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[1]*Laboratorio de Citogenética y Evolución, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina;* [2]*Member of the Carrera del Investigador Científico Consejo Nacional de Investigaciones Cientificas y Tecnicas (CONICET), Buenos Aires, Argentina;* [3]*Departamento de Zoología, Universidade Federal do Rio Grande do Sul, Porto Alegre RS, Fellowship of National Research Council (CNPg) Brazil*

Cytogenetic studies in Pentatomidae (Heteroptera): A review

P. J. Rebagliati[1], L. M. Mola[1,2], A. G. Papeschi[1,2] and J. Grazia[3]

Abstract

The suborder Heteroptera constitutes one of the most important insect groups because most species are plants feeders and cause damage on many plants of economic importance. One of the most important cytogenetic characteristics of Heteroptera is the holokinetic nature of the chromosomes. One particular feature of some species of Pentatomidae is the regular presence of an abnormal meiosis in one testicular lobe (harlequin lobe). From the 28 species cytogenetically analysed from Argentine material, 21 present the diploid number $2n = 14$, four species present a reduced number ($2n = 12$) and another three species possess an increased diploid number ($2n = 16$); among all these only three present an harlequin lobe. In the present work, a bibliographic review of the chromosome number and sex determining system of 294 species and subspecies belonging to 121 genera within the subfamilies Asopinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae and Podopinae is presented. The male diploid numbers range from six to 27 with a mode in 14 chromosomes; this last diploid number is present in 85% of the species. The sex chromosome determining system is XY/XX except in three species: *Macropygium reticulare* (Fabricius, 1803), *Rhytidolomia senilis* (Say, 1832) and *Thyanta calceata* (Say, 1832) which present derived sex chromosome systems. Furthermore, the cytogenetic relationships with the other families of Pentatomoidea are discussed.

Key words: Heteroptera – Pentatomidae – Holokinetic chromosomes – Chromosome numbers – Sex chromosome determining systems – Harlequin lobe

Introduction

The suborder Heteroptera constitutes one of the most important insect groups because most of its species are plant feeders during both nymphal and adult stages, and cause great damage on many plants of economic importance. With approximately 37 000 nominal species the suborder comprises eight infraorders, five of which include agronomically important species (Rizzo 1976; Saini 1992; Schuh and Slater 1995; Schaefer and Panizzi 2000; Triplehorn and Johnson 2005).

The superfamily Pentatomoidea includes 1080 genera and 5907 species belonging to 16 families. Cydnidae, Pentatomidae, Scutelleridae and Tessaratomidae are the most important since 94% of the species belong to them (Schaefer 1993; Schuh and Slater 1995; Schaefer and Panizzi 2000).

One of the largest families within Heteroptera is Pentatomidae including 4112 species (Schaefer and Panizzi 2000). They are called stinkbugs because they produce a disagreeable odour by means of scent glands that open in the region of the metapleuras. Schuh and Slater (1995) include eight subfamilies in this family: Asopinae, Cyrtocorinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae and Serbaninae. Packauskas and Schaefer (1998) treated Cyrtocoridae as a family, and J. Grazia (personal communication) removed Serbaninae of Pentatomidae. Most economically important phytophagous species belong to the subfamilies Edessinae and Pentatominae, and the latter contains the majority of species that are crop pests. The species belonging to Asopinae are predators, and some of them are important agents of biological control (Schaefer and Panizzi 2000).

Until present more than 1200 heteropteran species belonging to 42 families have been cytogenetically analysed (Ueshima 1979; Manna 1984; Schuh and Slater 1995). The diploid chromosome number ranges from four (*Lethocerus* sp., Belostomatidae) to 80 (four species of *Lopidea* Uhler, 1872, Miridae). Cytogenetic reports on Pentatomoidea refer to 391 species belonging to only nine families: Acanthosomatidae (12 species), Cydnidae (14 species), Dinidoridae (12 species), Plataspididae (16 species), Tessaratomidae (nine species), Thaumastellidae (two species), Scutelleridae (27 species), Urostylididae (five species), and Pentatomidae, which is by far the more studied (294 species) (Ueshima 1979; Manna and Deb-Mallick 1981; Nuamah 1982; Manna 1984; Dey and Wangdi 1988; Satapathy and Patnaik 1988, 1989; Jacobs 1989; Satapathy et al. 1990; González García et al. 1996; Rebagliati 2000; Rebagliati et al. 2001, 2002, 2003; Lanzone et al. 2003; Kerzhner et al. 2004).

One of the most important cytogenetic characteristics of Heteroptera is the holokinetic nature of its chromosomes, i.e. the presence of a diffuse kinetic activity, which contrasts with the monocentric nature (i.e. with a localized centromere) of the chromosomes of most organisms. Holokinetic chromosomes have been reported in other insect groups such as the so-called Homoptera, Phthiraptera, Lepidoptera, Odonata, Trichoptera, Psocoptera and Zoraptera (Hughes-Schrader and Schrader 1948; Blackman 1985; Mola 1995; Traut and Marec 1997; Tombesi et al. 1999; Kuztnezova et al. 2002), in some arachnids (Shanahan 1989; Rodríguez Gil et al. 2002) and in nematodes (Goday et al. 1992; Dernburg 2001). All organisms with holokinetic chromosomes show the same mitotic behaviour: chromosomes orientate at the metaphase plate with their long axes perpendicular to the spindle axis and sister chromatids migrate parallel to each other. However, the meiotic behaviour presents differences according to the group of organisms, since bivalents can divide pre- or post-reductionally (Battaglia and Boyes 1955; White 1973). In holokinetic systems, fusions and fragmentations are the most frequent chromosome rearrangements that cause variations in diploid number.

The male sex chromosomes described so far in Heteroptera are XY (approximately 75% of the species), XO, different

Table 1. Argentine species of Pentatomidae cytogenetically studied

Taxon	Number of specimens M	F	Localities (province)
Asopinae			
Podisus distinctus (Stål, 1860)	2	1	Iguazú National Park (Misiones)
Podisus nigrispinus (Dallas, 1851)	2	0	Gualeguaychú (Entre Ríos)
Discocephalinae			
Dinocoris prolineatus Becker and Grazia, 1985	11	30	Gualeguaychú (Entre Ríos)
Macropygium reticulare (Fabricius, 1803)	2	1	Colón (Entre Ríos)
Edessinae			
Edessa meditabunda (Fabricius, 1812)	14	0	Macomita (Tucumán)
	12	13	Gualeguaychú (Entre Ríos)
	2	2	Colón (Entre Ríos)
	2	1	Rosario del Tala (Entre Ríos)
	6	12	Gilbert (Entre Ríos)
	4	1	Pereyra Iraola Park (Buenos Aires)
	2	1	Martín García National Preserve (Buenos Aires)
Edessa rufomarginata (De Geer, 1773)	19	19	Benito Juarez (Buenos Aires)
	1	1	Gualeguaychú (Entre Ríos)
	1	0	Colón (Entre Ríos)
	0	1	Urdinarrain (Entre Ríos)
	0	1	Martín García National Preserve (Buenos Aires)
Edessa sp.	2	1	Gualeguaychú (Entre Ríos)
Pentatominae			
Acledra bonariensis (Stål, 1859)	1	0	Martín García National Preserve (Buenos Aires)
Acledra kinbergii (Stål, 1859)	0	1	Colón (Entre Ríos)
	1	1	Sierra de la Ventana (Buenos Aires)
	0	1	Gualeguaychú (Entre Ríos)
Acledra modesta (Stål, 1859)	3	0	Los Resortes (Cordoba)
Acrosternum armigerum (Stål, 1859)	2	0	Capital Federal (Buenos Aires)
Acrosternum bellum Rolston, 1983	0	2	Capital Federal (Buenos Aires)
	1	0	Elortondo (Santa Fé)
	1	0	Resistencia (Chaco)
Acrosternum herbidum (Stål, 1859)	1	0	Pereyra Iraola Park (Buenos Aires)
Arvelius albopunctatus (De Geer, 1773)	1	0	Gualeguaychú (Entre Ríos)
	4	0	Capital Federal (Buenos Aires)
Dichelops furcatus (Fabricius, 1775)	4	0	Mercedes (Corrientes)
	2	6	Gualeguaychú (Entre Ríos)
	0	2	Colón (Entre Ríos)
	1	1	Los Resortes (Cordoba)
	1	0	Bella Vista (Corrientes)
	4	0	Paraná (Entre Ríos)
	1	0	Martín García National Preserve (Buenos Aires)
	3	0	Pergamino (Buenos Aires)
	0	1	El Carrizal (Mendoza)
	1	0	Hughes (Santa Fé)
Dichelops melacanthus (Dallas, 1851)	2	0	Gualeguaychú (Entre Ríos)
	1	0	Colón (Entre Ríos)
Euschistus heros (Fabricius, 1798)	3	2	Iguazú National Park (Misiones)
Ladeaschistus sp.	1	0	Embalse Rio III (Cordoba)
Loxa deducta Walker, 1867	1	1	Iguazú National Park (Misiones)
	2	1	Capital Federal (Buenos Aires)
	0	1	El Carrizal (Mendoza)
	1	0	Almada (Entre Ríos)
	0	1	Gualeguaychú (Entre Ríos)
	2	0	Embalse Rio III (Cordoba)
Mecocephala maldonadensis Schwertner,Grazia and Fernandes, 2002	1	0	Tornquist Park (Buenos Aires)
Mormidea paupercula Berg, 1879	2	0	Gualeguaychú (Entre Ríos)
	1	0	Los Resortes (Cordoba)
	1	0	Capital Federal (Buenos Aires)
	2	1	Martín García National Preserve (Buenos Aires)
Mormidea quinqueluteum (Lichtenstein, 1796)	15	12	Gualeguaychú (Entre Ríos)
Nezara viridula (Linnaeus, 1758)	30	0	Rojas (Buenos Aires)
Oebalus ypsilongriseus (De Geer, 1773)	11	13	Capitán Solari, Resistencia (Chaco)
Piezodorus guildinii (Westwood, 1837)	4	0	Colón (Entre Ríos)
	1	4	Gualeguaychú (Entre Ríos)
	0	1	Urdinarrain (Entre Ríos)

Table 1. (Continued)

Taxon	Number of specimens M	F	Localities (province)
Piezodorus gvildinii (Westwood, 1837) cont.	3	4	Villa Angela (Chaco)
	0	4	Hughes (Santa Fe)
	0	0	Rojas (Buenos Aires)
Proxys albopunctulatus (Palisot de Beauvois, 1805)	3	1	Gualeguaychú (Entre Ríos)
Thyanta sp.1	2	1	Martín García National Preserve (Buenos Aires)
Thyanta sp.2	2	5	El Carrizal (Mendoza)

Table 2. Diploid and Haploid numbers of Pentatomidae

Taxon	2*n* (1)	*n*	References
Subfamily Asopinae			
Afrius yolofus (Guérin-Méneville, 1831) [= *Afrius purpureus* (Westwood, 1837)]	14	6A + XY	Nuamah (1982)
Apoecilus bracteatus (Fitch, 1856)			
[as *Podisus bracteatus* (2)]	14	–	Wilson (1906, 1909)
[as *Podisus crocatus* Uhler, 1897 (2)]	14	–	Wilson (1909)
Arma custos (Fabricius, 1794)	14	6A + XY	Schachow (1932b)
	–	6A + XY	Muramoto (1973b)
Dynorhynchus dybowskii Jakovlev, 1876	16	7A + XY	Muramoto (1981[(b)])
Macrorhaphis acuta Dallas, 1851	14	6a + XY	Nuamah (1982)
Oechalia grisea (Burmeister, 1834)	14	6A + XY	Heizer (1951)
	14F	6A + XX	
O. pacifica (Stål, 1859) (as *O. pacifica – type I*) (3)	14	6A + XY	Heizer (1950)
	14F	6A + XX	
O. patruelis (Stål, 1859)	12	5A + XY	Heizer (1950)
	12F	5A + XX	
Perillus bioculatus (Fabricius, 1775) (as *Mineus bioculatus*, 1775)	14	6A + XY	Wilson (1906)
P. confluens (Herrich-Schäeffer, 1840)	14	6A + XY	Montgomery (1901, 1906)
Picromerus bidens (Linnaeus, 1758)	14	6A + XY	Geitler (1939)
	12	5A + XY	Yosida (1946[(c)], 1956[(a)]),
P. nigridens (Fabricius, 1803)	14	6A + XY	Xavier and Da (1945), Miyamoto (1957[(a)])
Picromerus sp.	14	6A + XY	Dey and Wangdi (1985[(b)], 1988),
Podisus distinctus (Stål, 1860)	16	7A + XY	Rebagliati et al. (2002)
P. maculiventris (Say, 1832)			
[as *P. modestus* (Dallas, 1851)] (2)	16	–	Wilson (1906, 1909)
[as *P. spinosus* (Dallas, 1851)]	16	7A + XY	Montgomery (1901, 1906) Wilson (1905a, 1906, 1909)
	16F	–	Wilson 1906
P. nigrispinus (Dallas, 1851)	16	7A + XY	Rebagliati et al. (2002)
P. placidus Uhler, 1870 (3)	16	–	Wilson (1906, 1909)
Stiretrus anchorago (Fabricius, 1775)	14	–	Wilson (1909)
	14 F	–	
	14	6A + XY	Parshad (1957a[(a)])
Troilus luridus (Fabricius, 1775) (as Arma elector (Fabricius, 1794)	14	6A + XY	Miyamoto (1957[(a)]); Parshad (1957c)
Zicrona caerulea (Linnaeus, 1758)	14	6A + XY	Muramoto 1973a
Subfamily Discocephalinae			
Tribe Discocephalini			
Ablaptus amazonus Stål, 1864 (4)	14	6A + XY	Schrader (1960a)
Agaclitus dromedarius Stål, 1864 (4)	14	6A + XY	Schrader (1960a)
Antiteuchus macraspis (Perty, 1833) (as *Neodine macraspis*) (4)	14	6A + XY	Schrader (1946b, 1960a)
A. mixtus (Fabricius, 1787) (4)	14	6A + XY	Lanzone et al. (2003)
A. panamensis (Ruckes, 1959) (as *Mecistorhinus melanoleucus* Westwood, 1837) (4) (5)	14	6A + XY	Schrader (1946b, 1960a)
A. sepulcralis (Stål, 1868) (as *Mecistorhinus sepulcralis*) (4) (6)	14	6A + XY	Schrader (1946b, 1960a), Lanzone et al. (2003)
A. tripterus (Fabricius,1787) (as *Mecistorhinus tripterus*) (4) (7)	14	6A + XY	Schrader (1946b, 1960a), Lanzone et al. (2003)
Cataulax pudens (Distant, 1889) (as *Architas pudens*) (4)	14	6A + XY	Schrader (1960a)
Dinocoris rufitarsus Ruckes, 1958 (4)	14	6A + XY	Schrader (1960a)
D. (Praedinocoris) prolineatus Becker and Grazia, 1985 (4)	14	6A + XY	Rebagliati et al. (2001)
Discocephalessa humilis (Herrich-Schäeffer, 1843) (as *Platycarenus notulatus* (Stål, 1862))	14	6A + XY	Schrader (1946b)

Table 2. (Continued)

Taxon	2*n* (1)	*n*	References
Tribe Ochlerini			
Alitocoris parvus Sailer, 1950 (4)	14	6A + XY	Schrader (1960a)
A. schraderi Sailer, 1950 (4)	14	6A + XY	Schrader (1960a), Martin (1953)
Macropygium reticulare (Fabricius, 1803) (4)	15	6A + X_1X_2Y	Srivastava (1957), Schrader (1960a)
	16 F	6A + $X_1X_1X_2X_2$	Srivastava (1957)
	14	6A + XY	Rebagliati et al. (2001)
Moncus obscurus (Dallas, 1851) (4)	14	6A + XY	Schrader (1960a)
Schraderiellus cinctus (Ruckes, 1959) (4) (as *Schraderia cinctus*)	14	6A + XY	Schrader (1960a)
S. hughesae (Ruckes, 1959) (4) (as *Schraderia hughesae*)	14	6A + XY	Schrader (1960a)
Stalius tartareus (Stal, 1862) (as *Melanodermus tartareus*) (4)	14	6A + XY	Schrader (1960a)
Subfamily Edessinae			
Brachystethus rubromaculatus Dallas, 1851 (4)	14	6A + XY	Schrader (1946a, 1960a)
Edessa caldaria Distant, 1890	14	6A + XY	Schrader (1941a)
E. celsa Distant, 1890	14	6A + XY	Schrader (1941a)
E. costae Bergroth, 1891(as *E. Costallis*)	14	6A + XY	Schrader (1941a)
E. fuscidorsata Distant, 1881	14	6A + XY	Schrader (1941a)
E. irrorata Dallas, 1851	14	6A + XY	Schrader (1941a)
E. meditabunda (Fabricius, 1794)	14	6A + XY	Rebagliati et al. (2003)
E. pictiventris Stål, 1872	14	6A + XY	Schrader (1941a)
E. laticornis Stål, 1872	14	6A + XY	Schrader (1941a)
E. rufomarginata (De Geer, 1773)	14	6A + XY	Schrader (1941a), Rebagliati et al. (2003)
E. vinula Stål, 1862	14	6A + XY	Schrader (1941a)
Edessa sp.1	14	6A + XY	Schrader (1941a)
Edessa sp. 2	14	6A + XY	Schrader (1941a)
Edessa sp.	14	6A + XY	Present work
Peromatus notatus (Burmeister, 1835)	14	6A + XY	Schrader (1941b[(c)])
Subfamily Pentatominae			
Tribe Aeptini			
Aeptus singularis Dallas, 1851	14	6A + XY	Nuamah (1982)
Tribe Halyini			
Atelocera serrata (Fabricius, 1803)	14	6A + XY	Nuamah (1982)
Brochymena sp. 1	14	6A + XY	Montgomery (1901, 1906)
Brochymena sp. 2	14	6A + XY	Wilson (1905a)
Cahara jugatoria (Lethierry, 1891) (as *C. jugotoria*)	14	–	Dey and Wangdi (1988)
Dalpada consinna Westwood, 1837 (as *Dalpada clavata (Fabricius, 1798)*	14	6A + XY	Parshad (1957b)
D. confusa Distant, 1879	14	6A + XY	Parshad (1957b)
D. versicolor (Herrich–Schäeffer, 1840)	14	6A + XY	Rao (1954[(a)])
Dalpada sp.	14	6A + XY	Dey and Wangdi (1988)
Erthesina fullo Thunberg, 1783	14	6A + XY	Mittal and Leelamma (1981[(b)])
Halys dentata (Fabricius, 1775) (as *H. sulcata* Thunberg, 1783	14	6A + XY	Sharma and Parshad (1956[(c)]) Srivastava (1965[(c)]), Srivastava (1965)
	14	6A + XY	Manna (1951), Satapathy et al. (1990)
H. serricolis Westwood, 1837 (as *H. parvus* Chopra, 1974)	14	6A + XY	Mittal and Leelamma (1981[(b)])
Halys sp.	14	6A + XY	Sharma and Parshad (1956[(c)])
Tribe Lestonocorini			
Gynenica affinis Distant, 1880	16	7A + XY	Sathapathy and Patnaik (1989)
Tribe Myrocheini			
Dymantis grisea Jensen-Haarup, 1931	14	6A + XY	Nuamah (1982)
Tribe Pentatomini			
Acledra bonariensis (Stål, 1859)	12	5A + XY	Present work
A. kinbergii (Stål), 1859	14	6A + XY	Present work
A. modesta (Stål), 1859 (8)	14	6A + XY	Rebagliati et al. (2002)
Acrosternum armigerum (Stål, 1859)	14	6A + XY	Present work
A. bellum Rolston, 1983	14	6A + XY	Present work
A. graminea (Fabricius, 1787)	14	6A + XY	Satapathy and Patnaik (1988, 1989)
A. heegeri Fieber,1861	14	6A + XY	Nuamah (1982)
A. herbidum (Stål, 1859)	14	6A + XY	Present work
A. hilare (Say, 1832) (as *Nezara hilaris*) (9)	14	6A + XY	Hughes-Schrader and Schrader (1957) Montgomery (1901, 1906) Wilson (1905a, 1906)
	14 F		Wilson (1906, 1911)
A. marginatum (Palisot de Beauvois, 1805)	14	6A + XY	Hughes-Schrader and Schrader (1957)
A. pennsylvanicum (De Geer, 1773)	14	6A + XY	Hughes-Schrader and Schrader (1957)
A. scutellatum (Distant, 1890)	14	6A + XY	Hughes-Schrader and Schrader (1957)

Table 2. (Continued)

Taxon	2*n* (1)	*n*	References
Acrosternum sp. n.	14	6A + XY	Hughes-Schrader and Schrader (1956, 1957)
Adevoplitus longicomis (Ruckes, 1958) (as *Pseudevoplitus longicomis*) (4)	14	6A + XY	Schrader (1960a)
Adria parvula (Dallas, 1851)	14	6A + XY	Jande (1959)
Aelia acuminata (Linnaeus, 1758)	14	6A + XY	Schachow (1932b), Xavier and Da (1945)
A. fieberi Scott, 1874	14	6A + XY	Nishimura (1927[c]), Yosida (1950[c]), Miyamoto (1957[a])
A. rostrata Boheman, 1852 (=*glabana Ferrari, 1874 hom.jr.*)	14	6A + XY	Xavier and Da (1945), Yosida (1956[a])
Aeliomorpha sp. *griseoflava* (Stål, 1853)	14	6A + XY	Nuamah (1982)
A. lineatocollis Westwood, 1837	14	6A + XY	Mittal and Leelamma (1981[b])
Aenaria lewisi (Scott, 1874)	14	6A + XY	Jande (1959)
Aethemenes nigropunctata (Signoret, 1858) [as *A.chloris* (Westwood, 1837)]	14	6A + XY	Nuamah (1982)
Agonoscelis nubila (Fabricius, 1775) (10)	14	6A + XY	Satapathy and Patnaik (1988, 1989)
	14	6A + XY	Manna (1951)
	14	6A + XY	Dey and Wangdi (1988)
Andrallus spinidens (Fabricius, 1787)	14	6A + XY	Satapathy et al. (1990)
Antestia cruciata (Fabricius, 1775)	14	6A + XY	Manna (1951)
A. versicolor (Distant, 1881) (as *Farnya versicolor*)	14	6A + XY	Nuamah (1982)
Antestia sp.	14	6A + XY	Nuamah (1982)
Antestia sp. S. I.	14	6A + XY	Nuamah (1982)
Antestiopsis sp. S. I.	14	6A + XY	Nuamah (1982)
Arvelius albopunctatus (De Geer, 1773)	14	6A + XY	Bowen (1922b[c])
			Hughes-Schrader and Schrader (1956)
			Present work
Tribe Pentatomini			
Aspavia acuminata Montandon, 1894	14	6A + XY	Nuamah (1982)
A. armigera (Fabricius, 1781)	14	6A + XY	Nuamah (1982)
A. hastator (Fabricius, 1794)	14	6A + XY	Nuamah (1982)
A. ingens Distant, 1890	14	6A + XY	D. Leston (unpublished data)[a]
Banasa alboapicata (Stål, 1860)	26	12A + XY	Thomas and Yonke (1981)[b]
B. angulobata Thomas, 1990	26	12A + XY	Thomas and Yonke (1981)[b]
Banasa bidens schraderi Sailer 1959 [=*B. irata* (Fabricius, 1787)]	26	12A + XY	Schrader and Hughes-Schrader (1958)
B. calva (Say, 1832)	26	12A + XY	Wilson (1905b, 1907)
	26 F	–	Schrader and Hughes-Schrader (1958)
B. centralis Sailer, 1959	26F	–	Schrader and Hughes-Schrader (1958)
B. derivata Walker, 1867	26	12A + XY	Thomas and Yonke (1981[b])
B. dimidiata (Say, 1832)	16	7A + XY	Wilson (1907)
			Schrader and Hughes-Schrader (1958)
B. euchlora Stål, 1872	16	7A + XY	Schrader and Hughes-Schrader (1958)
B. excavata Thomas, 1988	26	12A + XY	Thomas and Yonke (1981[b])
B. lenticularis Uhler, 1894	16	7A + XY	Schrader and Hughes-Schrader (1958)
B. minor Sailer, 1859	26	12A + XY	Schrader and Hughes-Schrader (1958)
B. packardii (Stål, 1872)	26	12A + XY	Thomas and Yonke (1981[b])
B. panamensis Sailer, 1959	14	6A + XY	Schrader and Hughes-Schrader (1958)
	14F	–	Hughes-Schrader and Schrader (1957)
B. rolstoni Thomas and Yonke, 1981	16	7A + XY	Thomas and Yonke (1981[b])
B. salvini Distant, 1911 (as *B. rufifrons* Sailer, 1959)	26	12A + XY	Schrader and Hughes-Schrader (1958)
B. sordida Uhler, 1871	26	12A + XY	Thomas and Yonke (1981[b])
B. subcarnea Van Duzze, 1935	26	12A + XY	Thomas and Yonke (1981[b])
B. zeteki Sailer, 1959	26	12A + XY	Schrader and Hughes-Schrader (1958)
Bathycoelia rodhaini Schouteden, 1913	14	6A + XY	Nuamah (1982)
B. thalassina (Herrich-Schäeffer, 1844)	14	6A + XY	Nuamah (1982)
Benia sp. A	14	6A + XY	Nuamah (1982)
Carbula aspavia Distant, 1898	14	6A + XY	Parshad (1957b)
C. biguttata (Fabricius, 1794)	14	6A + XY	Satapathy and Patnaik (1988, 1989)
			Yosida (1956[a])
C. capito Stål, 1865	14	6A + XY	Nuamah (1982)
C. carbula (Distant, 1898)	14	6A + XY	Nuamah (1982)
C. humerigera (Uhler, 1860) (as *C. Abbreviata* Motschulsky, 1866) (11)	14	6A + XY	Yosida (1950[c])
			Takenouchi and Muramoto (1968[c]), 1970 [d],
C. indica (Westwood, 1837)	14	6A + XY	Dey and Wangdi (1988)
C. limpoponis (Stal 1853) (as *C. marginella* (Thumberg, 1822))	14	6A + XY	Nuamah (1982)
C. melacantha (Fabricius, 1781)	14	6A + XY	Nuamah (1982)
C. scutellata Distant, 1687	14	6A + XY	Mittal and Leelamma (1981)
C. socia (Walker, 1867)	14	6A + XY	Manna (1951, 1958[a])
			Satapathy and Patnaik (1988)

Table 2. (Continued)

Taxon	2*n* (1)	*n*	References
Carbula sp.	14	6A + XY	Manna (1951, 1958)
Carbula sp. *aff. sjostedti* Schouteden, 1910	14	6A + XY	Nuamah (1982)
Carpocoris fuscispinus (Boheman, 1849)	14	6A + XY	Schachow (1932b)
			Geitler (1939), Xavier and Da (1945)
C. melanocerus (Mulsant and Rey, 1852)	–	6A + XY	Geitler (1939)
C. pudicus (Poda, 1761)	14	6A + XY	Schachow (1932b)
C. purpureipennis (De Geer, 1773)	14	6A + XY	Oksala (1947[(c)]), Yosida 1950[(c)]
Caura pugillator (Fabricius, 1781)	14	6A + XY	Nuamah (1982)
Caystrus (Neodius) pallipes (Stål, 1871) (as *Neodius* sp.)	16	7A + XY	Parshad (1957b)
Chlorochroa juniperina [Linnaeus, 1758 (as *Pentatoma juniperina*)]	14	–	Wilson (1913)[(c)]
Codophila varia (Fabricius, 1787)	14	6A + XY	Schachow (1932b), Xavier and Da (1945)
Coenus delius (Say, 1832)	14	6A + XY	Montgomery (1901, 1906), Wilson (1905a)
	14	–	Wilson (1906)
	14F	–	Wilson (1906)
Coenus sp.	14	6A + XY	Hughes-Schrader and Schrader (1956)
Cosmopepla carnifex (Fabricius, 1798)(= *C. lintneriana* Kirkaldy, 1909)	16	7A + XY	Montgomery (1901, 1906)
Dichelops (Dicaereus) furcatus (Fabricius, 1775)	12	5A + XY	Rebagliati et al. (2001)
D. melacanthus (Dallas, 1851)	12	5A + XY	Rebagliati et al. (2002)
Diploxys bipunctata Amyot and Serville, 1843	14	6A + XY	Nuamah (1982)
D. Punctata Distant 1910 (as Amaxosana punctata)	14	6A + XY	Nuamah (1982)
Dolycoris baccarum (Linnaeus)	14	6A + XY	Schachow (1932b), Xavier and Da (1945)
			Takenouchi and Muramoto (1970[(c)])
D. indicus Stål, 1876	14	6A + XY	Manna (1951)
Dunnius sp.	16	7A + XY	Dey and Wangdi (1988)
Durmia haedula (Stål, 1865)	14	6A + XY	Nuamah (1982)
D. lutulenta (Stål, 1853)	14	6A + XY	Nuamah (1982)
Durmia sp.	14	6A + XY	Nuamah (1982)
Euschistus crassus Dallas, 1851	12	5A + XY	Foot and Strobell (1912[(c)])
			Hughes-Schrader and Schrader (1956)
E. euschistoides (Vollenhoven, 1868) (as *E. fissilis* Uhler, 1871)	14	6A + XY	Wilson (1905a, 1906)
	14 F	–	Wilson (1906)
E. heros (Fabricius, 1798)	14	6A + XY	Present work
E. ictericus (Linnaeus, 1763)	14	–	Wilson (1906)
	14	–	
E. crenator (Fabricius, 1794) (as *E. obscurus* (Palisot de Beauvois, 1805)	14	6A + XY	Hughes-Schrader and Schrader (1956)
E. servus (Say, 1832)	14	6A + XY	Wilson 1906. Foot and Strobell (1914)
			Hughes-Schrader and Schrader (1961)
	14 F		Wilson (1906)
E. tristigmus (Say, 1832)	14	6A + XY	Montgomery (1901, 1906), Wilson (1906)
	14	6A + XY	Hughes-Schrader and Schrader (1961)
	14 F		Wilson (1906)
E. variolarius (Palisot de Beauvois, 1805) (as *Pentatoma*) (12)	14	6A + XY	Montgomery (1897, 1898, 1901, 1906)
			Wilson 1906. Bowen (1922a)
			Foot and Strobell (1914)
	14 F		Wilson (1906)
Euschistus sp. 1	14	6A + XY	Wilson (1905a)
Euschistus sp. 2	14	6A + XY	Montgomery (1910[(c)]), (1911)[(c)]
Eysarcoris aeneus (Scopoli, 1763) (as *Eusarcaris aeneus*)	16	7A + XY	Schachow (1932b)
E. capitatus (Distant) (as *Stollia capitatus*)	14	6A + XY	Manna (1951)
E. fabricii Kirkaldy, 1909 [as *E. venustissimus* (Schrank, 1776)] (as	16	7A + XY	Schachow (1932b)
Eusarconis melanocephalus (Fabricius, 1775))	16	7A + XY	Xavier and Da 1945
E. fallax Breddin, 1913	14	6A + XY	Muramoto (1978)
E. guttiger (Thunberg, 1783) (as *E. guttuger*) (as *Stollia guttigera)*	14	6A + XY	Toshioka (1937[(c)])
			Satapathy and Patnaik (1988) Manna, (1951)
Eysarcoris sp. ? guttiger	14	6A + XY	Manna and Deb-Mallick (1981)
E. inconspicuus (Herrich-Schäfer, 1844) (13)	14	6A + XY	Nuamah (1982)
	14	6A + XY	Xavier and Da (1945)
	14	6A + XY	Parshad (1957b)
E. lewisi (Distant, 1883) (as *Eusarcoris lewisi*) (14)	14	6A + XY	Yosida (1946[(c)])
			Takenouchi and Muramoto (1964[(c)]), 1970[(d)]
E. montivagus Distant, 1902 (as *Eusarcocoris montivagus*)	14	6A + XY	Parshad (1957b)
E. parvus Uhler, 1896	14	6A + XY	Toshioka (1937[(c)]), Miyamoto (1957[(a)])
E. ventralis (Westwood, 1837)	14	6A + XY	Toshioka (1937[(c)]), Miyamoto (1957[(a)])
Eysarcoris sp. 1	14	6A + XY	Toshioka (1937[(c)])
Eysarcoris sp. 2	14	6A + XY	Miyamoto (1957[(a)])
Halyomorpha annulicornis (Signoret, 1858)	14	6A + XY	Nuamah (1982)

Table 2. (Continued)

Taxon	2*n* (1)	*n*	References
H. picus (Fabricius, 1799)			
[as *H. brevis* (Walker, 1867)]	14	6A + XY	Parshad (1957b)
(as *H. pica*) (15)	14	6A + XY	Yosida (1946)[c], Manna (1951)
			Nuamah (1982)
H. reflexa (Signoret, 1858)	14	6A + XY	Nuamah (1982)
Hermolaus amurensis Horvath, 1903 (as *Hemolatus amurensis*)	14	6A + XY	Muramoto (1973a)
Holcostethus limbolarius (Stål, 1872) (as *Peribalus*)	14	6A + XY	Montgomery (1901, 1906)
Homalogonia obtusa (Walker, 1868)	14	6A + XY	Takenouchi and Muramoto (1970[c])
Ladeaschistus sp.	14	6A + XY	Present work
Lelia decempunctata Motschulsky, 1859	14	6A + XY	Yosida (1946[c])
Lerida punctata (Palisot de Beauvois, 1805)	14	6A + XY	Nuamah (1982)
Loxa deducta Walker, 1867 (4)	14	6A + XY	Rebagliati et al. (2001)
L. flavicollis (Drury, 1773) [as *L. florida* Van Duzze (4)]	14	6A + XY	Schrader (1945a,b, 1960a)
	14 F	–	Schrader (1945b)
	–	8	Bowen (1922a)
L. viridis (Palisot de Beauvois, 1805) [as *L. picticornis* Horvath, 1925 (4)]	14	6A + XY	Schrader (1945a,b, 1960a)
	14 F	–	Schrader (1945b)
Loxa sp.	14	6A + XY	Hughes-Schrader and Schrader (1956)
Mayrinia variegata (Distant, 1880) (4)	14	6A + XY	Schrader (1945a, 1960a)
Mecocephala maldonadensis Schwertner, Grazia and Fernandes, 2002 (16)	12	5A + XY	Rebagliati et al. (2002)
Menida bengalensis (Westwood, 1837)	14	6A + XY	Banerjee (1958[c])
M. bengalensis (Westwood, 1837) [as *M. histrio* (Fabricius, 1787)]	14	6A + XY	Satapathy et al. (1990)
M. scotti Puton, 1886	14	6A + XY	Muramoto (1973b)
M. violacea Motschulsky, 1861 (as *Meuda violacea*)	14	6A + XY	Yosida (1950)[c], 1956[a]
Mormidea lugens (Fabricius, 1775)	14	6A + XY	Montgomery (1901, 1906)
M. paupercula Berg, 1879 (17)	14	6A + XY	Rebagliati et al. (2002), Present work
M. quinqueluteum (Lichtenstien, 1796)	14	6A + XY	Present work
Mormidea sp.	14	6A + XY	Hughes-Schrader and Schrader (1956)
Morna sp.	14	6A + XY	Muramoto (1979[b])
Neottiglossa leporina (Herrich-Schäeffer, 1830)	14	6A + XY	Xavier and Da (1945)
Neottiglossa pusilla (Gmélin, 1789)	14	6A + XY	Xavier and Da (1945)
Nezara antennata Scott, 1784	14	6A + XY	Nishimura (1927[c]), Miyamoto (1957[a]),
			Yosida (1950[c])
N. antennata Scott, 1789 (as *N. icterica* Horvath, 1889)	14	6A + XY	Manna and Deb-Mallick (1981)
			Dey and Wangdi (1990)
N. viridula (Linnaeus, 1758)	14	6A + XY	Wilson (1911), Xavier and Da (1945)
			Manna (1951), Yosida (1956[a])
			Hughes-Schrader and Schrader (1957)
			Nuamah (1982), Camacho et al. (1985)
			Papeschi et al. (2003)
Niphe subferruginea (Westwood, 1837)	14	6A + XY	Parshad (1957a[a])
Niphe sp. (*near N. subferruginea*)	16	7A + XY	Parshad (1957c)
Oebalus pugnax (Fabricius, 1775) (as *Solubea pugnax*) (18)	10		Wilson (1909)
	10F		Wilson (1909)
	10		Hughes-Schrader and Schrader (1961)
Oebalus ypsilongriseus (De Geer, 1773)	14	6A + XY	Present work
Palomena angulosa (Motschulsky, 1861)	16	7A + XY	Yosida (1946[c], 1956[a])
			Takenouchi and Muramoto (1970[c]), 1971[d]
P. prasina (Linnaeus, 1761)	16	7A + XY	Schachow (1932b)
			Geitler (1939), Xavier and Da (1945)
P. reuteri Distant, 1879	16	7A + XY	Parshad (1957b)
P. viridissima (Poda, 1761)	16	7A + XY	Schachow (1932b)
Parantestia immunda (Linnavouri, 1975) (as *Antestia sp.? immunda*)	14	6A + XY	Nuamah 1982
Pellaea stictica (Dallas, 1851)	14	6A + XY	Hughes-Schrader and Schrader (1957)
Pentatoma japonica (Distant, 1882) (as *Tropidocoris japonicum*)	14	6A + XY	Parshad (1957a[c]), Ueshima (1979[a])
P. rufipes (Linnaeus, 1758)	14	6A + XY	Geitler (1939), Yosida (1950[c])
	–	6A + XY	Takenouchi and Muramoto (1968)
Pentatoma semiannulata (Motschulsky, 1859) (as *P. armandi* Fallou, 1881)	14	6A + XY	Zhang and Zheng (1999)
Pentatoma sp. 1	14	–	Yosida (1946[c])
Peribalus sp.	14	6A + XY	Hughes-Schrader and Schrader (1956)
Piezodorus guildinii (Westwood, 1837)	14	6A + XY	Rebagliati et al. (2001)
P. hybneri (Gmélin, 1789)	14	6A + XY	Manna (1951), Nuamah (1982)
P. lituratus (Fabricius, 1794)	14	6A + XY	Schachow (1932b), Xavier and Da (1945)
Placosternum ficusius Distant, 1918 (as *Placosternum urus* Stål, 1876)	14	6A + XY	Parshad (1957b)
P. taurus (Fabricius, 1781)	14	6A + XY	Dey and Wangdi (1988)
Plautia brunnipennis (Montrouzier et Signoret, 1861)	14	6A + XY	Muramoto (1979[b])

Table 2. (Continued)

Taxon	2*n* (1)	*n*	References
P. crossota stali Scott, 1879	14	6A + XY	Takenouchi and Muramoto (1970[c], 1971[d])
P. crossota (Dallas, 1851) [as *P. fimbriata* (Fabricius, 1787)]	14	6A + XY	Manna (1951)
Plautia sp.	14	6A + XY	Dey and Wangdi (1988)
Priassus exemptus (Walker, 1865)	14	6A + XY	Parshad (1957b)
P. spiniger Haglund, 1868	14	6A + XY	Mittal and Leelamma (1981[b])
Proxys albopunctulatus (Palisot de Beauvois, 1805)	14	6A + XY	Rebagliati et al. (2001)
Rhynchocoris humeralis (Thunberg, 1783)	14	6A + XY	Mittal and Leelamma (1981[b])
Rhytidolomia juniperina (Linnaeus, 1758) (as *Pitedia juniperina*)	14	–	Southwood and Leston (1959)
R. saucia (Say, 1832)	14	6A + XY	Schrader (1940)
	14F	–	
R. senilis (Say, 1832) (as *Pentatoma senilis*) (19)	6	2A + NeoX–NeoY	Wilson (1913[c])
			Schrader (1940)
Sabaeus humeralis (Dallas, 1851)	14	6A + XY	Manna and Deb-Mallick (1981)
Sepontia misella (Stål, 1853)	14	6A + XY	Nuamah (1982)
Spermatodes sp.	16	7A + XY	Manna (1951)
Stagonomus bipunctatus (Linnaeus, 1758)	12	5A + XY	Xavier and Da (1945)
Staria lunata (Hahn, 1835)	14	6A + XY	Xavier and Da (1945)
Thyanta antiguensis (Westwood, 1837)	14	6A + XY	Schrader and Hughes-Schrader (1956)
T. calceata (Say, 1832) (as *T. custator* (Fabricius, 1803)'B form') (20)	27	12A + X_1X_2Y	Wilson (1911)
			Schrader and Hughes-Schrader (1956)
	28 F	12A + $X_1X_1X_2X_2$	Schrader and Hughes-Schrader (1956)
T. custator (Fabricius, 1803)	16	7A + XY	Schrader and Hughes-Schrader (1956)
T. pallidovirens (Stål, 1856) (as *T. custator* "A form") (21) (22)	16	7A + XY	Wilson (1911)
			Schrader and Hughes-Schrader (1956)
T. pallidovirens pallidovirens (Stål, 1856)	14	6A + XY	Ueshima (1963)
T. pallidovirens spinosa Ruckes, 1957 (= *T. custator acerra* McAtee, 1919)	14	6A + XY	Ueshima (1963)
T. perditor (Fabricius, 1794)	14	6A + XY	Schrader and Hughes-Schrader (1956)
	14 F	6A + XX	
T. pseudocasta Blatchley, 1926	14	6A + XY	Schrader and Hughes-Schrader (1956)
			Hughes-Schrader and Schrader (1956)
Thyanta sp. 1	16	6A + XY	Present work
Thyanta sp. 2	14	6A + XY	Present work
Tolumnia latipes (Dallas, 1851)	14	6A + XY	Dey and Wangdi (1988)
Trichopepla semivittata (Say, 1832)	14	6A + XY	Montgomery (1901, 1906)
Trichopepla sp. 1	–	6A + XY	Hughes-Schrader and Schrader (1956)
Trichopepla sp. 2	14	6A + XY	Wilson (1905a)
Tyoma verrucosa Montandon, 1894	14	6A + XY	Nuamah (1982)
Udonga montana (Distant, 1900)	14	6A + XY	Manna (1951)
Veterna sanguineirostris (Thunberg, 1822)	14	6A + XY	Nuamah (1982)
Tribe Rolstoniellini			
Rolstoniellus bhutanicus (Dalls, 1849) (as *Compastes bhutanicus*)	14	–	Dey and Wangdi (1988)
Tribe Sciocorini			
Dyroderes umbraculatus (Fabricius, 1775)	14	6A + XY	Xavier and Da (1945)
Sciocoris cursitans (Fabricius, 1794)	14	6A + XY	Xavier and Da (1945)
S. helferi Fieber, 1851	14	6A + XY	Xavier and Da (1945)
S. sulcatus Fiebre, 1851	14	6A + XY	Xavier and Da (1945)
Tribe Strachiini			
Bagrada cruciferarum Kirkaldy, 1909 [as *B. picta* (Fabricius, 1775)]	14	6A + XY	Manna and Deb-Mallick (1981)
			Rao (1954[a], 1958[c]), Dutt (1955)
Eurydema dominulus (Scopoli, 1763)	14	6A + XY	Geitler (1939)
E. festiva (Linnaeus, 1767) (23)	14	6A + XY	Schachow (1932b), Xavier and Da (1945)
E. fieberi Fieber, 1837	14	6A + XY	Geitler (1939), Xavier and Da (1945)
E. gebleri Kolenati, 1846	14		Kuznetsova and Petropavlovskaya (1976)
Eurydema lituriferum (Walker, 1867)	14	6A + XY	Parshad (1957b)
E. oleracea (Linnaeus, 1758) (24)	14	6A + XY	Schachow (1932b)
			Geitler (1939), Xavier and Da (1945)
E. ornatum (Linnaeus, 1758)	14	6A + XY	Geitler (1939), Xavier and Da (1945)
E. pulchrum (Westwood, 1837)	14	6A + XY	Ueshima (1979)
E. rugosum Motschulsky, 1861 (as *E. rugosa*) (25)	14	6A + XY	Nishimura (1927[c]), Yosida (1946[c])
			Takenouchi and Muramoto (1968)
E. ventrale Kolenati, 1816 (as *E. ornata V pectoralis*) (26)	14	6A + XY	Schachow (1932b)
			Geitler (1939)
			Kuznetsova and Petropavlovskaya (1976)
Murgantia sp.	14	6A + XY	Hughes-Schrader and Schrader (1956)
Stenozygum coloratum (Klug, 1845)	14	6A + XY	Leston and Wahrman (unpublished data[a])

Table 2. (Continued)

Taxon	2*n* (1)	*n*	References
Subfamily Phyllocephalinae			
Macrina juvenca (Burmeister, 1835)	14	6A + XY	Nuamah (1982)
Subfamily Podopinae			
Ancyrosoma leucogrammes (Gmélin, 1789) [as *A. albolineatum* (Fabricius, 1781)]	14	6A + XY	Schachow (1932a[(b)]), Xavier and Da (1945)
Graphosoma italicum (Müller, 1766)	14	6A + XY	Schachow (1932b) Geitler (1939), Xavier and Da (1945)
	–	6A + XY	González García et al. (1996)
G. rubrolineatum (Westwood, 1837)	14	6A + XY	Yosida (1950[(c)]) Takenouchi and Muramoto (1968[(a)], 1970[(c)])
G. semipunctatum (Fabricius, 1775) (as *G.semipunctata*)	14	6A + XY	Schachow (1932b)
Podops inuncta (Fabricius, 1775)	14	–	Southwood and Leston (1959[(c)])
Scotinophara coarctata (Fabricius, 1798)	12	5A + XY	Satapathy et al. (1990)
S. fibulata (Germar, 1839)	14	6A + XY	Nuamah (1982)
S. horvathi Distant, 1883	14	6A + XY	Toshioka (1934[(c)])
Scotinophara sp.	12	5A + XY	Jande (1959, 1960[(c)])
Storthecoris nigricepes Horovath, 1883	14	6A + XY	Mittal and Leelamma (1981[(b)])

(1) Male diploid number, except in (F) (females); (2) Ueshima (1979) gives as reference Wilson (1909), and Nuamah (1982); Wilson (1906), but these species are not cited in the original articles; (3) Two males presented multiple sex determining system: *O. pacifica* – type II ($2n = 17 = 6 + X_1X_2Y$) and *O. pacifica* – type III ($2n = 16 = 6 + X_1X_2X_3Y$); (4) Species with 'harlequin lobe'; (5) as *Mecistorhinus melanoleucus* in Schrader (1946b); (6) as *Mecistorhinus sepulcralis* in Schrader (1946b, 1960a); (7) as *Mecistorhinus tripterus* in Schrader (1946b, 1960a); (8) Cited in Rebagliati et al. (2002) as *Acledra* sp.; (9) as *Nezara hilaris* in Montgomery (1901, 1906); Wilson (1905a, 1906, 1911[(c)]); (10) as *Agonoscelis nubilis* in Manna (1951) and *A. subila* in Dey and Wangdi 1988; (11) as *C.abbereviata* in Yosida (1950[(c)]); (12) as *Pentatoma* in Montgomery (1897, 1898); (13) as *Eusarcoris inconspicuus* in Xavier and Da (1945) and *Eusarcocoris inconspicuous* in Parshad (1957b); (14) as *Eusarcoris lewisi* in Yosida (1946[(c)]); (15) as *H. pica* in Manna (1951); (16) cited in Rebagliati et al. (2002) as *Mecocephala sp.*; (17) Wrongfully reported in Rebagliati et al. (2002) with $2n = 16 = 14 + XY$; (18) as *Solubea pugnax* in Hughes-Schrader and Schrader (1961); (19) as *Pentatoma senilis* in Wilson (1913); (20) as *T. custator* 'B form' in Wilson (1911); (21) as *T. custator* 'A form' in Wilson (1911); (22) Cited as *T. pallidovirens accerra* in Ueshima (1963); (23) as *E. festivum* in Xavier and Da (1945); (24) as *E. oleraceum* in Geitler (1939[(c)]); (25) as *E. rugosa* in Takenouchi and Muramoto (1968); (26) as *E. ornata V pectoralis* in Geitler (1939).
[(a)]Cited in Nuamah 1982; [(b)]cited in Kerzhner et al. 2004; [(c)]cited in Ueshima 1979; [(d)]cited in Muramoto 1973a.

multiple systems X_nO, X_nY and XY_n, and less frequently neo-XY (in only five species) (Ueshima 1979; Manna 1984; Grozeva and Nokkala 1996; Grozeva 1997; Nokkala and Grozeva 1997; Bressa et al. 1999; Nokkala and Nokkala 1999).

Two hypotheses concerning the evolution of the sex determining systems have been proposed in Heteroptera. Ueshima (1979) suggested that the XY system derived from an ancestral X0 which is commonly encountered in primitive heteropteran taxa and in primitive insect orders as well. By contrast, Nokkala and Nokkala (1983) suggested that the X0 system derived from the XY, present in the majority of the species analysed, on the basis of the discovery of an Y chromosome in Saldidae. New evidences of primitive taxa support the latter suggestion (Nokkala and Nokkala 1984; Grozeva and Nokkala 1996). Nevertheless, Bressa et al. (1999) considered that the neo-XY system of *Dysdercus albofasciatus* Berg, 1878; could support Ueshima's hypothesis.

Another cytogenetic characteristic of many heteropteran species is the presence of a minute chromosome pair with a special meiotic behaviour. These m chromosomes are generally observed unpaired during early meiotic prophase and no chiasma is detected between them. It is uncertain which the origin of this chromosome pair is and which is their function in the genetic system of the species possessing them (Ueshima 1979). On the basis of its presence in the primitive infraorder Dipsocoromorpha, Grozeva and Nokkala (1996) suggested that the m chromosomes were present in the ancestral karyotype of the Heteroptera.

During male meiosis sex chromosomes are identified from early prophase onwards because they are positively heteropycnotic. After pachytene many species present a diffuse stage during which the bivalents decondense and the nucleus increases its size and acquires an interphase appearance. Immediately after the diffuse stage the cell entres diakinesis and bivalents show one or sometimes two chiasmata. At metaphase I autosomal bivalents arrange in a circle with the sex univalents at its centre. The asynaptic sex chromosomes lie side by side, segregating sister chromatids at anaphase I. The first meiotic division is therefore reductional for autosomes and m chromosomes, and equational for the sex chromosomes. The second meiotic division follows immediately after the first one without interkinesis. At metaphase II the autosomes dispose at the periphery of the spindle while the sex chromosomes associate non-chiasmatically forming a pseudo-bivalent that localizes at the centre of the ring of autosomes. At anaphase II, the X and Y segregate to opposite poles and second division is reductional for the sex chromosomes (Ueshima 1979).

Cytogenetic reports show that most Pentatomidae present a diploid number $2n = 14$ and a sex chromosome determining system XY/XX, without a pair of m chromosomes, and male meiosis follows this general pattern. However, one particular feature of some species of this family is the regular presence of an abnormal meiosis in one testicular lobe (harlequin lobe). Bowen (1922a,b cited in Ueshima 1979) and Schrader (1945a,b, 1946a,b, 1960a,b) were the first to report the presence of this harlequin lobe, and later Rebagliati et al. (2001) and Lanzone et al. (2003) also described it, summing up a total number of 22 species belonging to Pentatominae, Edessinae and Discocephalinae.

Table 3. Diploid chromosome number (autosomal number and sex chromosome determining system) in Pentatomoidea and subfamilies and tribes of Pentatomidae

Family	2*n* (males)	Number of species
Acanthosomatidae[1]		12
	10 + XY	9
	12 + XY	1
	14 + XY	1
	10 + XO	1
Cydnidae[1]		14
	10 + XY	8
	12 + XY	4
	24 + XY	1
	28 + X_1X_2Y	1
Dinidoridae[1]		12
	12 + XY	8
	18 + X_1X_2Y	1
	18 + XY	3
Plataspididae[1]		16
	8 + XY	1
	10 + XY	15
Tessaratomidae[1]		9
	10 + XY	7
	12 + XY	2
Thaumastellidae[1]		2
	16 + 2m + XY	1
	14 + 2m + XY	1[2]
	12 + 2m + X_1X_2Y	
Scutelleridae[1]		27
	10 + XY	27[3]
	12 + XY	1[3]
Urostylididae[1]		5
	12 + XY	2
	14 + XY	3
Pentatomidae		294
Asopinae		22
	10 + XY	2[4]
	12 + XY	16[4]
	14 + XY	4
	16 + XY	1
Discocephalinae		18
Discocephalini	12 + XY	11
Ochlerini	12 + XY	7[5]
	12 + X_1X_2Y	1[5]
Edessinae		15
	12 + XY	15
Pentatominae		228
Aeptini	12 + XY	1
Halyini	12 + XY	13
Lestonocorini	14 + XY	1
Myrocheini	12 + XY	1
Pentatomini	4 + NeoX–NeoY	1
	10	1
	10 + XY	6
	12 + XY	153
	14 + XY	19
	24 + XY	13
	24 + X_1X_2Y	1
Rolstoniellini	12 + XY	1
Sciocorini	12 + XY	4
Strachiini	12 + XY	13
Phyllocephalinae		1
	12 + XY	1
Podopinae		10
	12 + XY	8
	10 + XY	2

[1]Number of species and diploid chromosome numbers of all the families (except Pentatomidae) are taken from Muramoto (1973a,b); Ueshima (1979); Manna and Deb-Mallick (1981); Nuamah (1982); Manna (1984); Dey and Wangdi (1988); Jacobs (1989); Satapathy and Patnaik (1989); Satapathy et al. (1990) and Kerzhner et al. (2004).
[2]*Thaumastella manaquensis* has been cited with $2n = 14 + 2m + XY$ and $12 + 2m + X_1X_2Y$ in different populations.
[3]*Eurygaster maura* has been cited with $2n = 12$ and $2n = 14$ by different authors.
[4]*Picromerus bidens* has been cited with $2n = 12$ and $2n = 14$ by different authors.
[5]*Macropygium reticulare* has been cited with $2n = 12 + XY$ and $2n = 12 + X_1X_2Y$ by different authors.

Materials and Methods

The species of Pentatomidae we have cytogenetically analysed are listed in Table 1. Adult males were analysed following standard procedures (Rebagliati et al. 2001).

Results and Discussion

The chromosome number and sex chromosome determining system in all the species and subspecies of Pentatomidae cytogenetically analysed until present are listed in Table 2. The number of species, diploid numbers and sex chromosome determining systems of superfamily Pentatomoidea are summarized in Table 3. The detail at subfamily and tribe level is given only for Pentatomidae.

The 28 species cytogenetically analysed from Argentine material present a meiotic behaviour that agrees with the previous description for the family. With reference to the diploid number 21 species present $2n = 14$; four species [*Dichelops furcatus* (Fabricius, 1775), *Dichelops melacanthus* (Dallas, 1851), *Mecocephala maldonadensis* Schwertner, Grazia and Fernandes, 2002 and *Acledra bonariensis* (Stål, 1859)] present a reduced number ($2n = 12$) and another three species [*Podisus distinctus* (Stål, 1860), *Podisus nigrispinus* (Dallas, 1851) and *Thyanta* sp.1] possess an increased diploid number ($2n = 16$). All of them have a sex chromosome determining system XY/XX (Fig. 1). Among the analysed Argentinean species only *Dinocoris prolineatus* Becker and Grazia, 1985, *Loxa deducta* Walker, 1867 and *Macropygium reticulare* (Fabricius, 1803) present a harlequin lobe. The analysis of all of them suggests a common meiotic pattern. Among the meiotic traits that are altered in the harlequin lobe we can mention: meiotic pairing and chiasma formation, non-specific association of autosomes, an anomalous disposition of the chromosomes in the metaphase plate, chromosome segregation and cellular fusion. The final result is the production of sperm with an abnormal and highly variable chromosome number, which will affect the individual fertility (Fig. 2).

Within Pentatomidae 294 species and subspecies belonging to 121 genera from the subfamilies Asopinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae and Podopinae have been cytogenetically analysed. The male diploid numbers are between six and 27 with a mode in 14 chromosomes; the latter diploid number is present in 85% of the species. The sex chromosome determining system is XY/XX except in three species: *M. reticulare*, *Rhytidolomia senilis* (Say, 1832) and *Thyanta calceata* (Say, 1832) (Ueshima 1979; Manna and

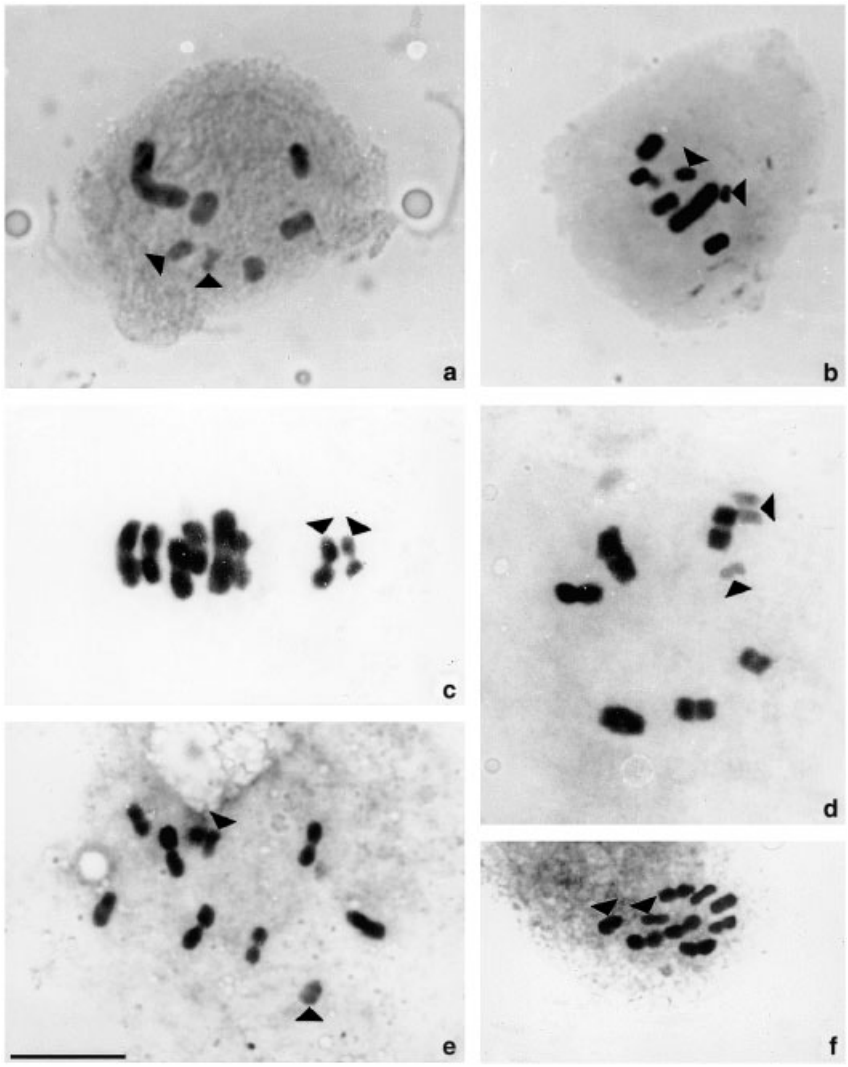

Fig. 1. (a) Prometaphase I of *Mecocephala maldonadensis* ($2n = 12 = 10 + XY$); (b) metaphase I of *Dichelops melacanthus* ($2n = 12 = 10 + XY$); (c) metaphase I of *Euschistus heros* ($2n = 14 = 12 + XY$); (d) prometaphase I of *Edessa sp.* ($2n = 14 = 12 + XY$); (e) diakinesis of *Podisus distinctus* ($2n = 16 = 14 + XY$); (f) prometaphase I of *Podisus nigrispinus* ($2n = 16 = 14 + XY$). Arrowheads point to the sex chromosomes. Bar = 10 μm

Deb-Mallick 1981; Nuamah 1982; Dey and Wangdi 1988; Satapathy and Patnaik 1988, 1989; Satapathy et al. 1990; Rebagliati 2000; Rebagliati et al. 2001, 2002, 2003; Lanzone et al. 2003; Kerzhner et al. 2004).

Within the subfamily Asopinae 22 species have been studied and the modal number is $2n = 14$ ($n = 6 + XY$) with a reduction in chromosome number in *Oechalia patruelis* (Stål, 1859) and a population of *Picromerus bidens* (Linnaeus, 1758) ($2n = 12$, $n = 5 + XY$); and an increase in chromosome number in all the species of *Podisus* Herrich-Schaeffer, 1853 ($2n = 16$, $n = 7 + XY$) and in *Dynorhynchus dybowskii* Jakovlev, 1876 ($2n = 18$, $n = 8 + XY$). Within Discocephalinae the 18 species cytogenetically analysed present $2n = 14$ ($n = 6 + XY$). In *M. reticulare*, Srivastava (1957) described $2n = 15$ ($n = 6 + X_1X_2Y$, male)/$2n = 16$ ($n = 6 + X_1X_1X_2X_2$, females), although according to Rebagliati et al. (2001) the third sex chromosome should be a B chromosome. The 15 species of the subfamily Edessinae and the unique species of Phyllocephalinae cytogenetically analysed show a constant diploid number and sex chromosome determining system $2n = 14$ ($n = 6 + XY$). Within the subfamily Pentatominae the study of 228 species reveals different diploid numbers from six in *R. senilis* ($2n = 4 +$ neoX–neoY) to 27 in *T. calceata* ($2n = 24 + X_1X_2Y$) with a modal number of 14, and a sex chromosome determining system XY/XX (Wilson 1911; Schrader 1940; Schrader and Hughes-Schrader 1956). The other numbers described are $2n = 10$ (in *Oebalus pugnax* Fabricius, 1775), $2n = 12$ ($n = 5 + XY$) in *A. bonariensis*, *D. furcatus*, *D. melacanthus*, *M. maldonadensis*, *Euschistus crassus* Dallas, 1851 and *Stagonomus bipunctatus* (Linnaeus, 1758); $2n = 16$ ($n = 7 + XY$) in 20 species of the genera *Banasa* Stål, 1860, *Caystrus* Stål, 1861, *Cosmopepla* Stål, 1867, *Dunnius* Distant, 1902, *Eysarcoris* Hahn, 1834, *Gynenica* Dallas, 1851, *Niphe* Stål, 1867, *Palomena* Mulsant and Rey, 1866, *Spermatodes* Bergroth, 1914 and *Thyanta* Stål, 1862, and $2n = 26$ ($n = 12 + XY$) in 13 species of *Banasa*.

Among the 10 species of Podopinae only *Scotinophara coarctata* Fabricius, 1798 and *Scotinophara* sp. show a reduction in the diploid number ($2n = 12$, $n = 5 + XY$).

Phylogenetic relationships among the 16 families of Pentatomoidea are under investigation (J. Grazia, personal communication). From a cytogenetic point of view, Schaefer (1993) stated that the presence of a pair of m chromosomes in Thaumastellidae (Jacobs 1989), which is lacking in all other families of Pentatomoidea, would suggest a relationship with species of Lygaeoidea, in which m chromosomes are widely present. Henry (1997) suggested that the presence of m chromosomes, although lost in a few taxa (Berytidae, Lygaeinae, and Piesmatidae), is a synapomorphy defining a broad group within the Pentatomomorpha, and that the

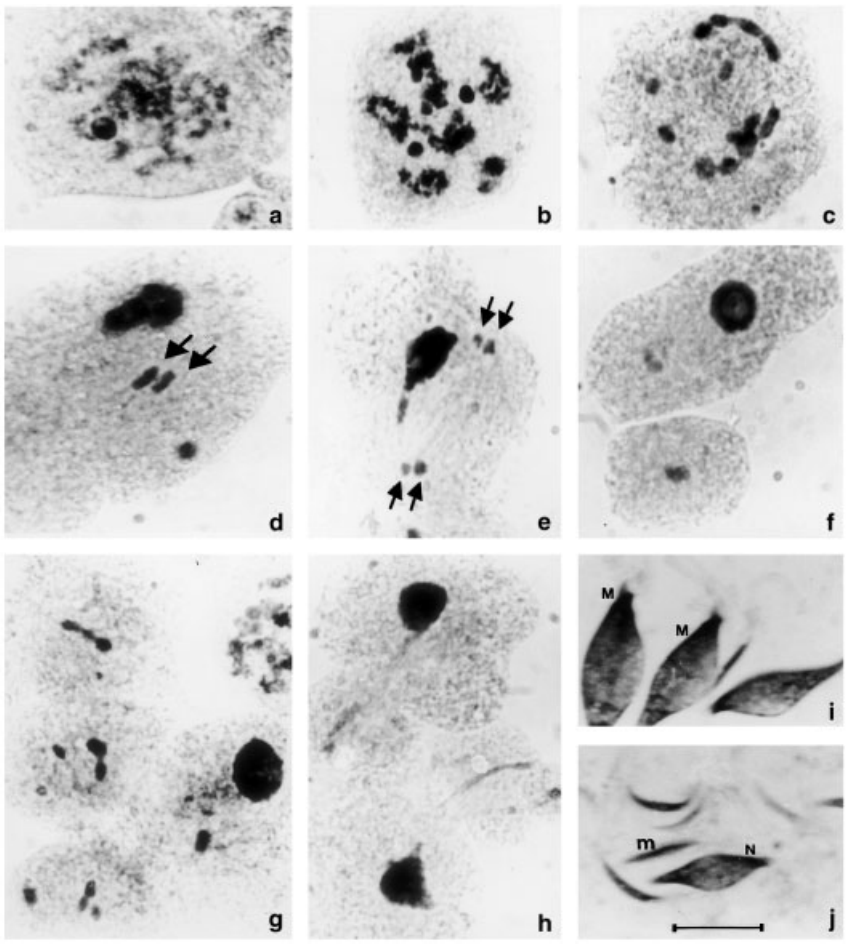

Fig. 2. Meiosis in the harlequin lobe of *Loxa deducta* ($2n = 14 = 12 + XY$): (a) leptotene–zygotene; (b) diplotene; (c) diakinesis, non-specific association of the chromosomes can be observed; (d) metaphase I, the autosomes are associated in a 'clump' and the sex chromosomes are separated; (e) anaphase I, the sex chromosomes segregate equationally, and one autosome leaves the 'clump'; (f and g) different cells types in metaphase II; (h) telophase II; (i) macrospermatids (M); (j) microspermatids (m); and normal spermatids (N). Arrow point to the sex chromosomes. Bar = 10 μm

Thaumastellidae, because of the presence of a pair of m chromosomes, may not belong to the Pentatomoidea. On the other hand, many synapomorphies to the Pentatomoidea are found in the Thaumastellidae (e.g. presence of foretibial apparatus, developed mandibular plates, base of head not forming a 'neck', post-ocular tubercles absent, structure of the female genitalia, and paired lateral trichobothria) (J. Grazia, personal communication). Taking into account the hypothesis of Grozeva and Nokkala (1996), that m chromosomes might be included in the ancestral karyotype of Heteroptera, the absence of m chromosomes in the family Pentatomidae could be assumed as a derived character.

According to Manna (1984) from a plesiomorphic karyotype $2n = 14$ (12 + XY) two branches evolved within Pentatomoidea; one of them includes the families that maintain this chromosome complement, e.g. Pentatomidae, while the other branch includes families with a reduction in diploid number. Acanthosomatidae, Cydnidae, Plataspididae, Scutelleridae and Tessaratomidae belong to this branch; all of them have a modal number $2n = 12$ (10 + XY) which could suggest a common origin. Dinidoridae and Urostylididae present the plesiomorphic chromosome number, although some species present an increase in the chromosome number. In Thaumastellidae, the two species analysed present an increased diploid number (Table 3).

The multiple sex chromosome system $X_1X_2Y/X_1X_1X_2X_2$ has been reported in unrelated species within Pentatomoidea, suggesting that the origin of these derived systems should have been independent. Only one species has been reported with an XO system (*Acanthosoma expansum* Horvath, 1905) and it would be desirable to reanalyse it. Within Pentatomidae the increase in diploid number through fragmentations of autosomes and/or sex chromosomes has been more frequent than its reduction through chromosome fusions (11% versus 4% of the total number of species cytogenetically analysed). The great uniformity in chromosome number and sex determining system found in Pentatomidae indicates that speciation within this family is not accompanied by a process of karyotype change.

Until present a total number of 22 species of 15 genera of Pentatomidae have been reported that present an harlequin lobe with abnormal meiosis. Although there is a common pattern in the meiotic behaviour, all the species that bear it present peculiar traits (Bowen 1922a,b; Schrader 1945a,b, 1946a,b; Martin 1953; Srivastava 1957; Ansley 1958; Schrader 1960a,b; Rebagliati et al. 2001; Lanzone et al. 2003).

Rolston (1981) includes the genera *Alitocoris* Sailer, 1850, *Macropygium* Spinola, 1837, *Melanodermus* Stål, 1867 (*Ochlerus* Spinola, 1837), *Moncus* Stål, 1867 and *Schraderia* Ruckes, 1959 (*Schraderiellus* Rider, 1998) in the tribe Ochlerini (Discocephalinae), which were previously included in the tribe Halyini (Pentatominae). Although no direct relationship between the presence of the harlequin lobe and a particular taxonomic rank seems to exist, according to this new classification 11 of the 15 genera with harlequin lobe belong to Discocephalinae {only *Discocephalessa humilis* Herrich-Schaeffer, 1843 [as *Platycarenus notulatus* (Stål, 1862)] of this family

does not possess it}. On the other hand, only *Loxa* Amyot and Serville, 1843 (three species) *Mayrinia* Horvath, 1925 (one species) and *Adevoplitus* Grazia and Becker, 1997 (*Pseudevoplitus* Ruckes, 1958) (one species) within Pentatomini (the tribe most vastly studied of Pentatominae) and *Brachystethus rubromaculatus* Dallas, 1851 within Edessinae show this abnormal meiosis. It is necessary to widen the cytogenetic analysis to more species from different regions in order to determine whether any relationship with the environment does exist, and to clarify its evolutionary and/or biological meaning.

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Zusammenfassung

Cytogetische Untersuchungen an Pentatomidae (Heteroptera). Ein Review

Die Untergruppe Heteroptera bildet eine sehr wichtige Insektengruppe, weil die meisten Arten Pflanzenfresser sind und daher schadhaft für viele wirtschaftlich bedeutende Pflanzen. Eine der wichtigsten cytogenetischen Eigenschaften von Heteroptera ist die holokinetische Natur ihrer Chromosomen. Ein Merkmal einiger Pentatomiden-Arten ist das reguläre Vorkommen einer anormalen Meiosis in einem Teil der Hodenlappen (harlequin lobe). Von den 28 cytogenetisch untersuchten Arten (argentinisches Material) weisen 21 die diploide Zahl von $2n = 14$ auf, vier eine reduzierte Zahl von $2n = 12$ und drei andere haben die größere Zahl von $2n = 16$. Von diesen haben nur drei den harlequin lobe. In der vorliegenden Arbeit befassen wir uns mit der bibliographischen Revision der Chromosomenzahlen und des geschlechtsbestimmenden Systems von 294 Arten und Unterarten, die zu 121 Gattungen der Subfamilien Asopinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae und Podopinae gehören. Die Zahlen diploider Männchen liegen zwischen 6 und 27; am häufigsten sind es 14, eine Zahl, die in 85% der Arten vorhanden ist. Das geschlechtsbestimmende System ist XY/XX, außer in drei Arten: *M. reticulare* (Fabricius, 1803), *Rhytidolomia senilis* (Say, 1832) und *Thyanta calceata* (Say, 1832). Außerdem werden die cytogenetischen Beziehungen mit den anderen Familien der Pentatomoidea behandelt.

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Authors' addresses: Lic. Pablo J. Rebagliati (for correspondence), L.M. Mola and A.G. Papeschi, Laboratorio de Citogenética y Evolución, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes y Costanera Norte C1428EHA Buenos Aires, Argentina. E-mail: gchu@bg.fcen.uba.ar; J. Grazia, Av. Bento Gonçalves 9.500, Campus do Vale, Prédio 43435, Sala 223., 91501-970 Porto Alegre RS, Brazil. E-mail: jocelia@uprgs.br