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New cytogenetic data on Nabidae (Heteroptera: Cimicomorpha), with a discussion of karyotype variation and meiotic patterns, and their taxonomic significance

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Abstract. As a part of ongoing cytogenetic studies on the bug family Nabidae (Heteroptera), the karyotypes and meiotic patterns of male *Nabis (Aspilaspis) viridulus* Spinola, 1837, *N. (A.) indicus* (Stål, 1873) (subfamily Nabinae) and *Prostemma guttula* (Fabricius, 1787) (subfamily Prostemmatinae) are described.

N. viridulus and *N. indicus* differ from *P. guttula* in their chromosome numbers, which are 2n = 32 + XY and 2n = 26 + XY, respectively, and behaviour of the sex chromosomes in male meiosis, which, respectively, show "distance pairing" and "touch-and-go pairing" in spermatocyte metaphase II. The karyotype of 2n = 34 and "touch-and-go pairing" are considered to be plesiomorphic characters in Nabidae. The evolutionary mechanisms that might underlie different chromosome numbers, the taxonomic significance of karyotype variation and the distribution of meiotic patterns in the family, are discussed.

INTRODUCTION

Nabidae (damsel bugs) are predators with a world wide distribution. Taxonomically, the family belongs to the superfamily Cimicoidea, infraorder Cimicomorpha. Nabidae include approximately 400 species in about 20 genera and four subfamilies (Kerzhner, 1981, 1996). There are chromosome data for 24 species and 5 genera of the subfamilies Nabinae and Prostemmatinae (Ueshima, 1979; Kuznetsova & Maryańska-Nadachowska, 2000 and references therein). All these species have an XY sex-determining system, but different chromosome numbers of 2n = 18, 34, 38; 26–28 in *Pagasa fusca* (Stein, 1857), and several values in the range of 18 to 40 in different populations of *Himacerus apterus* (Fabricius, 1798). Owing to the statistical predominance of 2n = 18 (16 + XY) this karyotype was proposed as the modal and ancestral one for the family (Leston, 1957; Ueshima, 1979; Thomas, 1996; Kuznetsova & Maryańska-Nadachowska, 2000). The other karyotypes are thought to be derivates, with 2n = 32 + XY, showing doubling of the autosome number compared with 2n = 16 + XY (the phenomenon known as "pseudopolyploidy" after Battaglia, 1956, or "autosomal polyploidy" after Kuznetsova & Maryańska-Nadachowska, 2000) as originated by a polyploidy (Thomas, 1996).

The meiotic behaviour of the sex chromosomes in the Nabidae species is reported to differ from that observed in other Heteropteran species as they show "distance pairing" at the second male meiotic division instead of the orthodox "touch-and-go pairing" (Nokkala & Nokkala, 1984; Kuznetsova & Maryańska-Nadachowska, 2000).

Here, as a part of ongoing cytogenetic studies on Nabidae (Nokkala & Nokkala, 1984; Kuznetsova & Maryańska-Nadachowska, 2000; Grozeva & Nokkala, 2003; Grozeva et al., 2004), we present information on the karyotypes and male meiotic patterns in another three nabid species: *Nabis (Aspilaspis) viridulus* Spinola, 1837, *N. (A.) indicus* (Stål, 1873) (subfamily Nabinae, tribe Nabini) and *Prostemma guttula* (Fabricius, 1787) (subfamily Prostemmatinae, tribe Prostemmatini). The ancestral karyotype and male meiotic pattern of Nabidae are suggested. The evolutionary mechanisms that might have resulted in the different chromosome numbers, the taxonomic significance of the variation in karyotype and the distribution of meiotic patterns in the family, are discussed.

MATERIAL AND METHODS

Males of *Nabis* (*Aspilaspis*) *viridulus* (7) and *N.* (*A.*) *indicus* (6) were collected in Israel; males of *Prostemma guttula* (4) were collected in Bulgaria. They were fixed in the field in 3 : 1 ethanol-acetic acid mixture.

Males of all three species had 7 follicles per testis. Testicular follicles were dissected and squashed under a coverslip in a drop of 45% acetic acid. The coverslips were removed after freezing with dry ice; slides were dehydrated in freshly prepared 3 : 1 fixative for 20 min and air-dried.

For staining, the Feulgen-Giemsa procedure of Grozeva & Nokkala (1996) was applied as follows: slides were immersed in 1 N HCl at room temperature for 20 min, hydrolysed in 1N HCl at 60°C for 8 min and stained with Schiff's reagent for 20 min. Slides were thoroughly rinsed with distilled water, then rehydrated in Sorensen's phosphate buffer for 10 min and stained with 2% Giemsa solution in the same buffer for 15–20 min. When appropriately stained, slides were rinsed briefly with dis-

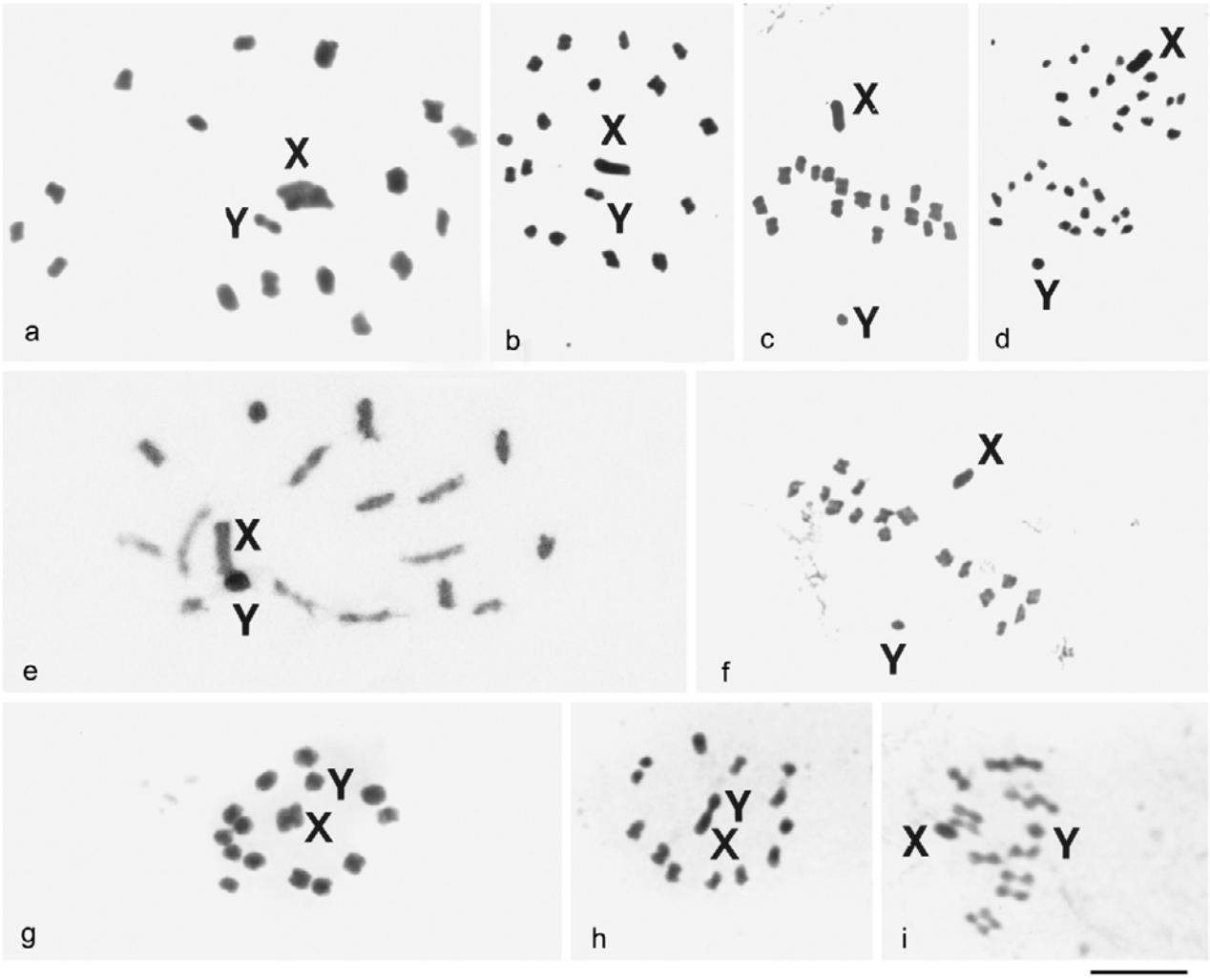

Fig. 1. a–d – male meiotic chromosomes of *Nabis* (*Aspilaspis*) *viridulus*, 2n = 34 (32 + XY): a – metaphase I; b – metaphase II; polar view; c – metaphase II, equatorial view; d – anaphase II / telophase II transition, two daughter plates; e, f – male meiotic chromosomes of *Nabis* (*Aspilaspis*) *indicus*, 2n = 34 (32 + XY): e – prometaphase I; f – metaphase II, equatorial view; g–i – male meiotic chromosomes of *Prostemma guttula*, 2n = 28 (26 + XY): g – metaphase I; h – metaphase II, polar view; i – metaphase II / anaphase II transition, equatorial view. Scale = 10 μm

tilled water, air dried and mounted in Entellan (Merck, Darmstadt, Germany).

Chromosome spreads were analysed using an Olympus BH 2 light microscope with an OM-4 camera.

RESULTS

The meiotic karyotypes of *N. viridulus* and *N. indicus* are similar. At first metaphase (MI) in both species the spermatocytes have 16 autosomal bivalents plus X and Y-chromosomes, indicating a diploid karyotype of 2n = 32 + XY (Figs 1a, e). Bivalents were of a gradually decreasing size. The X was the largest and the Y was one of the medium-sized chromosomes.

In the bivalents, the homologues were aligned in parallel with no chiasmata between them. As in the great majority of Heteroptera (Ueshima, 1979), the first division was reductional for the autosomal bivalents, whereas the sex chromosomes underwent equational separation in anaphase I (AI) and segregation in AII (postreduction). Each MII cell therefore contained both X and Y chromosomes (Fig. 1b). When viewed from the pole, MII plates were "radial" with the sex chromosomes lying in the centre of the ring formed by the autosomes. The sex chromosomes were spaced separately from each other without any visible links between them. Viewed from the side, the sex chromosomes showed a bipolar co-orientation, the so-called "distance pairing". The sex chromosomes moved towards the poles ahead of the autosomes (Figs 1c, f). During AII, they segregated resulting in spermatocyte II nuclei with 16 autosomes plus an X or a Y chromosome (Fig. 1d).

In *P. guttula*, spermatocyte MI had 13 autosomal bivalents plus X and Y chromosomes, consequently male diploid karyotype was defined as 2n = 26 + XY (Fig. 1g). All bivalents were achiasmatic and graded in size. The X was the largest and the Y a medium-sized chromosome. MII plates were "radial" with the sex chromosomes lying in centre of the ring formed by the autosomes (Fig. 1h). At this stage, the sex chromosomes formed a pseudobivalent by so-called "end-to-end" pairing, or more prop-

TABLE 1. Chromosome numbers of Nabidae.*

NN	Taxa	2n
	NABINAE	
1.	NABINI	18
	Nabis (s.str.) punctatus Costa, 1847	
2.	*N. (s.str.) brevis* Scholtz, 1847	18
3.	*N. (s.str.) ericetorum* Scholtz, 1847	18
4.	*N. (s.str.) ferus* (Linnaeus, 1758)	18
5.	*N. (s.str.) pseudoferus* Remane, 1949	18
6.	*N. (s.str.) meridionalis* Kerzhner, 1963	18
7.	*N. (s.str.) rugosus* (Linnaeus, 1758)	18
8.	*N. (s.str.) stenoferus* Hsiao, 1964	18
9.	*N. (Tropiconabis) kinbergii* Reuter, 1872	18
10.	*N. (Dolichonabis) limbatus* Dahlbom, 1851	18
11.	*N. (Dolichonabis) tesquorum* (Kerzhner, 1968)	18
12.	*N. (Reduviolus) americoferus* Carayon, 1961	18
13.	*N. (Milu) reuteri* Jakovlev, 1876	18
14.	*N. (Limnonabis) ussuriensis* Kerzhner, 1962	18
15.	*N. (Limnonabis) lineatus* Dahlbom, 1851	18
16.	*N. (Nabicula) flavomarginatus* Scholtz, 1847	18
17.	*N. (Aspilaspis) pallidus* Fieber, 1861	34
18.	*N. (Aspilaspis) viridulus* Spinola, 1837**	34
19.	*N. (Aspilaspis) indicus* (Stal, 1873)**	34
20.	*N. (Halonabis) sareptanus* Dohrn, 1862	34
21.	*Lasiomerus annulatus* (Reuter, 1872)	18
22.	*Himacerus (Himacerus) apterus* (Fabricius, 1798)	18*** 38***
23.	*H. (Aptus) mirmicoides* (O. Costa, 1834)	34
24.	*H. (Aptus) maracandicus* (Reuter, 1890)	38
25.	*Hoplistoscelis sordidus* (Reuter, 1872)	18
	PROSTEMMATINAE	
26.	PROSTEMMATINI	28
	Pagasa fusca (Stein, 1857)	
27.	*Prostemma guttula* (Fabricius, 1787)	28

*The most plausible chromosome numbers of the species are given; for other chromosome numbers, place of origin of samples, references and remarks, see Table 1 in Kuznetsova & Maryańska-Nadachowska, 2000 and the Discussion in this paper. **New data; ***for comments, see Discussion.

erly "touch-and-go" pairing. In early AII, the sex chromosomes segregated polewards ahead of the autosomes (Fig. 1i).

DISCUSSION

Chromosome numbers

The three species studied, *N. viridulus*, *N. indicus* and *P. guttula*, have relatively high numbers of chromosomes compared to the family Nabidae as a whole. With these results, the karyotypes of 27 nabid species are known: *Nabis* (20), *Lasiomerus* (1), *Himacerus* (3), *Hoplistoscelis* (1) [subfamily Nabinae, tribe Nabini], *Pagasa* (1) and *Prostemma* (1) [subfamily Prostemmatinae, tribe Prostemmatini]. In these species, a total of four karyotype patterns were established with confidence: 2n = 18 (16 + XY); 2n = 28 (26 + XY); 2n = 34 (32 + XY); 2n = 38 (36 + XY). (Table 1; for additional information, see Table 1 in Kuznetsova & Maryańska-Nadachowska, 2000).

All but one (2n = 28) of the karyotypes appear to be characteristic of the subfamily Nabinae. In this group, 18 species, belonging to the genera *Nabis*, *Lasiomerus* and *Hoplistoscelis*, have 2n = 18. A karyotype of 2n = 34 is found in five species: *N.* (*Aspilaspis*) *pallidus* Fieber, 1861, *N.* (*A.*) *viridulus* and *N.* (*A.*) *indicus*; *N.* (*Halonabis*) *sareptanus* Dohrn, 1862; *Himacerus* (*Aptus*) *mirmicoides* (O. Costa, 1834). Although a population of the latter species from Caucasus shows some chromosome number polymorphism (2n = 34–38) (Kuznetsova & Maryańska-Nadachowska, 2000), the 2n = 34 karyotype, initially reported from England (Leston, 1957), was recently confirmed for populations of this species from Germany and the North Caucasus, Russia (Grozeva et al., 2004). The same chromosome number polymorphism (2n = 34–38) was reported for *H.* (*Aptus*) *maracandicus* (Reuter, 1890) in Kazakhstan (Kuznetsova & Maryańska-Nadachowska, 2000), however, a 2n = 38, without polymorphism, was recorded for this species in Turkmenia (Schachow, 1932). We are inclined to believe that *H. mirmicoides* and *H. maracandicus* have, respectively, 2n = 34 and 2n = 38 in their standard sets. An unusual range of chromosome numbers was reported for a third *Himacerus species – H.* (*Himacerus*) *apterus*, which has dissimilar chromosome numbers in different populations. Two European populations (England, The Netherlands) of this species are reported to have 2n = 18 (16 + XY) (De Meijere, 1930; Leston, 1957). However, three populations in the Far East have high chromosome numbers: 2n = 34–38 (32–36 + XY) in the Far East of Russia (Kuznetsova & Maryańska-Nadachowska, 2000), 2n = 38 (36 + XY) (Yoshida, 1950) and 2n = 40 (38 + XY) (Takenouchi & Muramoto, 1968) in Japan. The 2n = 28 karyotype is probably characteristic of the subfamily Prostemmatinae. Kuznetsova & Maryańska-Nadachowska (2000) reported 2n = 26–28 for *Pagasa fusca*, although they did not establish the chromosome number with certainty. This species most likely shares 2n = 28 with *Prostemma guttula*, as reported in the present study.

Male meiotic patterns

Male meiosis in the Nabidae is characterized by a number of significant peculiarities such as the absence of chiasmata; postreduction of sex chromosomes, which separate equationally in AI while segregate reductionally in AII; "distance pairing" of sex chromosomes in MII (Ueshima, 1979; Nokkala & Nokkala, 1984; Kuznetsova & Maryańska-Nadachowska, 2000). Unlike the first two characters, sex chromosome "distance pairing" is thought to be a unique characteristic of Nabidae (Nokkala & Nokkala, 1984; Kuznetsova & Maryańska-Nadachowska, 2000). Typical of "distance pairing" is that the sex chromosomes do not associate in MII. They orientate towards opposite poles forming a kind of "distance bivalent" and segregate in AII. The rest of the Heteroptera display the "touch-and-go" pairing of sex chromosomes in MII (Ueshima, 1979). In this case, sex chromosomes associate as a pseudo-bivalent in MII and segregate polewards in AII. Regular segregation of achiasmatic sex chromosomes apparently involves an achiasmatic segregation mechanism. This mechanism is known to be responsible for the regular segregation of the m-chromosomes in Heteroptera (Nokkala, 1986), the prereductional segregation of sex chromosomes in the family Tingidae (Heteroptera) (Jande, 1960), the regular segregation of the B chromo-

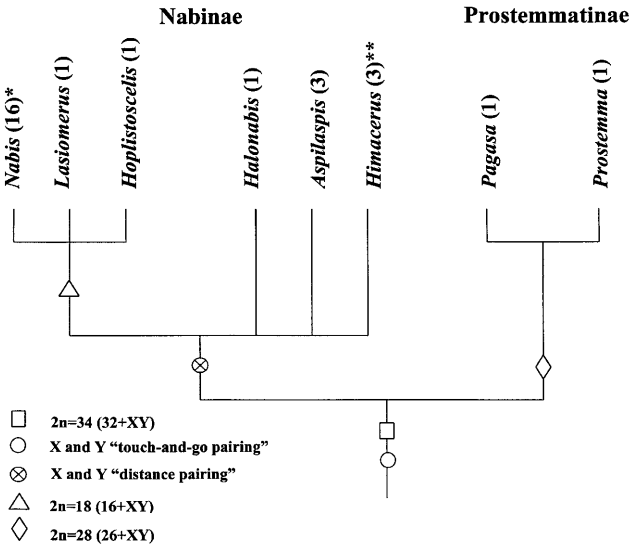

Fig. 2. Distribution of chromosome numbers, male meiotic patterns and the relationships between some genera of the Nabinae and Prostemmatinae subfamilies (family Nabidae) based on cytogenetic evidence. * – given in brackets is the number of species studied; ** – the initial karyotype of 2n = 34 (32 + XY) is inherited by *Himacerus mirmicoides*; *H. maracandicus* acquired 2n = 38 (36 + XY) through autosome fissions; the karyotype recorded for *H. apterus* is questionable (see Discussion).

some from the Y chromosome (Nokkala et al., 2000) and segregation of X and Y chromosomes (Nokkala et al., 2003) in Psylloidea (Sternorrhyncha).

Meiosis in *N. viridulus*, *N. indicus* and *P. guttula* is principally that typically found in nabids, including "distance pairing" of sex chromosomes discovered in two *Nabis* species. However, *P. guttula* appeared to show "touch-and-go" pairing in MII. Based on the evidence available at the time for the subfamily Nabinae, Kuznetsova & Maryańska-Nadachowska (2000) suggested that "distance pairing" is an autapomorphy of Nabidae within the infraorder Cimicomorpha. However, the new data for the subfamily Prostemmatinae presented here indicate that this pattern is probably only characteristic of the subfamily Nabinae.

Possible evolutionary mechanisms that underlie the differences in chromosome number

Bugs display holocentric (more often referred to as holokinetic) chromosomes, sharing this chromosome pattern with their relatives the Homoptera (within Hemiptera), Thysanoptera, Psocoptera and Phthiraptera, as well as with the phylogenetically distant orders Dermaptera, Odonata, Lepidoptera and Trichoptera (for references, see White, 1973). Quite recently, holocentric chromosomes were also discovered in Zoraptera (Kuznetsova et al., 2002).

It is commonly supposed that holocentric chromosomes have diffuse centromeres (or relatively large centromeres; see Wolf, 1996), which facilitate chromosome fission (fragmentation) and fusion. Such chromosomal rearrangements may be the basic mechanisms by which karyotypes in insects with holocentric chromosomes evolve (White, 1973; Kuznetsova, 1975; Blackman, 1980; Wolf, 1996).

Because of its predominance, the 2n = 18 karyotype is proposed as the modal and ancestral one for Nabidae (Leston, 1957; Ueshima, 1979; Thomas, 1996; Kuznetsova & Maryańska-Nadachowska, 2000). All the other karyotypes are regarded as derivatives, with 2n = 34 (32 + XY) representing "autosomal polyploidy" (Kuznetsova & Maryańska-Nadachowska, 2000) resulting from a doubling of the autosomes in the 2n = 18 (16 + XY) karyotype. Some authors (Leston, 1957; Thomas, 1996) argue that true polyploidy occurred during speciation in Nabidae.

However, it is often impossible to suggest with confidence the mechanism responsible for the different chromosome numbers in related species. In some cases, chromosome size is inversely related to chromosome number. That is, the chromosomes in low chromosome number karyotypes are noticeably larger than those in high chromosome number karyotypes suggesting fusion/fission rearrangements. Some well-documented examples of this are known in the superfamilies Aphidoidea and Coccoidea (Sternorrhyncha), where cytogenetic studies were carried out on mitotic chromosomes (Kuznetsova, 1975; Blackman, 1980; Cook, 2000). However, such examples are very rare in Heteroptera, where cytogenetic studies were mainly done on meiotic divisions. Because of their non-uniform spiralization, meiotic chromosomes provide inconclusive evidence of differences in chromosome size, and this is also true for Nabidae.

As indicated above, the karyotypes with 2n = 16 + XY and 2n = 32 + XY occur in the genera *Himacerus* and *Nabis*, with no intermediate numbers of autosomes. At an early stage in the study of chromosomes in nabids, when data on species with 2n = 18 prevailed, plus a few data on species with 2n = 34, the karyotype of 2n = 18 was thought to be ancestral and that with 2n = 34 a result of polyploidy (Leston, 1957; Thomas, 1996; Kuznetsova & Maryańska-Nadachowska, 2000). Leston (1957), and particularly Thomas (1996), invoked true polyploidy as an evolutionary mechanism in Nabidae and some other heteropteran families. To explain why the putative polyploid species each have a single rather than two pairs of sex chromosomes, Thomas suggested that their asynaptic pattern and postreduction in meiosis may have prevented the sex chromosomes from doubling up.

However, the hypothesis that the ancestral nabid karyotype was 2n = 34 and that 2n = 18 originated from it by autosomal fusions is in better agreement with the data on related groups and the common mechanisms of karyotype evolution. Chromosome numbers close or even equal to 34 are characteristic of the families closely related to Nabidae: Miridae, Anthocoridae and Cimicidae, including their primitive members (Ueshima, 1979). A character state found both within and outside a group should be considered plesiomorphic unless and until there is strong contrary evidence (Rasnitsyn, 1996). Although polyploidy is suggested for some groups of Heteroptera (Tho-

mas, 1996), how it evolved is unclear and even its existence is doubted (Jacobs, 2002). Autosomal fusions are a common mechanism of karyotype evolution and, hence, an easier explanation of the karyotype variability in nabids. If 2n = 34 is the ancestral number of chromosomes in nabids, the higher number of chromosomes (2n = 38) in *Himacerus maracandicus*, can be considered as a result of fission of 4 autosomes, the reduced number of chromosomes (2n = 28) in Prostemmatinae the result of fusion of 6 autosomes, and the prevailing karyotype of 2n = 18 the fusion in pairs of all the autosomes, i.e. 16 fusion events.

The fusion hypothesis is new for Nabidae, and it needs to be substantiated. Applying modern cytogenetic and molecular techniques could improve our understanding of the mechanisms of chromosome evolution in Nabidae, and especially the phenomenon of "autosomal polyploidy". It should be noted, however, that our first attempt at this (using C-banding, Ag-NOR-banding and DNA sequence specific fluorochromes CMA_3 and DAPI) did not result in a deeper insight into the problem (Grozeva & Nokkala, 2003; Grozeva et al., 2004). At the moment we prefer to use the term "autosomal polyploidy" not "pseudopolyploidy", since the former describes a phenomenon and its formative mechanisms are open to further investigation.

Correlation between chromosome numbers, male meiotic patterns and the morphological characters of higher taxa

Nabidae (Cimicomorpha, Cimicoidea) consist of 4 subfamilies: Velocipedinae, Medocostinae, Nabinae and Prostemmatinae. The first two are very small and are sometimes considered to be families (see Kerzhner, 1996), and their karyotypes are unknown. Although information on nabid cytogenetics is scant, differences in chromosome number and meiotic pattern correspond (with some exceptions) with the superspecies grouping of the family (Fig. 2).

In Prostemmatinae, two tribes with a total of four genera are recognized (Kerzhner, 1981). The cytogenetically studied genera, *Prostemma* (Old World) and *Pagasa* (New World), belong to the more primitive tribe, Prostemmatini. As discussed above, male *Prostemma guttula* show the orthodox (in the context of Heteroptera) "touch-and-go" sex chromosome pairing at meiosis. They most probably retain this pattern from the common nabid ancestor. Nabinae then acquired "distance pairing" as an apomorphic character. The representatives of the genera *Prostemma* and *Pagasa* have 2n = 28, a karyotype unknown in Nabinae.

Nabinae include more than 2/3 of the species in the family Nabidae. The systematics of the supraspecies of Nabinae, especially that of the largest genus *Nabis*, is controversial and repeatedly revised (Kerzhner, 1981, 1996). At present, the division of *Nabis* s. lato into five genera (*Himacerus, Nabis, Stenonabis, Lasiomerus* and *Hoplistoscelis*) (Kerzhner, 1996) rather than 19 (Kerzhner, 1981) is accepted. Chromosome data for all of these genera are available with the exception of *Stenonabis*.

In *Himacerus*, as few as three species, that is, about 20% of the species assigned to this genus, have been karyotyped. *H. mirmicoides* and *H. maracandicus*, although belonging to the same subgenus *Aptus*, have different chromosome numbers, respectively, 2n = 34 and 2n = 38. As discussed above, the Western European and Far Eastern populations of *H. apterus* (subgenus *Himacerus*) have low (2n = 18) and high (2n = 34–40) chromosome numbers, respectively. However, it should be emphasized that in three other European populations of this species 2n = 38 (unpublished), so the populations in England and the Netherlands (Leston, 1957; De Meijere, 1930) need to be re-investigated.

The two species, *L. annulatus* (Reuter, 1872) and *H. sordidus* (Reuter, 1872) of the genera *Lasiomerus* and *Hoplistoscelis*, both of which occur in the New World, have 2n = 18.

In the genus *Nabis* s. str., the subgenera *Nabis* (8 species karyotyped), *Tropiconabis* (1), *Dolichonabis* (1), *Reduviolus* (1), *Milu* (1), *Limnonabis* (2) and *Nabicula* (1) all have 2n = 18. In contrast, the small subgenera *Aspilaspis* (3 species karyotyped) and *Halonabis* (1) have 2n = 34. Based on morphological criteria, *Aspilaspis* and *Halonabis* appear to be closely related, which is well supported by their similar karyotypes. They were treated previously as separate genera (Kerzhner, 1981). This separation is supported by their chromosome numbers different from that of other subgenera of *Nabis* (Fig. 2).

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