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Meiotic Karyotypes in Males of Nineteen Species of Psylloidea (Hemiptera) in the Families Psyllidae and Triozidae

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Meiotic karyotypes in males of 16 species (assigned to 9 genera and 7 subfamilies) of the family Psyllidae and 3 species (assigned to 3 genera of the subfamily Triozinae) of the family Triozidae are described for the first time. The first data on the genus *Ligustrinia* are presented. All the species were shown to exhibit the modal karyotype for psyllids, 2n = 24 + X, except *Bactericera nigricornis* and *Arytainilla spartiophila*, in which 2n = 24 + XY and 2n = 22 + X were found, respectively. The karyotype of *Ctenarytaina eucalypti* (Psyllidae, Spondyliaspidinae) was reinvestigated, and the karyotype 2n = 10 + X, characteristic of Spondyliaspidinae, was revealed. The karyotypes of *Strophingia fallax*, *S. arborea*, and *Craspedolepta topicalis* were studied using the C-banding technique.

Key words: Psylloidea, karyotypes, sex determining chromosome systems, C-banding.

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Psyllids or jumping plant-lice (Hemiptera, Sternorrhyncha, Psylloidea) are generally mono- or oligophagous (in their larval stages) phloem-sucking insects, with dicotyledons as their predominant host-plants. Psyllids are distributed across all zoogeographic realms from sea to alpine level, being the most numerous in south temperate and tropical latitudes. The approximately 2600 described species of Psylloidea (GEGECHKORI & LOGINOVA 1990) probably are a small fraction of their actual diversity (BURCKHARDT 1989). Many psyllids are gall-formers, and several species are known to be pests on cultivated plants. Several further species can regionally or sporadically reach pest status (BURCKHARDT 1994).

The systematics of this family has changed radically just recently, during the last 20 years. According to BURCKHARDT (1994), in a phylogenetic classification the Psylloidea can be subdivided into the following 6 families: Calophyidae Vondraček, Carsidaridae Crawford, Homotomidae Heslop-Harrison, Phacopteronidae Burckhardt, Psyllidae Löw, and Triozidae Löw. Of these families, the four first are small and mostly tropical, whereas Psyllidae and Triozidae are both cosmopolitan and include the bulk of the psyllid species. Relationships are poorly explored and although some genera have been revised, there are plenty of species and higher taxa that still haven't found their proper position in the system.

Karyotypic characters may be helpful for taxonomy due to their low level of intraspecies variation. However, karyotypes are presently known for a minor portion of insect species. In Psylloidea, only 171 species (i.e. 6.5 % of the world psyllid fauna) have been studied to date. Chromosome data are available for 54 genera (i.e. 27 % of the 200 accepted genera) and for all of the families except Phacopteronidae (reviewed by MARYAŃSKA-NADACHOWSKA 2002; see also MARYAŃSKA-NADACHOWSKA & GŁOWACKA 2005).

Psyllid karyotypes seem to display high evolutionary stability as indicated by 129 studied species (i.e., approx. 75%) which share the chromosome complement 2n = 24 + XX/XO. It has been suggested that this karyotype is the most primitive in Psylloidea (KUZNETSOVA *et al.* 1995). Deviating karyotypes, which occur sporadically in this group, sometimes define genera and even higher

taxa. One of these occurs in the subfamily Spondyliaspidinae Heslop-Harrison (Psyllidae), in which all the studied species were shown to have a low chromosome number, 2n = 6+XX/X0 through 2n = 10 + XX/X0, with a single species, *Ctenarytaina eucalypti* (Maskell, 1890), displaying 2n = 20 + X (MARYAŃSKA-NADACHOWSKA *et al*. 1992).

The above-mentioned deviation from the norm encountered in *C. eucalypti* seemed intriguing, so one of the aims of this study was to reinvestigate the karyotype of this species. This paper also aimed at providing more information on the karyotypes of Psylloidea by investigating 18 further species assigned to the families Psyllidae and Triozidae.

Material and Methods

Adult males of various ages were used in the study. Field collections were carried out in Portugal (Madeira Island) in 2005 (during January and February), in Spain in 2005 (in July), and in Russia (Maritime Territory and Siberia) in 2004 (between July and mid-August). In each species, the specimens studied belonged to a single population, except for *Cacopsylla intacta*, in which specimens from two populations were investigated (Table 1). A total of 19 species, 16 of which belong to 9 genera and 7 subfamilies of Psyllidae, whereas 3 belong to 3 genera of the subfamily Triozinae of Triozidae, were studied. Table 1 lists the species

Table 1

Chromosome numbers and sex chromosome systems of 19 species of Psylloidea

Taxa	2n (♂)	Collection localities	Specimen numbers
Psyllidae Löw			
Aphalarinae Löw			
Craspedolepta flava (Kuwayama, 1908)	2n = 24+X	Russia, Maritime Territory	3
C. kerzhneri Loginova, 1963	2n = 24+X	Russia, Maritime Territory	2
C. lineolata Loginova, 1962	2n = 24+X	Russia, Maritime Territory	4
C. terminata Loginova, 1962	2n = 24+X	Russia, Maritime Territory	5
C. topicalis Loginova, 1962	2n = 24+X	Russia, Maritime Territory	5
Arytaininae Crawford			
Arytainilla spartiophila (Förster, 1848)	2n = 22+X	Spain	2
Livilla nervosa Hodkinson et Hollis, 1987	2n = 24+X	Portugal, Madeira Island	1
L. pyrenaea (Mink, 1859)	2n = 24+X	Spain	1
L. retamae (Puton, 1878)	2n = 24+X	Portugal, Madeira Island	1
Diaphorininae Vondráček			
Diaphorina putonii Löw, 1879	2n = 24+X	Spain	3
Euphyllurinae Bekker-Migdisova			
Ligustrinia herculeana Loginova, 1967	2n = 24+X	Russia, Maritime Territory	2
Psyllinae Löw			
Psylla ginnali Konovalova et Loginova, 1985	2n = 24+X	Russia, Maritime Territory	2
Cacopsylla intacta (Loginova, 1964)	2n = 24+X	Russia, Eastern Siberia, Irkutsk Region*	3
		Russia, Western Siberia, Gorno-Altaisk Territory**	1
Spondyliaspidinae Heslop-Harrison			
Ctenarytaina eucalypti (Maskell, 1890)	2n = 8 +X	Portugal, Madeira Island	2
Strohpingiinae White et Hodkinson			
Strophingia arborea Loginova, 1976	2n = 24+X	Portugal, Madeira Island	1
S. fallax Loginova, 1976	2n = 24+X	Portugal, Madeira Island	1
Triozidae Löw			
Bactericera nigricornis (Förster, 1848)	2n = 24+XY	Russia, Maritime Territory	3
Trichochermes grandis Loginova, 1965	2n = 24+X	Russia, Maritime Territory	2
Trioza elaeagni (Scott, 1880)	2n = 24+X	Portugal, Madeira Island	1

*South-western part of the Baikal Lake coast, east from the Angara River mouth, Listvyanka village, mouth of the Pokhabikha river

**Spurs of Kuminskiy ridge, Edigan river, 3 km to the west from Edigan village

studied, with taxonomic assignment, the number of specimens from which chromosome preparations were obtained and their countries of origin. The karyotypes of all the species, except *C. eucalypti*, have not been previously recorded. The genus *Ligustrinia* Loginova, 1973 is described for the first time. Specimens were fixed in Carnoy solution (glacial acetic acid : ethanol 1:3). Chromosome slides were prepared from testes. Testes follicles were extracted from the abdomen on a slide, separated and squashed in a drop of 45% acetic acid under a coverslip. The preparations were first examined using a phase-contrast microscope. The best preparations with well spread chromosomes were made permanent using the dry ice technique (CONGER & FAIRECHILD 1953). The preparations were frozen on a block of dry ice and the coverslip was removed with a sharp blade, after which the preparations were fixed in freshly prepared Carnoy and air-dried. The preparations were routinely stained using the Feulgen-Giemsa technique by GROZEVA and NOKKALA (1996), detailed in an earlier paper of this series (KUZNETSOVA *et al.* 1997b). C-banding treatment was performed according to SUMNER's technique (1972), whereas DAPI staining was made in accordance to SCHWEIZER (1976). The technique of fluorescent banding had not been previously used on psyllid chromosomes.

Results

Diploid chromosome numbers and sex determining chromosome systems in males of 19 species studied in the present work are listed in Table 1 Other information on male meiotic karyotypes is as follows:

Craspedolepta Enderlein, 1921

The karyotypes of the five studied species (*C. flava*, *C. kerzhneri*, *C. lineolata*, *C. terminata*, *C. topicalis*) are all similar in chromosome number, sex determining chromosome system, and gross chromosome morphology. In male metaphase I (MI) of each species there are 12 autosomal bivalents and a univalent X chromosome, as shown for *C. topicalis* (Fig. 1). The bivalents form a gradual size series. The size of the X chromosome is relatively consistent between species, being similar to that of a group of larger-sized semi-bivalents. The sister second metaphases (MII) contain 12 or 13 double-stranded chromosomes as shown for *C. flava* (Fig. 2). C-banding was successful only for *C. topicalis*, which showed two large C-bands of unclear localization and a number of tiny C-bands in early diplotene (Fig. 3), while no bands at later stages. The large bands are most likely located in two middle-sized bivalents as indicated by the two DAPI-positive signals observed in these bivalents in late diplotene (Fig. 4).

Arytainilla Loginova, 1972

In males of *A. spartiophila*, MI contains 11 autosomal bivalents and a univalent X chromosome (Fig. 5). The bivalents form a more or less gradual size series, whereas the X chromosome is close in size to the middle-sized semi-bivalents. One of the middle-sized bivalents is slightly heteromorphic in all seven MI examined.

Livilla Curtis, 1836

The karyotypes of the three studied species (*L. nervosa*, *L. pyrenaea*, *L. retamae*) are all similar in chromosome number and sex determining chromosome system. In male MI of each species there are 12 autosomal bivalents forming a more or less gradual size series, and a univalent X chromosome, which is the largest element of the complement, at least in *L. nervosa* (Fig. 6). During diakinesis, the X chromosome is positively heteropycnotic, and bivalents each show a single terminal or near terminal chiasma (Fig. 7).

Diaphorina Löw, 1879

In males of *D. putonii*, MI contains 12 autosomal bivalents and a X univalent (Fig. 8). Bivalents form a more or less gradual size series. The X chromosome is the largest element of the complement, also evident from the MII cells (Fig. 9).

Ligustrinia Loginova, 1967

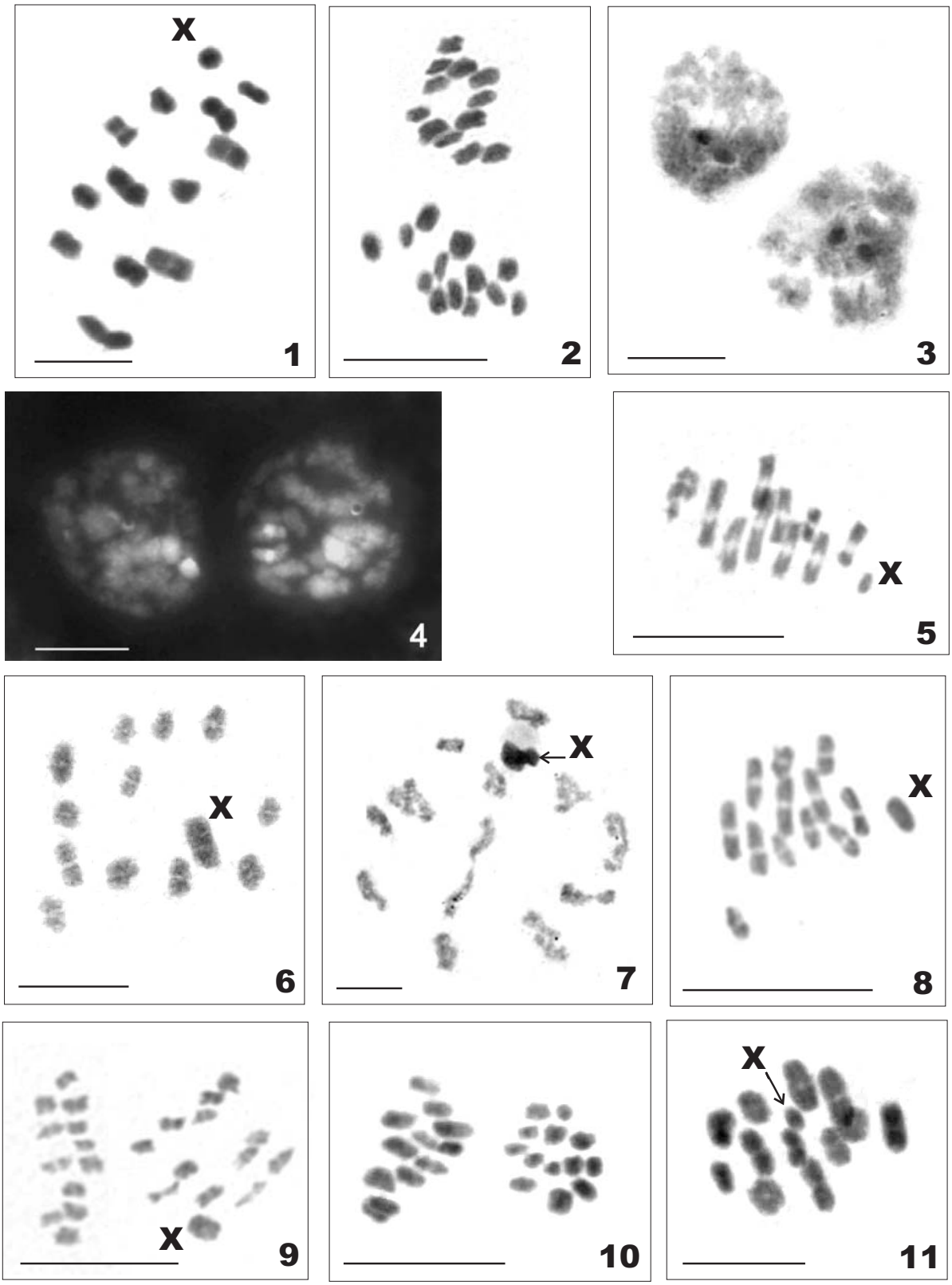
In males of *L. herculeana*, only MII were available for observations. Fig. 10 shows two sister MII plates each with 12 or 13 chromosomes suggesting $2n = 24 + X$.

Psylla Geoffroy, 1862

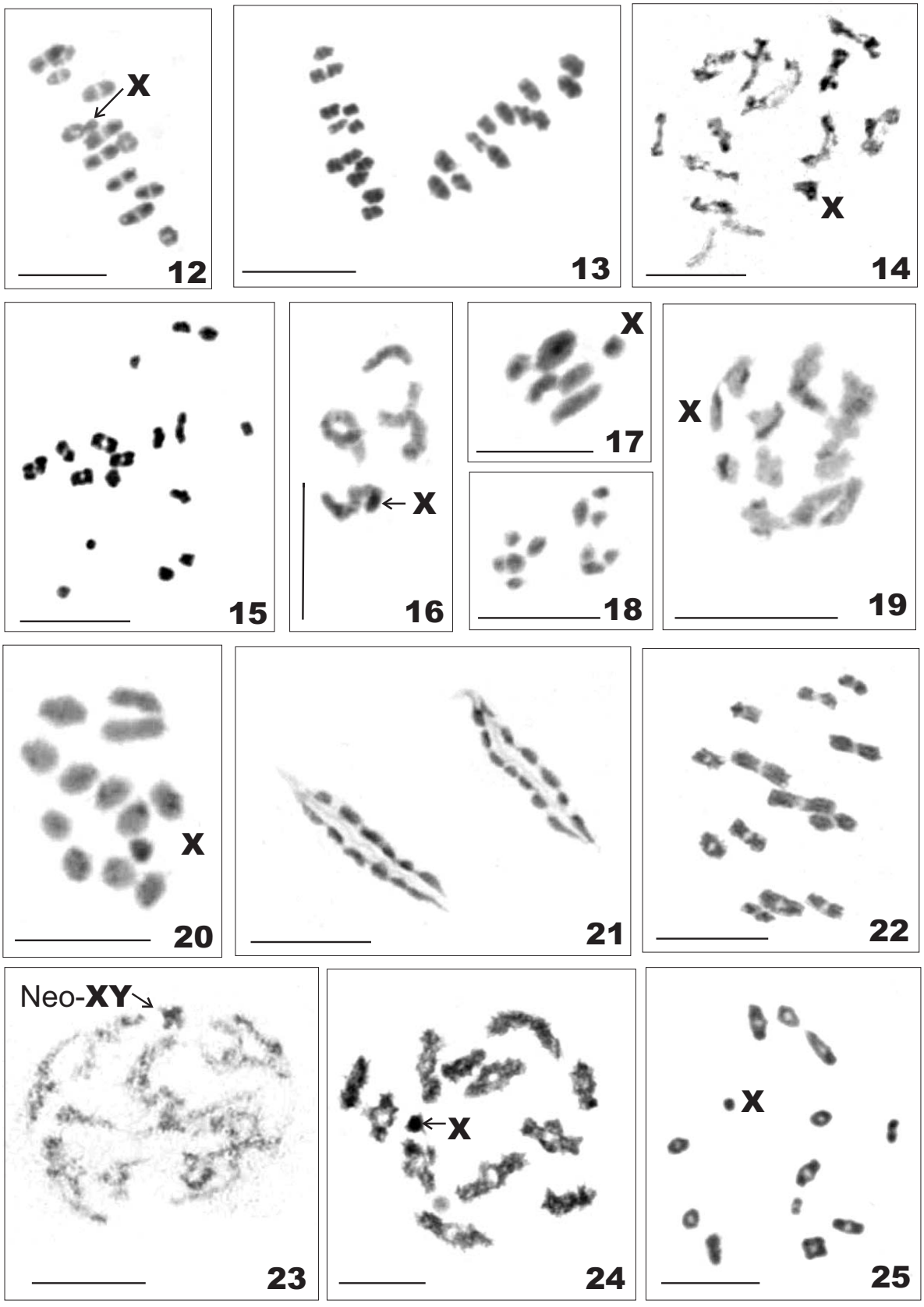
In MI of *P. ginnali*, there are 12 autosomal bivalents and a univalent X chromosome (Fig. 11). Bivalents form a more or less gradual size series. The X chromosome is similar in size to small semi-bivalents.

Cacopsylla Ossiannilsson, 1970

In *C. intacta*, two distant populations, one from the Gorno-Altaysk Territory, whereas another from the Irkutsk Region of Russia (Table 1), were studied. In three males from the first population all MI



Figs 1-11. Male meiotic karyotypes of psyllid species. Fig. 1. *Craspedolepta topicalis* metaphase I. Fig. 2. *C. flava* metaphase II. Figs 3 & 4. *C. topicalis* early diplotene. Fig. 3. C-bands. Fig. 4. DAPI-signals. Fig. 5. *Arytainilla spartiophila* metaphase I. Figs 6 & 7. *Livilla nervosa*. Fig. 6. metaphase I. Fig. 7. late diakinesis; Figs 8 & 9. *Diaphorina putonii*. Fig. 8. metaphase I. Fig. 9. metaphase II. Fig. 10. *Ligustrinia herculeana* two metaphases II with 12 and 13 chromosomes, respectively. Fig. 11. *Psylla ginnali* metaphase I. Bars = 10 μm.



Figs 12-25. Male meiotic karyotypes of psyllid species. Figs 12-15. *Cacopsylla intacta*. Figs12 & 13. Gorno-Altaysk Territory population. Fig. 12. metaphase I. Fig. 13. Two metaphases II with 12 and 13 chromosomes, respectively. Figs 14 & 15. Irkutsk Region population. Fig. 14. diakinesis. Fig. 15. metaphase I. Figs 16-18. *Ctenarytaina eucalypti*. Fig.16. diakinesis. Fig. 17. metaphase I. Fig. 18. Two metaphases II with 5 and 6 chromosomes, respectively. Fig. 19. *Strophingia arborea* diakinesis. Figs 20 & 21. *S. Fallax*. Fig. 20. metaphase I. Fig. 21. spermatids. Figs 22 & 23. *Bactericera nigricornis*. Fig. 22. metaphase I. Fig. 23. early diplotene. Fig. 24. *Trichochermes grandis* diakinesis. Fig. 25. *Trioza elaeagni* metaphase I. Bars = 10 μm.

cells showed 12 autosomal bivalents and a univalent X chromosome (Fig. 12), whereas all MII cells displayed 12 or 13 chromosome respectively (Fig. 13). The bivalents formed a gradual size series, and the X chromosome seemed to be fairly small. In two studied males from the Irkutsk population, in diakineses, 12 bivalents, each with only terminal, near terminal or very rarely interstitial chiasma, and a positively heteropycnotic X chromosome were observed (Fig. 14), however in all MI cells examined some bivalents resembled univalents (Fig. 15).

Ctenarytaina Ferris & Klyver, 1932

In males of C. e*ucalypti*, diakinesis and MI show 5 autosomal bivalents and a univalent X chromosome (Figs 16, 17). The bivalents form a more or less gradual size series with the greatest differences in size between the two first and three subsequent bivalents. The X chromosome seems to be one of the medium-sized elements of the complement. The sister MII cells each contain 5 chromosomes (autosomes only) or 6 chromosomes, respectively, including the X chromosome (Fig. 18).

Strophingia Enderlein, 1914

The karyotypes of the two species studied (*S. arborea*, *S. fallax*) are similar showing 12 autosomal bivalents and a univalent X chromosome in diakinesis and MI (Figs 19, 20). Bivalents form a more or less gradual size series. The X chromosome is similar in size to the medium-sized semi-bivalents. It is interesting that at the forward end of each maturing sperm of *S. fallax* the chromosomes, 12 or 13 in number respectively, are visibly arranged in two lines within the spermatids (Fig. 21). C-banding was obtained for both species. In *S. fallax*, there are prominent terminal C-bands in all the bivalents except two middle-sized bivalents, and an interstitial C-band in the X chromosome (Fig. 20). In *S. arborea*, four middle-sized bivalents appear lightly C-banded at the chromosome ends, whereas the X shows dark C-banding over its majority (Fig. 19).

Bactericera Puton, 1876

In males of *B. nigricornis*, MI shows 12 autosomal bivalents and a heteromorphic XY bivalent (Fig. 22). The autosomal bivalents gradually decrease in size, and the XY bivalent is similar in size to the smallest of these. During diplotene, the sex bivalent is positively heteropycnotic and cross-shaped with the typical appearance of that forming a single chiasma (Fig. 23).

Trichochermes Crawford, 1914

In *T. grandis*, diplotene shows 12 autosomal bivalents having each a terminal or near terminal chiasma, and a univalent X chromosome, which is round in shape and positively heteropycnotic at this stage (Fig. 24).

Trioza Förster, 1848

In males of *T. elaeagni*, MI contains 12 autosomal bivalents and a X univalent (Fig. 25). Bivalents form a more or less gradual size series. The size of the X chromosome is similar to that of a group of small semi-bivalents.

Discussion

This paper provides data on karyotypes in males of 19 psyllid species from the families Psyllidae and Triozidae. In the first, 16 species belong to 11 genera and 7 subfamilies, whereas in the second, 3 species belong to three genera of the largest subfamily Triozinae. With the exception of *C. eucalypti*, all the species and the genus *Ligustrinia* have not been previously studied. Most of these unrelated species showed 2n = 24 + X (see Table 1), whereas three species were found to display different karyotypes. Of these, *Arytainilla spartiophila* has 2n = 22 + X, *Ctenarytaina eucalypti* 2n = 8 + X, and *Bactericera nigricornis* 2n = 24 + XY.

In all but one case, one population with 1 to 5 specimens per species was studied and no polymorphism was detected. In *Cacosylla intacta*, in two studied males from the population in the Irkutsk Region, all 20 MI cells examined were found to display a number of bivalents as univalents. These meiotic abnormalities may be related to environmental conditions, since the three males originating from the Gorno-Altaysk Territory population showed no deviations from normal meiosis. Further studies are required investigate this suggestion.

A predominance of the karyotype 2n = 24 + X in the material investigated was expected. This karyotype is known to represent the modal class of chromosome complement in Psylloidea and is encountered, with a few exceptions, in every genus and each higher taxa of the superfamily (reviewed by MARYAŃSKA-NADACHOWSKA 2002; see also MARYAŃSKA-NADACHOWSKA & GŁOWACKA 2005). In many genera of Psyllidae and Triozidae, a variation in chromosome number and, rarely, in sex determining chromosome system occurs. In some cases the cause and significance of this variation are not clear at this stage, however, examination of additional members of these genera will probably reveal differences of taxonomic significance. Such seems to be the case for the genera *Craspedolepta*, *Cacopsylla*, *Aritainilla*, *Livilla* (Psyllidae), and *Trioza* (Triozidae) from the present study. Within these genera, the majority of studied species dis-

plays 2n = 24 + X, however, individual species deviate from the norm. These include *A. spartiophila* with 2n = 22 + X from the present study as well as *C. bulgarica* (Klimaszewski, 1961) with 2n = 12 + X, *P. corcontum* Šulc, 1909 with 2n = 20 + X, *L. radiata* (Förster, 1848) with 2n = 20 + X, *T. ilicina* (de Stefani Perez, 1902), and *T. remota* Förster, 1848 with 2n = 14 + X. Autosome fusions seem to have contributed to the karyotype evolution of the above-listed genera, each having the putative ancestral complement 2n = 24 + X.

For some higher taxa enough data are presently at hand to permit some inferences about the patterns of their chromosome evolution. In the genus *Bactericera*, all hitherto studied species were found to share a common autosome number 24, in diploid complement, however their karyotypes are distinguished by differences in sex determining chromosome system, that is XO in *B. acutipennis* (Zetterstedt, 1828), *B. femoralis* (Förster, 1848), *B. maura* (Förster, 1848), and *B. reuteri* (Šulc, 1913) whereas XY in *B. curvatinervis* (Förster, 1848), *B. salicivora* (Reuter, 1876), *B. striola* (Flor, 1961), and also in *B. nigricornis* (Förster, 1848) from the present study.

The occurrence of the XY system in a group with predominantly the XO system is usually considered as a result of a fusion between the formerly univalent X chromosome and an autosome in a XO ancestor. When such a fusion does occur, in the derived karyotype the number of autosomes would be reduced. A situation like this has been described in *Psylla corcontum* (SUOMALAINEN & HALKKA 1963) and, as a polymorphism, also in *Cacopsylla sorbi* (Linnaeus, 1758) and *C. mali* (Schmidberger, 1836), which all possess lower diploid chromosome numbers as compared to their congeners (GROZEVA & MARYAŃSKA-NADACHOWSKA 1995; MARYAŃSKA-NADACHOWSKA *et al*. 1996). In addition, when recently formed, the neo-Y must still be homologous with the original autosomal part of the neo-X and must therefore be chiasmatically associated with it in meiotic prophase, as it is the case in all XY *Bactericera* species (KUZNETSOVA *et al.* 1997b; MARYAŃSKA-NADACHOWSKA *et al.* 2001), including *B. nigricornis* (present study). It has been speculated that the only possible way of producing the karyotype 2n = 24 + neo-XY in the genus *Bactericera* is that of fission of one autosome pair in the initial karyotype 2n = 24 + X, resulting in the rise of karyotype 2n = 26 + X followed by the X-autosome fusion (KUZNETSOVA *et al.* 1997b). The hypothetic karyotype 2n = 26 + X has not yet been encountered in the genus *Bactericera*, however, quite recently it was for the first time revealed in Psylloidea (in *Pauropsylla tricheata* Pettey 1924, Triozidae), representing the highest chromosome number so far recorded for psyllids (MARYAŃSKA-NADACHOWSKA & GŁOWACKA 2005).

Without regard to its origin, the neo-XY sex determination in *Bactericera* suggests a common origin. Consequently, in this morphologically-based monophyletic genus (BURCKHARDT & LAUTERER 1997), two lines of evolution are in existence as indicated by cytogenetical characters. Clearly further combined cytogenetical and morphological studies of the *Bactericera* genus would be useful.

There is an obvious discrepancy between the results of this study carried out on *C. eucalypti* from Madeira Island and those obtained by MARYAŃSKA-NADACHOWSKA *et al.* (1992) for a South African population of this species, the chromosome number of which was found to be 2n = 20 + X, unique for the predominantly Australian subfamily Spondyliaspidinae (Psyllidae) when compared with the results from the other species studied to date. However from Figure 8 presented in MARYAŃSKA-NADACHOWSKA *et al.* (1992) for *C. eucalypti*, it is obvious that two closely spaced MII plates with 5 and 6 chromosomes respectively, were mistaken for a MI resulting in an erroneous count of 2n = 21. *C. eucalypti* has been introduced to other parts of the World, including South Africa, southern Europe, British Isles, Macronesia, California, Colombia and Bolivia, where it damages *Eucalyptus globulus* and other glacous leaved eucalypts (HOLLIS 2004). In Madeira it first found in August 1989, but it was probably introduced earlier (FRANQUINHO AGUIAR & MARTIN 1999). The results for *C. eucalypti* obtained in the present paper are in broad agreement with those recorded for the other spondyliaspidine species. Sixteen further studied species in 10 genera of Spondyliaspidinae, which are sometimes considered as an independent family Spondyliaspididae (BECKER-MIGDISOVA 1973; MORGAN 1984; WHITE & HODKINSON 1985), all were found to share low chromosome numbers, 7 through 11, in male karyotypes, and chromosome number, 2n = 10 + X, encountered in males of *C. eucalypti*, fits well in this range.

In organisms displaying holokinetic chromosomes, like Psylloidea, the identification of chromosome markers is very important, since these chromosomes lack markers like centromeres. Differentiation staining techniques provide some useful information on structure and rearrangements of holokinetic chromosomes, which is however of limited or no taxonomical significance. Relatively many studies were successfully analyzed the amount and distribution of heterochromatin in holokinetic chromosomes of different insect groups (KUZNETSOVA *et al.* 2003; NECHAYEVA *et al.* 2004; WALLER & ANGUS 2005; CRINITI *et al.* 2005), including studies carried out on Psylloidea. In *Rhinocola aceris* (Linnaeus, 1758), several types of

B chromosomes could be identified based on heterochromatin distribution (MARYAŃSKA-NADACHOWSKA 1999). In *Aphalara calthae* (Linnaeus, 1758), C-banding was found to enable all the bivalents to be distinguished from each other due to their different C-band patterns (KUZNETSOVA *et al*. 1997a), whereas in *A. rumicicola* Klimaszewski, 1968 clearly defined C-bands were revealed only in two autosomal pairs allowing their identification in the karyotype. In the present study, the closely related species, *Strophingia fallax* and *S. arborea*, likewise showed differences in C-band patterns. The first species displayed prominent terminal bands in all but two bivalents and an interstitial band in the X chromosome, whereas in the second species four bivalents possessed small terminal bands, and the X showed dark C-banding over its majority. In *Craspedolepta topicalis*, the two observed heterochromatin blocks, putatively located on a pair of middle-sized bivalents, were DAPI-positive indicating that they are AT rich. Further studies involving more specimens and different populations are required to draw inferences about the genuine C-band distribution in each species.

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