$0 sex-mechanism while two others, *Anhomoeus sulcatus* (Distant) and *Ochrochira aberrans* (Distant) have X0.

Sex chromosome mechanism with multiple X is thought to have originated through fragmentation of ancestral X (Papeschi & Bressa, 2006).

Cytogenetically, Coreidae is characterized by the presence of microchromosomes with a few exceptions. During the present study, a pair of microchromosomes has been found to be present in four and absent in two species. When present, they remain as univalents during diplotene and subsequently associate to form a pseudobivalent that is placed in the centre of the autosomal ring at metaphase I. In *Ochrochira aberrans* (Distant), microchromosomes are exceptionally large, almost equal to the smallest autosome but can be easily distinguished from the latter through their meiotic behavior. Similar observations have been reported in *Ochrochira rubrotincta* (Miller) by Sands (1982). In *Acanthocoris anticus* Walker and *Anoplocnemis compressa* Dallas, microchromosomes are absent as has earlier been reported in *Acanthocoris scabrator* (Fabricius) and *Anoplocnemis phasiana* Fabricius (Manna, 1951; Sands, 1982; Dey & Wangdi, 1990). However, these are present in *Acanthocoris sordidus* Thunberg (Yosida, 1944).

In Coreidae, during diplotene, single chiasma per bivalent is the most prevalent condition (Cattani *et al*., 2004; Franco *et al*., 2006; Souza *et al*., 2007; Bressa *et al*., 2008). However, in a few species, occasionally one or two bivalents are seen with two chiasmata (Manna, 1951; Parshad, 1957b; Dutt, 1957; Sands, 1982; Papeschi *et al*., 2003). In the present study, too, ring bivalents with two chiasmata are seen only in *Cletomorpha raja* Distant and *Cletus pallescens* Walker (Gonocerini), while in rest of the species, single chiasma per bivalent is observed.

In all the species, arrangement of chromosomes at metaphase I plate is of typical coreid type, *i.e.* all the autosomal bivalents form a ring, microchromosomes, if present, lie in the centre as pseudobivalent and sex chromosomes are placed outside the ring. At metaphase II, sex element (X or $X_1X_2$) remains apart from the autosomal group and moves to one of the poles as a laggard during anaphase II. In *Acanthocoris anticus* Walker, at metaphase I, two types of plates are observed, the one of typical coreid type while in the other, one or two autosomal bivalents lie within the ring formed by rest of the bivalents. Similar observation has been made in *A. scabrator* (Fabricius) by Manna (1951).

In the present study, the chromosome complement of *Clavigralla scutellaris* (Westwood) is 2n = 13 = 10A + 2m + X0. Behavior of chromosomes during meiosis is similar to Coreinae. Earlier, diploid number of only four species is known out of which, three have the same number while one has 2n = 22. Sex mechanism is X0 in all (Schachow, 1932; Xavier, 1945; Takenouchi & Muramoto, 1964; Muramoto, 1973, 1978).

With the present study, seven more species have been added to the pre-existing cytogenetic data on Coreidae and now the total number of cytogenetically known species comes to 123 (see online supplementary material, Table S1). Also, the tribe Anhomoeini has been introduced to cytogenetic world for the first time. It is revealed from the chromosomal data until now that the diploid number in Coreidae ranges from 13 to 29 with 52 species having 2n = 21 which is considered to be the modal number of the family. The most common sex mechanism is X0 present in 86 species, whereas $X_1X_20$ is reported in 29 species and $X_1X_2X_30$ in one population of *Coreus marginatus* (Linnaeus). Y-chromosome is absent throughout Coreidae with the only exception found in three species belonging to the genus *Metapodius* of the tribe Acanthocephalini. A pair of microchromosomes is present in 94 species, absent in 11 species and not reported in 18 species.

In the subfamily Coreinae, 2n = 21 is observed in 52 out of 118 species. Within Coreinae, tribes Acanthocerini, Anhomoeini, Chelinidini, Cloresmini and Daladerini invariably maintain the modal number of 2n = 21 (18A + 2m + X0) while in Mictini, Homoeocerini and Anisoscelini, this number is retained as the dominant number with a few deviations. In Mictini and Homoeocerini, deviations are reported in autosome number, microchromosomes as well as sex mechanism, whereas Anisoscelini is homogeneous for the presence of microchromosomes and X0 sex mechanism but deviates with respect to autosome number. In Coreini, Gonocerini, Acanthocorini, Colpurini and Acanthocephalini, complements are highly heterogeneous. In Coreini, deviations from the modal number have been reported in autosomes as well as sex chromosome. The most common complement is 2n = 22 shown by eight out of 21. Dominant sex mechanism is X0 (13 out of 21). A pair of microchromosomes is present in all studied species, except *Acanonicus hahni* (Stal). For Gonocerini, autosome number has decreased to 14 (as the commonest number), while X multiplicity is frequent suggesting fusion of autosomes and fragmentation of X to be the mode of evolution of this tribe. The tribe Acanthocephalini represents an exception due to possessing the number of supernumeraries being in association with Y chromosomes, as seen in *Metapodius terminalis* (Dallas), *M. granulosus* (Dallas) and *M. femoratus* Fabricius. The diploid number is increased in Petascelini, Spartocerini and Chariesterini and decreased in Nematopodini and Discogastrini. For Petascelini and Spartocerini, increase is seen for both autosomes and X chromosome while for Chariesterini, only autosome number is increased. In six species of the tribe Nematopodini, autosome number is decreased while in Discogastrini, autosome number of 18 is retained but overall chromosome number has decreased due to absence of microchromosomes.

For very less explored Pseudophloeinae, the most common number is 2n = 13 present in four out of five species.

## ACKNOWLEDGEMENTS

The authors are thankful to the Department of Science and Technology, New Delhi, India for providing financial support (Grant No. 96915) to carry out the present study.

## ONLINE SUPPLEMENTARY MATERIAL

Supplementary data associated with this research paper are presented on the online version of this manuscript (www.jbr.gr).

## REFERENCES

Arakaki RLM, Souza HV, Castanhole MMU, Bicudo HEMC, Itoyama MM, 2010. Cytogenetic evidence for *de novo* synthesis of rRNA and involvement of nucleolar material in the organization of cell structures during spermiogenesis of *Chariesterus armatus* (Heteroptera, Coreidae). *Genetics and Molecular Research*, 9: 1877-1885.

Banerjee MK, 1958. A study of the chromosomes during meiosis in twenty-eight species of Hemiptera (Heteroptera, Homoptera). *Proceedings of the Zoological Society of Calcutta*, 11: 9-37.

Bressa MJ, Larramendy ML, Papeschi AG, 2005. Heterochromatin characterization in five species of Heteroptera. *Genetica*, 124: 307-317.

Bressa MJ, Franco MJ, Toscani MA, Papeschi AG, 2008. Heterochromatin heteromorphism in *Holhymenia rubiginosa* (Heteroptera: Coreidae). *European Journal of Entomology*, 105: 65-72.

Carr DH, Walker JE, 1961. Carbol-fuchsin as a stain for human chromosomes. *Stain Technology*, 36: 233-236.

Cattani MV, Greizerstein EJ, Papeschi AG, 2004. Male meiotic behaviour and nucleolus organizer regions in *Camptischium clavipes* (Fabr.) (Coreidae, Heteroptera) analyzed by fluorescent banding and *in situ* hybridisation. *Caryologia*, 57: 267-273.

Das C, 1958. 'Lampbrush' phase during meiosis in a species of *Cletus* (Coreidae: Heteroptera-Hemiptera). *Cytologia*, 23: 80-85.

Dey SK, Wangdi T, 1985. Meiotic chromosomes and sex mechanism in males of twelve species of Heteroptera. *Entomon*, 10: 327-328.

Dey SK, Wangdi T, 1988. Chromosome number and sex chromosome system in forty-four species of Heteroptera. *Chromosome Information Service*, 45: 5-8.

Dey SK, Wangdi T, 1990. Banding patterns of the holocentric chromosomes in some species of Heteroptera. *Cytologia*, 55: 181-186.

Dursun A, Fent M, 2009. A study on the Coreidae (Insecta: Heteroptera) of the Kelkit Valley, Turkey. *Acta Entomologica Serbica*, 14: 13-25.

Dutt MK, 1957. Cytology of three species of Coreid bugs with special reference to multiple sex chromosome mechanism. *Genetica*, 29: 110-119.

Foot K, Strobell EC, 1907. The "Accessory Chromosome" of *Anasa tristis*. *Biological Bulletin*, 12: 119-126.

Fossey A, Liebenberg H, 1995. Meiosis and nucleolar structures in the stink bug *Carlisis wahlbergi* Stal (Coreidae: Heteroptera). *Cytobios*, 81: 7-15.

Franco MJ, Bressa MJ, Papeschi AJ, 2006. Karyotype and male meiosis in *Spartocera batatas* and meiotic behaviour of multiple sex chromosomes in Coreidae (Heteroptera). *European Journal of Entomology*, 103: 9-16.

Geitler L, 1939. Das heterochromatin der Geschlechtschromosomen bei Heteropteren. *Chromosoma*, 1: 197-229.

Jande SS, 1959. Chromosome number and sex mechanism in twenty seven species of Indian Heteroptera. *Research Bulletin of Panjab University*, 10: 215-217.

Kaur R, 2007. Cytological studies on the three species of family Coreidae (Insecta: Hemiptera: Heteroptera). M.Sc. Dissertation, Punjabi University, Patiala.

Kaur H, Semahagn BK, 2010. Meiosis in three species of Heteroptera from Ethiopia (East Africa). *Cytologia*, 75: 141-147.

Kaur H, Chhabra S, Suman V, Gupta M, 2006. Chromosomes and their behavior in two families of the sub-order Heteroptera. *Cytologia*, 71: 111-118.

Leston D, 1956. Chromosome number and the systematics of the Pentatomomorpha (Hemiptera). *Proceedings of 10th International Congress on Entomology*, 2: 911-918.

Manna GK, 1951. A study of the chromosomes during meiosis in forty three species of Indian Heteroptera. *Proceedings of the Zoological Society of Calcutta*, 4: 1-166.

Manna GK, 1984. Chromosomes in evolution in Heteroptera. In: Sharma AK, Sharma A, eds. *Chromosomes in evolution of eukaryotic groups*. CRC Press, Boca Raton, Florida, USA: 189-225.

Manna GK, Deb Mallick S, 1981. Meiotic chromosome constitution in forty one species of Heteroptera. *Chromo-*

*some Information Service*, 31: 9-11.

Meyer JR, 2005. Hemiptera Suborder Heteroptera. Department of Entomology NC State University. Last Updated March 8, 2005. Available on: http://www.cals.ncsu.edu/course/ent425/compendium/hetero~1.html#class.

Montgomery TH, 1901. A study of the chromosomes of the germ cells of Metazoa. *Transactions of the American Philosophical Society*, 20: 154-236.

Montgomery TH, 1906. Chromosomes in the spermatogenesis of the Hemiptera-Heteroptera. *Transactions of the American Philosophical Society*, 21: 97-173.

Muramoto N, 1973. A list of the chromosome numbers of heteropteran insects of Japan. *Chromosome Information Service*, 14: 29-31.

Muramoto N, 1978. A chromosome study of thirty Japanese Heteropterans (Heteroptera). *Genetica*, 49: 37-44.

Muramoto N, 1979. A chromosome study of fifteen species of Heteropteran insects (Heteroptera). *La Kromosoma*, 14: 390-397.

Nokkala S, 1986. The mechanisms behind the regular segregation of the m-chromosomes in *Coreus marginatus* L. (Coreidae, Hemiptera). *Hereditas*, 105: 73-85.

Papeschi AG, Mola LM, 1990. Meiotic studies in *Acanonicus hahni* (Stål) (Coreidae, Heteroptera). I. Behavior of univalents in desynaptic individuals. *Genetica*, 80: 31-38.

Papeschi AG, Bressa MJ, 2006. Evolutionary cytogenetics in Heteroptera. *Journal of Biological Research-Thessaloniki*, 5: 3-21.

Papeschi AG, Mola LM, Bressa MJ, Greizerstein EJ, Lía V, Poggio L, 2003. Behavior of ring bivalents in holocentric systems: alternative sites of spindle attachment in *Pachylis argentinus* and *Nezara viridula* (Heteroptera). *Chromosome Research*, 11: 725-733.

Parshad R, 1957a. Chromosome number and sex mechanism in twenty species of the Indian Heteroptera. *Current Science Bangalore*, 26: 125.

Parshad R, 1957b. Cytological studies in Heteroptera IV. Chromosome complement and meiosis in twenty six species of the Pentatomoidea, Lygaeoidea and Coreoidea with a consideration of the cytological bearing on the status of these superfamilies. *Research Bulletin of the Panjab University*, 133: 521-559.

Parshad R, 1958. Structure of the Heteropteran kinetochore. The behavior of the long chromosomes in some Lygaeid and Coreid bugs during mitosis and meiosis. *Cytologia*, 23: 25-32.

Paulmier FC, 1899. The spermatogenesis of *Anasa tristis. Journal of Morphology*, 15: 224-272.

Piza SdT, 1945. Estudoscitoldgosem Hemipterisda familia Corediae. *Luiz de Queiroz*, 2: 119-148.

Piza SdT, 1946. Comportamento dos cromossômios na meiose de Euryophthalmus rufipennis Laporte (Hemiptera-Pyrrhocoridae). *Anais da escola superior de agricultura "Luiz de Queiroz"*, 3: 27-54.

Piza SdT, 1956. Normally dicentric insect chromosomes. *Proceedings of Xth International Congress of Entomology*, 2: 945-951.

Piza SdT, 1957. Contribution of *Scaptocoris castaneus* to the kinetochore problem in Hemiptera. *Cytologia*, 22: 404-411.

Sands VE, 1982. Cytological Studies of the Coreidae and Alydidae (Hemiptera: Heteroptera). I. Male meiosis in the Malaysian species. *Caryologia*, 35: 291-305.

Satapathy SN, Patnaik SC, 1989. Chromosome numbers in forty one species of Indian Heteroptera. *Chromosome Information Service*, 47: 3-5.

Satapathy SN, Nahak U, Patnaik SC, 1990. Chromosome numbers in seventeen species of Heteroptera (Hemiptera, Insecta). *Chromosome Information Service*, 48: 20-22.

Schachow SD, 1932. Abhandlung über haploide Chromosomengarnituren in den Samendrüsen der Hemiptera. *Anatomischer Anzeiger*, 75: 1-46.

Schaefer CW, Mitchell PL, 1983. Food plants of the Coreoidea (Hemiptera: Heteroptera). *Annals of the Entomological Society of America*, 76: 591-615.

Schaefer CW, Panizzi AR, 2000. *Heteroptera of economic importance*. CRC Press, Florida.

Schuh RT, Slater JA, 1995. *True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History*. Cornell University Press, Ithaca, New York.

Souza HV, Arakaki RLM, Dias LN, Murakami AS, Costa, LAA, Bicudo HEMC, Itoyama MM, 2007. Cytogenetical aspects of testicular cells in economically important species of Coreidae family (Heteroptera). *Cytologia*, 72: 49-56.

Souza HV, Souza FB, Maruyama SRC, Castanhole MMU, Itoyama MM, 2009. Meiosis, spermatogenesis and nucleolar behavior in the seminiferous tubules of Alydidae, Coreidae and Rhopalidae (Heteroptera) species. *Genetics and Molecular Research*, 8: 1383-1396.

Takenouchi Y, Muramoto N, 1964. A study of chromosomes in five species of heteropteran bugs. *Journal of Hokkaido Gukugei University of Education*, 15: 1-8.

Takenouchi Y, Muramoto N, 1967. A survey of the chromosomes in twenty one species of heteropteran insects. *Journal of Hokkaido University of Education*, 18: 1-15.

Takenouchi Y, Muramoto N, 1970. A study of chromosomes in five species of heteropteran insects. *Journal of Hokkaido University of Education*, 21: 9-13.

Thomas DB, 1987. Chromosome evolution in the Heteroptera (Hemiptera): agmatoploidy *versus* aneuploidy. *Annals of the Entomological Society of America*, 80: 720-730.

Toscani MA, Pigozzi MI, Bressa MJ, Papeschi AG, 2008. Synapsis with and without recombination in the male meiosis of the leaf-footed bug *Holhymenia rubiginosa* (Coreidae, Heteroptera). *Genetica*, 132: 173-178.

Toshioka S, 1934. On the chromosomes in Hemipterous insects II. *Zoological Magazine*, 46.

Toshioka S, 1935. On the chromosome of some Hemipterous insects III. *Zoological Magazine*, 47.

Ueshima N, 1979. Hemiptera II: Heteroptera. In: John B, ed. *Animal cytogenetics*. Gebrüder Borntraeger, Berlin-Stuttgart: 117.

Wilson EB, 1905. Studies on chromosomes I. The behavior of idiochromosomes in Hemiptera. *Journal of Experimental Zoology*, 2: 371-405.

Wilson EB, 1906. Studies on chromosome III. The sexual differences of the chromosome groups in Heteroptera, with some considerations of the chromosome-groups in Hemiptera with some considerations of the determination and inheritance of sex. *Journal of Experimental Zoology*, 3: 1-140.

Wilson EB, 1907a. The case of *Anasa tristis*. *Science*, 25: 191-193.

Wilson EB, 1907b. Notes on the chromosome groups of *Metapodius* and *Banasa*. *Biological Bulletin*, 12: 303-313.

Wilson EB, 1909a. Studies on chromosomes IV. The “accessory” chromosome in *Syromastes* and *Pyrrhocoris* with a comparative review of the types of sexual differences of the chromosome groups. *Journal of Experimental Zoology*, 6: 69-99.

Wilson EB, 1909b. The female chromosome groups in *Syromastes* and *Pyrrhocoris. Biological Bulletin*, 16: 199-204.

Wilson EB, 1909c. Studies on chromosomes V. The chromosomes of *Metapodius*. A contribution to the hypothesis of the genetic continuity of chromosomes. *Journal of Experimental Zoology*, 6: 147-205.

Wilson EB, 1910. Studies on chromosomes VI. A new type of chromosome combination in *Metapodius*. *Journal of Experimental Zoology*, 9: 53-78.

Wilson EB, 1911. Studies on chromosomes VII. A review of the chromosomes of *Nezara* with some general considerations. *Journal of Morphology*, 22: 71-110.

Wilson EB, 1932. Polyploidy and metaphase patterns. *Journal of Morphology*, 53: 443-603.

Xavier CM, 1945. Cariologia comparada de alguns Hemipteros Heteropteros (Pentatomidoes, Coreideos). *Memorias de Estudos do Museu Zoologio de universidade de Coimbra*, 163: 1-105

Yosida T, 1944. Researches on the chromosomes of twenty species in the heteropterous insects. *Igaku and Seibutsugaku*, 5: 729-732.

Yosida T, 1946. A chromosome survey in twenty species of Heteropteran insects, with special reference to the morphology of sex chromosome. *La Kromosomo*, 2: 57-63.

Yosida T, 1947. Unusual type of the nucleolus observed in a bug *Acanthocoris sordidus*. *Journal of Faculty of Sciences of Hokkaido University*, 9: 243-249.

Yosida TH, 1950. A chromosomal survey in twelve species of the Hemiptera. *Iden-no-sogokenkyu*, 1: 85-91.