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Karyotype evolution in Reduviidae (Insecta: Heteroptera) with special reference to Stenopodainae and Harpactorinae

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Abstract. Heteropteran insects are characterized by holokinetic chromosomes, and, in most species, the post-reductional meiotic division of sex chromosomes and the presence of one chiasma per bivalent. The Reduviidae have a modal diploid autosomal number of 20 with a range between 12 to 34, and both simple and multiple sex chromosome systems (XY/XX, X0/XX, X_nY/X_nX_n). Within this family cytogenetic reports on 127 species belonging to 11 subfamilies are available. Stenopodainae (10 species) have a diploid autosomal number of 20/22 plus different multiple sex chromosome systems; in Harpactorinae 33 species belonging to 18 genera have been cytogenetically analysed, and the modal diploid number of the subfamily is $2n=28=24+X_1X_2X_3Y$ (male). In the present work we analyse the karyotype and male meiosis of *Stenopoda cinerea* Laporte, 1833 ($2n=25=20+X_1X_2X_3X_4Y$) (male) (Stenopodainae); *Zelus* sp. prope *leucogrammus* (Perty, 1834) (2n=26=24+XY) (male), *Apiomerus lanipes* (Fabricius, 1803) (2n=24=22+XY) (male), *Cosmoclopius nigroannulatus* (Stål, 1860) and *C. poecilus* (Herrich-Schaeffer, 1848) ($2n=28/30=24+X_1X_2X_3Y/24+X_1X_1X_2X_2X_3X_3$) (male/female) (Harpactorinae). Considering the cytogenetic characteristics of Reduviidae two evolutionary trends can be observed within the family: a reduction in the number of autosomes through fusion mechanisms, and an increase in the number of sex chromosomes through fragmentations (multiple systems). Furthermore, the presence of multiple sex chromosome systems is much more frequent in Harpactorinae and Stenopodainae than in the other subfamilies. These cytogenetic trends support a previously proposed phylogeny based on morphological, ecological and behavioural traits (Ambrose, 1999).

Key words: Heteroptera, Reduviidae, holokinetic chromosomes, karyotype evolution, sex chromosomes.

Introduction

Reduviidae are the largest family of predaceous land Heteroptera, and contain about 930 genera and 6500 species placed in 22 subfamilies. The size of these predatory assassin bugs ranges from relatively small and extremely delicate insects of only a few millimetres in length, such as members of the genus *Empicoris* Wolff, 1811 (Emesinae) to very large and formidable animals such as *Arilus* Hahn, 1831 (Harpactorinae), which may attain a length of nearly 40 mm (Schuh, Slater, 1995). Most reduviids are general predators and they occur worldwide. Being larger than many other preda-

Table 1. Available cytogenetic data on species belonging to the subfamilies Stenopodainae and Harpactorinae.

Species	2n♂	2n♀	n (♂)	References
Stenopodainae				
Oncocephalus impudicus Reuter, 1882	23	-	10A+X_1X_2Y	Jande, 1959b
O. naboides Walker, 1873	26	-	11A+$X_1X_2X_3Y$	Manna, Deb-Mallick, 1981
O. nubilus Van Duzee, 1914	26	-	11A+$X_1X_2X_3Y$	Ueshima, 1979
Oncocephalus sp. 1	23	24	10A+X_1X_2Y	Jande, 1959b
Oncocephalus sp. 2	24	-	10A+$X_1X_2X_3Y$	Jande, 1959b
Oncocephalus sp. 3	23	-	10A+X_1X_2Y	Manna, Deb-Mallick, 1981
Oncocephalus sp. 4	23	-	10A+X_1X_2Y	Satapathy, Patnaik, 1989
Pnirontis modesta Banks, 1910	25	-	10A+$X_1X_2X_3X_4Y$	Payne, 1912
Pygolampis foeda Stål, 1859	24 25	- -	11A+XY 11A+X_1X_2Y	Banerjee, 1958 (NW India) Jande, 1959b (Calcutta)
Stenopoda cinerea Laporte, 1833	25	-	10A+$X_1X_2X_3X_4Y$	Present work
Harpactorinae				
Acholla ampliata Stål, 1872 *(*as *A. multispinosa)*	32	-	16(M I)	Payne,1909, Mongomery, 1901
A. multispinosus De Geer, 1773	26	30	10A+$X_1X_2X_3X_4X_5Y$	Payne, 1909, Payne, 1910, Troedsson, 1944
Apiomerus crassipes Fabricius, 1803	24	-	11A+XY	Payne, 1912
A. flaviventris Herrich-Schaeffer, 1846	24	-	11A+XY	Ueshima, 1979
A. lanipes (Fabricius, 1803)	24	-	11A+XY	Present work
A. spissipes Say, 1825	24	-	11A+XY	Ueshima, 1979
Apiomerus sp.	24	-	11A+XY	Ueshima, 1979
Arilus cristatus Linnaeus, 1763	26	28	12A+$X_1X_2X_3Y$	Payne, 1909, Montgomery, 1901, Troedsson, 1944
Coranus fuscipennis Reuter, 1881	27	-	12A+X_1X_2Y	Jande, 1959b
Cosmoclopius nigroannulatus (Stål, 1860)	28	30	12A+$X_1X_2X_3Y$	Present work
C. poecilus (Herrich-Schaeffer, 1848)	28	30	12A+$X_1X_2X_3Y$	Present work
Cydnocoris crocatus Stål, 1866	27		12A+X_1X_2Y	Dey, Wangdi, 1988
Fitchia spinulosa Stål, 1872	27	28	12A+X_1X_2Y	Payne, 1909
Heniartes huacapistana Wygodzinsky, 1947	24	-	11A+XY	Ueshima, 1979
Lophocephala guerini Laporte, 1833	27	-	12A+X_1X_2Y	Satapathy, Patnaik, 1989
Polididus armatissimus Stål, 1859	12 14	- -	5A+XY 6A+XY	Banerjee, 1958; Payne, 1909, Toshioka, 1936 Jande, 1960

Table 1. Continuation.

Polididus sp.	12	-	5A+XY	Manna, Deb-Mallick, 1981
Pselliopus cinctus Fabricius, 1776	28	30	$12A+X_1X_2X_3Y$	Payne, 1912
Rhynocoris fuscipes (Fabricius, 1787)	28	-	$12A+X_1X_2X_3Y$	Dey, Wangdi, 1988, Satapathy, Patnaik, 1989, Manna, 1951
R. marginatus (Fabricius, 1781)	28	-	$12A+X_1X_2X_3Y$	Satapathy, Patnaik, 1989, Banerjee, 1958, Jande, 1959a.
Rhynocoris sp.	28	-	$12A+X_1X_2X_3Y$	Dey, Wangdi, 1988
Rocconota annulicornis Stål, 1872	27	-	$12A+X_1X_2Y$	Payne, 1909
Sinea complexa Caudell, 1900	28	30	$12A+X_1X_2X_3Y$	Payne, 1909
S. confusa Caudell, 1901	28	30	$12A+X_1X_2X_3Y$	Payne, 1909
S. diadema Fabricius, 1776	- 28	- 30	16 (M I) $12A+X_1X_2X_3Y$	Montgomery, 1901 Payne, 1909, Troedsson, 1944
S. rileyi Montandon, 1893	26	-	$10A+X_1X_2X_3X_4X_5Y$	Payne, 1909
S. spinipes Herrich-Schaeffer, 1846	28	30	$12A+X_1X_2X_3Y$	Payne, 1909
Sycanus collaris (Fabricius, 1785)	28	-	$12A+X_1X_2X_3Y$	Jande, 1959b
Sycanus sp.	28	-	$12A+X_1X_2X_3Y$	Manna, 1951
Velinus nodipes (Uhler, 1860)	28	30	$12A+X_1X_2X_3Y$	Toshioka, 1933, Yosida, 1947
Vesbius purpureus (Thunberg, 1784)	26	-	12A+XY	Manna, Deb-Mallick, 1981
Zelus exsanguis Stål, 1862 (as *Diplacodus exsanguis)*	26	26	12A+XY	Payne, 1909
Zelus sp. prope *leucogrammus* (Perty, 1834)	26	-	12A+XY	Present work

ceous land bugs and encompassing in their development a greater range of size, reduviid predators consume not only more prey but also a wider array of prey. Hence, they are important mortality factors and should be conserved and augmented for their utilization in biocontrol programs. Within Reduviidae the species belonging to Triatominae are distinctive for their blood-sucking habits, and several of them are vectors or potential vectors of Chagas' disease (Schaefer, Panizzi, 2000).

Cytogenetic reports are available for 122 species of Reduviidae. Apart from the general features of heteropteran insects (holokinetic chromosomes, post-reductional meiotic division of sex chromosomes, one chiasma per bivalent in male meiosis), reduviids are characterized by a modal diploid number of autosomes of 20 with a range between 10 to 34, and both simple and multiple sex chromosome systems: XY/XX (46.34%) and X_nY/X_nX_n (51.22 %); only 3 species have an X0/XX system (Ueshima, 1979).

In the present work we studied the karyotype and male meiosis of *Stenopoda cinerea* Laporte, 1833 (Stenopodainae), *Zelus* sp. prope *leuco-*

Table 2. Number, date and provenance of adult male and female specimens.

Taxa	No. of males	No. of females	Date of collection	Provenance (Argentina)
Stenopoda cinerea	4	-	01.I.05	Villaguay, Prov. Entre Ríos
Apiomerus lanipes	8	-	01.I.05	Villaguay, Prov. Entre Ríos
Zelus sp. prope *leucogrammus*	5	-	09.II.97	Mercedes, Prov. Corrientes
Cosmoclopius nigroannulatus	4	1	27-28.I.03	Arroyo Tabay, Prov. Misiones
	1	-	22.II.01	Isla Martín García, Prov. Bs. As.
	1	1	27-28.I.03	San Ignacio, Prov. Misiones
	2	-	V.06	Gualeguaychú, Prov. Entre Ríos
	-	1	X.06	Esperanza, Prov. Santa Fe
Cosmoclopius poecilus	3	-	16.I.03	La Paz, Prov. Entre Ríos

grammus (Perty, 1834), *Apiomerus lanipes* (Fabricius, 1803), *Cosmoclopius nigroannulatus* (Stål, 1860) and *C. poecilus* (Herrich-Schaeffer, 1848) (Harpactorinae). Previous cytogenetic studies in the subfamily Stenopodainae report a diploid number of 20/22 autosomes plus different multiple sex chromosome systems (Table 1). Within Harpactorinae 29 species belonging to 16 genera have been cytogenetically analysed, and the modal diploid autosomal number of the subfamily is 24 with both simple and multiple sex chromosome systems (Table 1). Considering the available cytogenetic characteristics of Reduviidae together with the results here presented the evolutionary karyotypic trends within the family were analysed.

Material and methods

Specimens

The number of male and female individuals of *Stenopoda cinerea* (Stenopodainae), *Apiomerus lanipes*, *Zelus* sp. prope *leucogrammus*, *Cosmoclopius nigroannulatus* and *C. poecilus* (Harpactorinae), and their provenance are indicated in Table 2.

Chromosome preparations

Some individuals were fixed in the field in 3:1 (ethanol:glacial acetic acid) and other specimens were brought alive to the laboratory. Gonads were dissected under a binocular microscope. Gonads fixed in 3:1 were used for slides by squash procedures and standard staining techniques (haematoxylin staining).

Results

In the five species here analysed the male meiosis follows the general heteropteran pattern. During early prophase I the sex chromosomes are recognized because they are positively heteropycnotic. After pachytene the cells enter a diffuse stage during which the autosomes decondense completely. At diplotene the autosomal bivalents recondense, and in most species they present only one chiasma. At metaphase I the autosomal bivalents and the sex univalents arrange at the equatorial plane, and at anaphase I the sex univalents segregate equationally, while the autosomes divide reductionally. At metaphase II the autosomes are arranged to form a ring and the sex

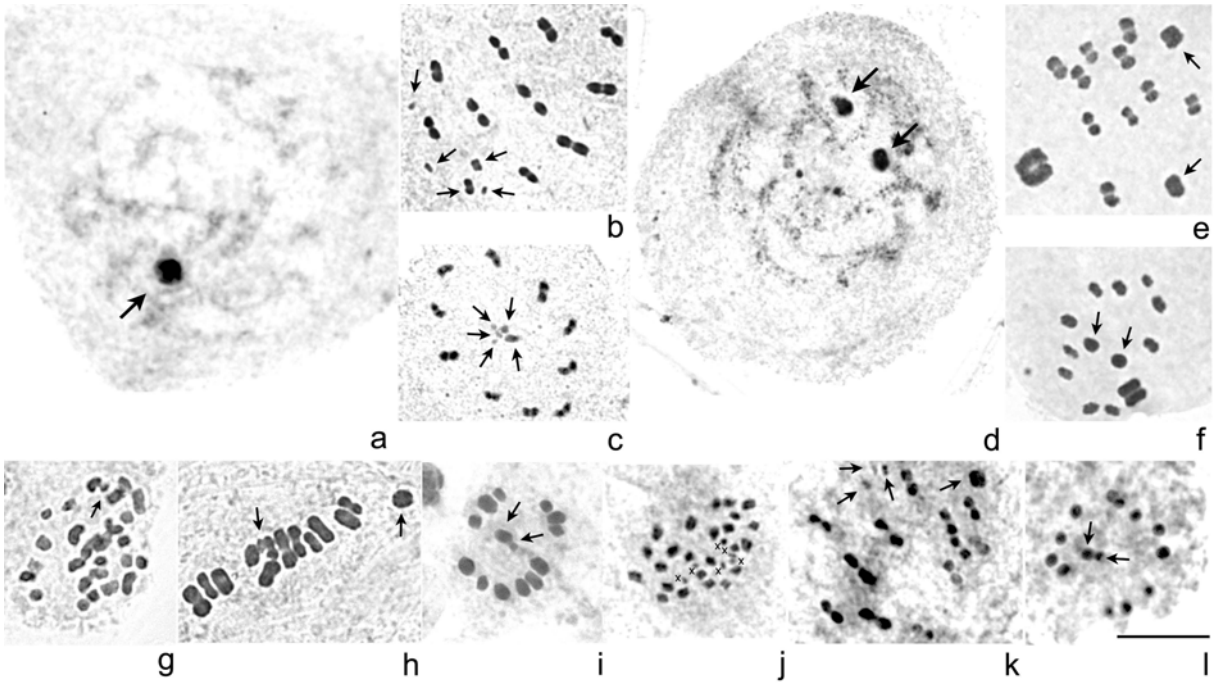

Fig. 1, a-l. a-c - *Stenopoda cinerea*; **a** - diffuse stage, **b** - metaphase I, **c** - metaphase II. **d-f** - *Apiomerus lanipes*; **d** - diffuse stage, **e** - metaphase I, **f** - metaphase II. **g-i** - *Zelus* sp. prope *leucogrammus*; **g** - spermatogonial prometaphase, **h** - metaphase I, **i** - metaphase II. **j-l** - *Cosmoclopius nigroannulatus*; **j** - oogonial prometaphase, **k** - metaphase I , **l** - metaphase II . Arrows show sex chromosomes. Bar=10 μm.

chromosomes associate in a pseudobivalent or pseudomultivalent, which lies at the centre of the ring of autosomes and divides reductionally at anaphase II.

The presence and duration of the diffuse stage, the number and position of chiasmata and the arrangement of the autosomal bivalents and the sex univalents at metaphase I are features that differ among the species.

Stenopoda cinerea has 2n=25=20+X_1 $X_2X_3X_4Y$ (male); autosomes decrease gradually in size and three out of the five sex chromosomes are very small. In the male meiosis of this species a long diffuse stage is observed (Fig. 1, a), bivalents present only one chiasma at terminal position, and at metaphase I the sex univalents are located at the periphery of the plate (Fig. 1, b). At metaphase II the sex pseudopentavalent lies at the centre of the ring of autosomes (Fig. 1, c).

Apiomerus lanipes has 2n=22+XY (male) (Fig. 1, d-f). Among the autosomes one pair is remarkably larger, and the X and Y sex chromosomes are the second largest, and similar in size. Male meiosis presents a long diffuse stage (Fig. 1, d), and at diakinesis each bivalent presents one chiasma at terminal position, except for the largest pair that shows two terminal/subterminal chiasmata. At metaphase I the eleven bivalents plus the X and Y univalents arrange disorderly at the equatorial plane (Fig. 1, e). At metaphase II the autosomes dispose in a ring, and the XY pseudobivalent lies at its centre (Fig. 1, f).

Zelus sp. prope *leucogrammus* presents 2n=26=24+XY (male) (Fig. 1, g-i). The X chromosome is the smallest of the complement and the Y cannot be recognized at mitotic prometaphase

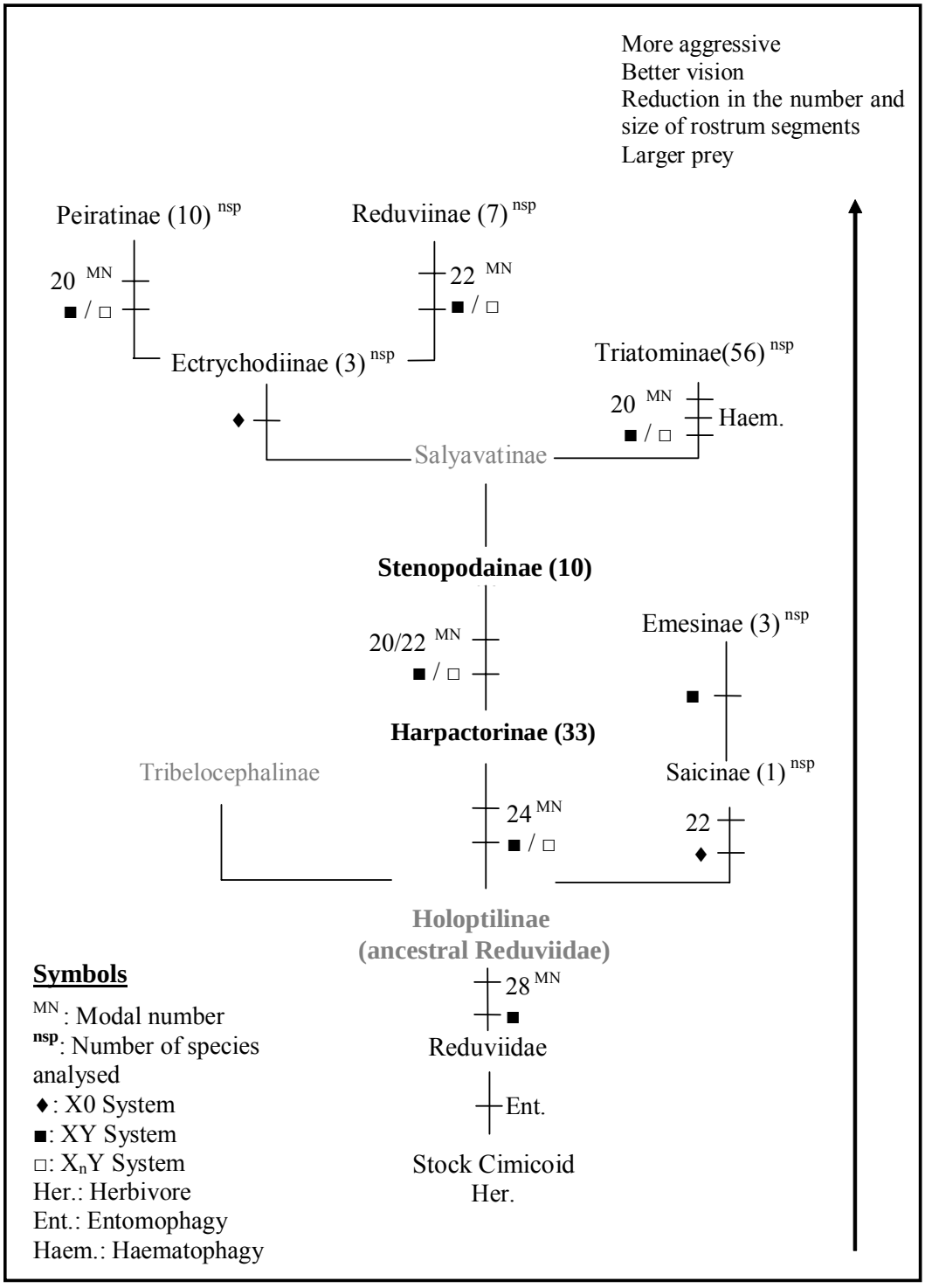

Fig. 2. Origin and evolution of the Reduviidae (modified from Ambrose, 1999) and cytogenetic characteristics of members of the family (modal autosomal diploid number, sex chromosome system and number of species cytogenetically analysed in each subfamily).

because it is similar in size to the autosomes. During male meiosis no diffuse stage is detected, and chromosomes do not show any particular arrangement at the first meiotic metaphase plate (Fig. 1, h); however, the metaphase II arrangement is the typical heteropteran one with the sex chromosomes associated in a pseudobivalent and in the centre of the autosomal ring (Fig. 1, i).

Cosmoclopius nigroannulatus and *C. poecilus* share the same cytogenetic characteristics and male meiotic behaviour. They have 2n=28/30=24+$X_1X_2X_3Y$/ 24+$X_1X_1X_2X_2X_3X_3$ (male/female) (Fig. 1, j-l). At spermatogonial prometaphase the sex chromosomes can be readily distinguished: the Y chromosome is the largest of the complement and the X chromosomes are the smallest ones. In female mitosis the six sex chromosomes are also easily detected (Fig. 1, j). In these species the diffuse stage is also very long, and at diplotene/diakinesis it is evident that autosomal bivalents present only one terminally located chiasma. At metaphase I the 12 autosomal bivalents generally dispose in a ring, and the sex univalents lie at its centre, although this arrangement is not always observed (Fig. 1, k). At metaphase II the sex multivalent is placed in the centre of the autosomal ring (Fig. 1, l).

Discussion

With the present contribution, 127 species from 11 subfamilies of Reduviidae are now cytogenetically known; 56 of them belong to Triatominae (44.09%), 33 to Harpactorinae (25.98%), 10 to Peiratinae (7.87%) and 10 to Stenopodainae (7.87%). The remaining species (14.17%) are evenly distributed among other seven subfamilies: Bactrodinae (1 species), Ectrychodiinae (3), Emesinae (3), Hammacerinae (1), Phymatinae (2), Reduviinae (7) and Saicinae (1). No cytogenetic reports are available on species of the remaining eleven subfamilies (Ueshima, 1979; Manna, 1984).

The Stenopodainae are characterized by the autosomal diploid number of 20/22 (n=10A/11A) and multiple sex chromosome systems X_nY/ X_nX_n (Table 1). *Stenopoda cinerea* constitutes the tenth species of the subfamily cytogenetically analysed and its chromosome number and male meiotic behaviour agree with previous reports in other species of the subfamily. It deserves attention that among the sex chromosomes three Xs are remarkably smaller than the remaining X and Y chromosomes.

Although Harpactorinae are the largest reduviid subfamily, only 33 species have been cytogenetically studied. The modal diploid autosomal number is 24 (n=12A) and both simple and multiple sex chromosome systems are found (Table 1). Under the hypothesis that the modal karyotype probably represents the ancestral one, *Zelus* sp. prope *leucogrammus*, *Z. exsanguis* (Stel, 1862) and *Vesbius purpureus* (Thunberg, 1784) should represent the original karyotype of the subfamily (2n=24+XY). On the other hand, *Apiomerus lanipes* shows a reduction in the autosomal number from 24 to 22; concomitantly, one autosomal pair is remarkably larger than the others suggesting that it has originated through an autosomal fusion. The five species of *Apiomerus* cytogenetically known are karyotypically similar suggesting that the autosomal fusion should be synapomorphic for the genus within Harpactorinae. Finally, *Cosmoclopius nigroannulatus* and *C. poecilus* show the modal diploid autosomal number of the subfamily and multiple sex chromosomes (2n=24+$X_1X_2X_3Y$). The Y chromosome is strikingly large and completely heterochromatic, and the Xs are very small and of similar size.

Considering 2n=24+XY as the ancestral karyotype of the subfamily, some evolutionary trends can be detected: reduction in autosomal number in some genera through fusion mechanisms, and fragmentation of the X chromosome to give rise to multiple sex chromosome systems. If multiple Xs have adaptive advantages cannot be as-

Table 3. Distribution of the different sex chromosome systems in Reduviidae. [1]*Triatoma dimidiata* (Latreille, 1811), *T. picturata* Usinger, 1939 and *T. tibiamaculata* (Pinto, 1926) described with sex chromosome systems XY and X_1X_2Y (polytypism). [2]*Acholla ampliata* Stål, 1872 with no reference to sex chromosome system. [3]*Pygolampis foeda* Stål, 1859 described with sex chromosome systems XY and X_1X_2Y. [4]*Microtomus conspicillaris* (Drury, 1926) with no reference to sex chromosome system. [5]*Phymata wolffii* Stål, 1876 with no reference to sex chromosome system.

Subfamilies	No. of species analysed	Sex chromosomes X_nY					
		X0	n=1	n=2	n=3	n=4	n=5
Triatominae [1]	56	-	31	26	1	1	-
Harpactorinae [2]	33	-	11	5	14	-	2
Stenopodainae [3]	10	-	1	5	3	2	-
Reduviinae	7	-	3	3	-	1	-
Bactrodinae	1	-	1	-	-	-	-
Ectrychodiinae	3	2	1	-	-	-	-
Emesinae	3	-	3	-	-	-	-
Hammacerinae [4]	1	-	-	-	-	-	-
Phymatinae [5]	2	-	-	-	-	-	-
Peiratinae	10	-	7	3	-	-	-
Saicinae	1	1	-	-	-	-	-
Total	**127**	**3**	**58**	**42**	**18**	**4**	**2**

certained at present.

The other two subfamilies of Reduviidae cytogenetically more deeply analysed are Triatominae and Peiratinae. The Triatominae are highly homogeneous with 20 autosomes (only three species out of 56 have 18 autosomes, and one, 22). The sex chromosome mechanisms are principally XY/XX (52.54%) and $X_1X_2Y/X_1X_1X_2X_2$ (44.07%), and just two species possess other X_nY mechanisms (Table 3). Within Peiratinae, the autosomal number is also 20; the most frequent sex chromosome system is XY, and three species have X_1X_2Y (Table 3) (Ueshima, 1979; Manna, 1984).

Karyotype evolution in Reduviidae

Reduviidae together with Cimicidae are the two heteropteran families in which multiple sex chromosome systems of the X_nY type have reached their broadest distribution and variation. Thus, in any discussion on karyotype evolution in these families the autosomal number and the sex chromosomes should be considered separately on behalf of a better understanding of the evolutionary trends.

Ambrose (1999) proposed a phylogeny on the origin and evolution of assassin bugs in which Stenopodainae might have evolved from the Harpactorinae, and the Peiratinae and Reduviinae should be considered as derived groups of aggressive predators (Fig. 2). According to this author, who analysed morphological characters, feeding habits, habitats and predatory behaviours of Reduviidae, the predaceous reduviids should have originated from the cimicoid ancestral stock characterized by herbivory and a four-segmented rostrum through saprophagy. During the course of evolution of carnivorous reduviids from the saprophagous cimicoid stock, the rostrum might have undergone reduction from four to three segments, and the shortening of the segments. The ancestral reduviids (Holoptilinae) were probably timid predators, which searched for small prey at random. From these timid predators such as holoptilines, emesines, saicines, tribelocephalines, stenopodaines and some harpactorines, aggressive reduviid predators or assassin bugs might have evolved gradually from Emesinae with poor vision to Harpactorinae with good vision. The salyavatines might have evolved from the aggressive harpactorines and stenopodaines, and represent the primitive predatory status, while Reduviinae represent the advanced predatory status. Ectrychodiinae that feed exclusively on millipedes (myriophagy) might have evolved from salyavatines, and Peiratinae might have also evolved from salyavatines in a different line adapted for entomophagy. Triatominae could have evolved from the Salyavatinae to haematophagy.

From a cytogenetic point of view the Cimicoidea have an autosomal diploid number of 28, and assuming that the ancestral diploid number for Reduviidae should have been the same (Holo-

ptilinae), the evolutionary trend within the family should have involved a reduction in autosomal number: 24 in Harpactorinae, 20/22 in Stenopodainae, 22 in Reduviinae, and 20 in Triatominae and Peiratinae (Fig. 2).

With respect to the sex chromosome systems it is generally agreed that multiple systems have originated from simple systems through chromosome fragmentations (Papeschi, 1996). In Reduviidae the frequency of the different systems (from X_1X_2Y to $X_1X_2X_3X_4X_5Y$) is not homogeneously distributed among subfamilies (Table 3). Two species of Ectrychodiinae and the only species of Saicinae have an X0/XX system, with a pre-reductional male meiotic behaviour of the X chromosome, at least in the former species. The simple system XY/XX is present in 46.09% of the species and the remaining species show different degrees of X chromosome multiplicity: X_1X_2Y (32.82%), $X_1X_2X_3Y$ (14.06%), $X_1X_2X_3X_4Y$ (3.13%) and $X_1X_2X_3X_4X_5Y$ (1.56%). From the 18 species with $X_1X_2X_3Y$, 14 belong to Harpactorinae and 3 to Stenopodainae; of the 4 species with $X_1X_2X_3X_4Y$, two belong to Stenopodainae, and the 2 species with $X_1X_2X_3X_4X_5Y$ belong to Harpactorinae. It can be observed that the multiple systems are more frequent in Harpactorinae and Stenopodainae than in the other subfamilies.

The analysis of sex chromosome systems is also in agreement with the phylogeny proposed by Ambrose (1999). During karyotype evolution in Reduviidae some genera belonging to the different subfamilies, Emesinae, Harpactorinae, Stenopodainae, Peiratinae, Reduviinae and Triatominae, maintained the ancestral sex chromosome system XY/XX, while in other genera the original X fragmented giving rise to different multiple systems (X_nY). Furthermore, in only three species of Ectrychodiinae and Saicinae a simple system X0 is observed probably originated through the primary loss of the Y chromosome (Fig. 2).

Summarizing, two different mechanisms occurred during karyotype evolution of Reduviidae: the reduction in autosomal number through fusions, and the increase in the number of sex chromosomes through fragmentations (multiple systems). Although the fragmentation of the X chromosome is a characteristic of the family, the phenomenon is far more frequent in Harpactorinae and Stenopodaine than in other subfamilies.

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References

Ambrose D.P. 1999. Assassin bugs. Enfield. VIII + 336 p.

Banerjee M.R. 1958. A study of the chromosomes during meiosis in twenty-eight species of Hemiptera (Heteroptera, Homoptera) // Proc. Zool. Soc. Calcutta. 11: 9-37.

Dey S.K., Wangdi T. 1988. Chromosome number and sex chromosome system in forty-four species of Heteroptera // *Chromosome Inform. Serv.* 45: 5-8.

Jande S.S. 1959a. Chromosome number and sex mechanism in nineteen species of Indian Heteroptera // *Res. Bull. Panjab Univ.* (N.S.). 10: 415-417.

Jande S.S. 1959b. Chromosome number and sex mechanism in twenty-seven species of Indian Heteroptera // *Res. Bull. Panjab Univ.* (N.S.). 10: 215-217.

Jande S.S. 1960. Pre-reductional sex chromosomes in the family Tingidae (Gymnocerata-Heteroptera) // *Nucleus*. 3: 209-214.

Manna G.K. 1951. A study of the chromosomes during meiosis in forty-three species of Indian Heteroptera // *Proc. Zool. Soc. Bengal*. 4: 1-116.

Manna G.K. 1984. Chromosomes in evolution in Heteroptera, (pp. 189-225) // Sharma A.K., Sharma A. (Eds). *Chromosomes in evolution of eukaryotic groups*. *II*. Boca Raton.

Manna G.K., Deb-Mallick S. 1981. Meiotic chromosome constitution in forty-one species of Heteroptera // *Chromosome Inform. Serv.* 31: 9-11.

Montgomery T.H. 1901. Further studies on the chromosomes of the Hemiptera Heteroptera // *Proc. Acad. Nat. Sci. Philadelphia*. 53: 261-271.

Papeschi A.G. 1996. Sex chromosome polymorphism in

species of *Belostoma* (Belostomatidae, Heteroptera) // *Hereditas*. 124: 269-274.

Payne F. 1909. Some new types of chromosome distribution and their relation to sex // *Biol. Bull.* 16: 116.

Payne F. 1910. The chromosomes of *Acholla multispinosa* // *Biol. Bull.* 18: 174-179.

Payne F. 1912. I. A further study of the chromosomes of the Reduviidae. II. The nucleolus in the young oocytes and the origin of the ova in *Gelastocoris* // *J. Morphol.* 23: 347.

Satapathy S.N., Patnaik S.C. 1989. Chromosome numbers in forty-one species of Indian Heteroptera // *Chromosome Inform. Serv.* 47: 3-5.

Schaefer C.W., Panizzi A.R. 2000. Heteroptera of economic importance. Florida. 828 p.

Schuh R.T., Slater J. 1995. True bugs of the world (Hemiptera: Heteroptera): classification and natural history. New York. 349 p.

Toshioka S. 1933. On the chromosomes in Hemiptera - Heteroptera. I. Chromosomes in *Velinas* Uhler // *Oyo-dobutsugaku-zasshi*. 5: 218-224.

Toshioka S. 1936. On the chromosome types in several families of Heteroptera // *Oyo-dobutsugaku-zasshi*. 8: 167-168.

Troedsson P.H. 1944. The behaviour of the compound sex chromosomes in the females of certain Hemiptera Heteroptera // *J. Morphol.* 45: 103-147.

Ueshima N. 1979. Hemiptera II: Heteroptera. *Animal Cytogenetics. 3: Insecta 6*. Berlin-Stuttgart. V+117 p.

Yosida T. 1947. Unusual type of the nucleolus observed in a bug, *Acanthocoris sordidus* // *J. Fac. Sci. Hokkaido Univ. (Zool.)*. 9: 243-249.

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