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Meiotic karyotypes and structure of testes in males of 12 species of Psyllidae: Acizziinae, Carsidaridae and Triozidae (Hemiptera: Psylloidea) from Australia

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Abstract The structure of the internal reproductive system of males of 12 Australian species of Psylloidea is described. These are *Acizzia loranthacae* Taylor, *A. acaciaebaileyanae* (Froggatt) and two undescribed species of *Acizzia* Heslop-Harrison (Psyllidae: Acizziinae), *Protyora sterculiae* (Froggatt) (Carsidaridae), *Aacanthocnema dobsoni* (Froggatt), three undescribed species of *Trioza* Förster, *Schedotrioza apicobystra* Taylor, *S. distorta* Taylor and *S. multitudinea* (Maskell) (Triozidae). Chromosome numbers were determined for all but the last three species. All species karyotyped had diploid chromosome numbers of 2n = 25 (24 + X) in males. Aspects of the karyology and morphology of the male internal reproductive system are discussed, and some comments on the placement of the Australian psylloid fauna within the higher classification of the Psylloidea are presented.

Key words Carsidaridae, chromosome number, karyology, male reproductive system, Psyllidae: Acizziinae, Psylloidea, Triozidae.

INTRODUCTION

The karyology of some 125 species from 51 psylloid genera and the structure of the male internal reproductive organs of 182 species from 60 psylloid genera have been studied (Maryańska-Nadachowska *et al*. 1992, 2001; Głowacka *et al*. 1995; Kuznetsova *et al*. 1997a; Matcharashvili & Kuznetsova 1997). Chromosome numbers and the number of testicular follicles and arrangement of spermatocysts within a follicle were found to be of taxonomic and phylogenetic significance.

The Psylloidea, like other hemipterous insects, possess holokinetic chromosomes in which a localised centromere is absent and kinetic activity is diffused along the length of the chromosome (White 1973; Kuznetsova 1979; Blackman 1980, 1987). This attribute has important evolutionary implications: if a chromosome breaks, the portions are still able to move independently into the daughter cells and may be perpetuated in the genome. In the case of monokinetic chromosomes (with localised centromeres), fragments left without centromeres are lost. Organisms with holokinetic chromosomes would thus be expected to have greater variation in their karyotypes. Additional variability in karyotypes occurs in insects with thelytokous reproduction; that is, Aphididae where chromosome fusions are perpetuated by independent parthenogenetic lines (Blackman 1980, 1987). In the Psylloidea chromosome numbers lie between 2n = 7 and 2n = 26 in males with a clear mode of 2n = 25. The great majority of genera show few if any variations in chromosome numbers.

Recently the karyotypes of 16 species, and the internal reproductive system of 17 species of Australian Psyllidae: Spondyliaspidinae (Hemiptera: Psylloidea) have been investigated (Maryańska-Nadachowska *et al*. 2001), representing the first comprehensive study of this kind, not only for the subfamily, but for the Australian region as well. All species displayed unusually low chromosome numbers of 2n = 11, 9 and 7 in males, the latter two being the lowest chromosome numbers recorded for any Psylloidea. In all species there was only one follicle per testis. Most Psylloidea have two follicles per testis although up to five have been recorded (Głowacka *et al*. 1995). These characters indicated that Australian Spondyliaspidinae constitute a compact, specialised taxon that has undergone intensive rearrangements of its genetic structure during its evolution.

The present study describes the karyotypes and male internal reproductive system of nine species, and the reproductive system of an additional three species from Australia. Species examined belong to the families Psyllidae: Acizziinae (four species, all *Acizzia* Heslop-Harrison); Carsidaridae (one species); and Triozidae (seven species). This is the first comprehensive study for these taxa from Australia; data on the genera *Protyora* Kieffer (Carsidaridae) and *Aacanthocnema* Tuthill and Taylor and *Schedotrioza* Tuthill and Taylor (Triozidae) are reported for the first time.

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MATERIALS AND METHODS

All species for the present study were collected and identified (by GST) in Australia. For cytological studies, specimens of adult male psyllids were dropped live into freshly prepared Carnoy's fixative (25% glacial acetic acid in ethanol). The locations of collection sites and sample sizes are given in Table 1. Karyological and anatomo-morphological studies were carried out by AM and VGK. Pretreatment, preparation of slides and staining of chromosome were made according to the protocol described by Maryańska-Nadachowska *et al*. (1992).

Morphology of the male internal reproductive system, including number of testicular follicles and the arrangement of spermatocysts within a follicle, was examined using the technique described in Maryańska-Nadachowska *et al*. (2001).

The karyotypes of nine species belonging to four genera (*Acizzia*, *Protyora*, *Aacanthocnema* and *Trioza*) of the families Psyllidae: Acizziinae, Carsidaridae and Triozidae were examined. The male internal reproductive organs of these, and of an additional three species of *Schedotrioza* (Triozidae), were studied.

Voucher specimens, slide material mounted in Gurr's DePex mounting medium (as per method in Taylor 1999), specimens preserved in 70% ethanol, and specimens used in cytogenetic studies (in Carnoy's fixative), have been deposited in the Waite Insect and Nematode Collection, Adelaide University.

RESULTS

Psyllidae: Acizziinae

Acizzia loranthacae Taylor

Seven males were studied. Male diploid karyotype was 2n = 25 (24 + X). Males had four elongate and tubiform follicles in each of the paired testes. Three zones of differentiation were observed within the follicle: germarium (premeiotic divisions); growth (meiotic divisions); and spermiogenesis. In the last two zones the spermatocyte cysts, bundles of spermatids and bundles of mature sperms were aligned in one row.

Cells in metaphase I (MI), anaphase I (AI) and in metaphase II (MII) were available for analysis. MI showed 12 autosomal bivalents and the univalent X chromosome (Fig. 1a). Each bivalent was held together with one terminal chiasma. The X was comparatively large and similar in size to one of the larger half-bivalents. In AI, diverging autosomes showed free telomeres facing the poles, this arrangement indicating the kinetic activity of the telomeres in psyllid meiosis. This was also the case for the X, which moved to one pole behind the autosomes (Fig. 1b). As a result of AI, two types of MII plates were available: those with 12 autosomes and those with 12 autosomes and the X (Fig. 1c,d).

Table 1 Species of Australian Psyllidae: Acizziinae, Carsidaridae, and Triozidae with host plant, collection data and number of specimens examined, number of chromosomes (2n) and number of follicles per testis

Species	Host plant	Collection site and date (number examined)	No. chromosomes 2n (metaphase I)	No. follicles per testis
Psyllidae: Acizziinae				
Acizzia loranthacae Taylor	*Amyema pendulum* on *Eucalyptus camaldulensis*	SA, Ambleside (near Hahndorf), 22.ix.1997 (7 males)	24 + X	4
Acizzia acaciaebaileyanae (Froggatt)	*Acacia baileyana*	SA, Adelaide, Urrbrae, Waite Campus, 22.ix.1997 (11 males)	24 + X	2
Acizzia sp. 1	Myoporaceae	SA, Adelaide, Urrbrae, Waite Campus, 4.xi.1997 (7 males)	24 + X	4
Acizzia sp. 2	*Acacia pendula*	SA, Adelaide, Urrbrae, Waite Campus, 22.ix.1997 (9 males)	24 + X	4
Carsidaridae: Carsidarinae				
Protyora sterculiae (Froggatt)	*Brachychiton* sp.	SA, Clare, 1.xi.1998 (6 males)	24 + X	1
Triozidae: Triozinae				
Aacanthocnema dobsoni Froggatt	*Allocasuarina verticillata*	SA, Adelaide, Seaview Downs, 26.ix.1997 (6 males)	24 + X	2
Trioza sp. 1	*Allocasuarina verticillata*	SA, Adelaide, Seaview Downs, 26.ix.1997 (6 males)	24 + X	2
Trioza sp. 2	*Casuarina cristata*	SA, Adelaide, Urrbrae, Waite Campus, 22.ix.1997 (7 males)	24 + X	2
Trioza sp. 3	*Allocasuarina verticillata*	SA, Adelaide, Seaview Downs, 26.ix.1997 (6 males)	24 + X	2
Schedotrioza apicobystra Taylor	*Eucalyptus cosmophylla*	SA, Bridgewater, 29.x.1997, 30.x.1998 & 13.ix.1999 (6 males)	–	2
Schedotrioza distorta Taylor	*Eucalyptus leucoxylon*	SA, Adelaide, Urrbrae, Waite Campus, 24.x.1997 (7 males)	–	2
Schedotrioza multitudinea (Maskell)	*Eucalyptus obliqua*	SA, Mylor, 21.x.1998 (7 males)	–	2

All collected by GST. SA, South Australia

Acizzia acaciaebaileyanae (Froggatt)

Eleven males were studied. Male diploid karyotype was 2n = 25 (24 + X). Males had two follicles in each testis. The follicles were elongate and tubiform with slender apical ends. Within the follicle three zones of differentiation were observed: the spermatocyte cysts, bundles of spermatids and bundles of mature sperms were aligned in one row.

Cells in diplotene and in diakinesis/MI were available for analysis. In diplotene, 12 bivalents and one conspicuous heteropycnotic body were visible (Fig. 2a,b). Each bivalent was held together with one terminal chiasma. Among the bivalents, the largest could be readily distinguished. The heteropycnotic body was comparatively large, its large size and heteropycnotic state maintained up to diakinesis/MI stage (Fig. 2c,d). This body was considered to represent the univalent X-chromosome.

Acizzia sp. 1

Seven males were studied. The male diploid karyotype was 2n = 25 (24 + X). Males had four follicles in each testis. The follicles were elongate and tubiform with slender apical ends. Within the follicle three zones of differentiation were observed: the spermatocyte cysts, bundles of spermatids and bundles of mature sperms were aligned in one row.

Cells in MI and AI were available for analysis. MI showed 12 autosomal bivalents and the univalent X chromosome (Fig. 3a). The largest bivalent was readily distinguishable. Each bivalent was held together with one terminal chiasma. The X was comparatively large, its size close to that of one of the larger half-bivalents. At early AI, chromatin connections were seen between diverging chromosomes of bivalents; the sex univalent moved to one pole suggesting segregation in the first division (Fig. 3b).

Acizzia sp. 2

Nine males were studied. Male diploid karyotype was 2n = 25 (24 + X). Males had four elongate and tubiform follicles in each testis. Within the follicle spermatocyte cysts, bundles of spermatids and bundles of mature sperms were aligned in one row.

Cells in MI were available for analysis. MI showed 12 autosomal bivalents and the univalent X-chromosome (Fig. 4). Bivalents were comparatively evenly sized, each with one terminally located chiasma.

Carsidaridae: Carsidarinae

Protyora sterculiae (Froggatt)

Six males were studied. Male diploid karyotype was 2n = 25 (24 + X). Males had one follicle in each testis. Each follicle was elongate and cone-shaped, tapering more towards the apex than towards the basal end. Within the follicle three zones of differentiation were observed. In the last two zones the spermatocyte cysts, bundles of spermatids and bundles of mature sperms were well distinguished but were not arranged into definite rows.

Cells in diakinesis, MI and AI were available for analysis. In diakinesis, 12 autosomal bivalents and the univalent X-chromosome were seen (Fig. 5a,b). Bivalents four and five were clearly larger than the others. Each of the bivalents displayed one chiasma that was mainly terminally or subterminally located. In one nucleus, one of the large bivalents showed an interstitial chiasma. In many diakineses some univalents and different kinds of chromosome translocations were observed (Fig. 5c–e) but all MI and AI nuclei proved to be normal. At MI, 12 autosomal bivalents and the univalent X-chromosome were observed (Fig. 5f). In this stage and in AI (Fig. 5g), but in contrast to diakinesis, it was impossible to differentiate between the largest bivalents.

Triozidae: Triozinae

Aacanthocnema dobsoni Froggatt

Six males were studied. Male diploid karyotype was 2n = 25 (24 + X). Males had two follicles in each testis. The follicles were elongate and tubiform with a slender apical end. Three zones of differentiation were observed inside the follicle: spermatocyte cysts, bundles of spermatids and mature sperm were aligned in several poorly defined rows.

Cells in late MI were available for analysis. MI exhibited 12 autosomal bivalents and the univalent X-chromosome (Fig. 6). Bivalents were comparatively small and evenly sized, each with one terminal chiasma. The X was split into chromatids in all cells studied.

Trioza sp. 1

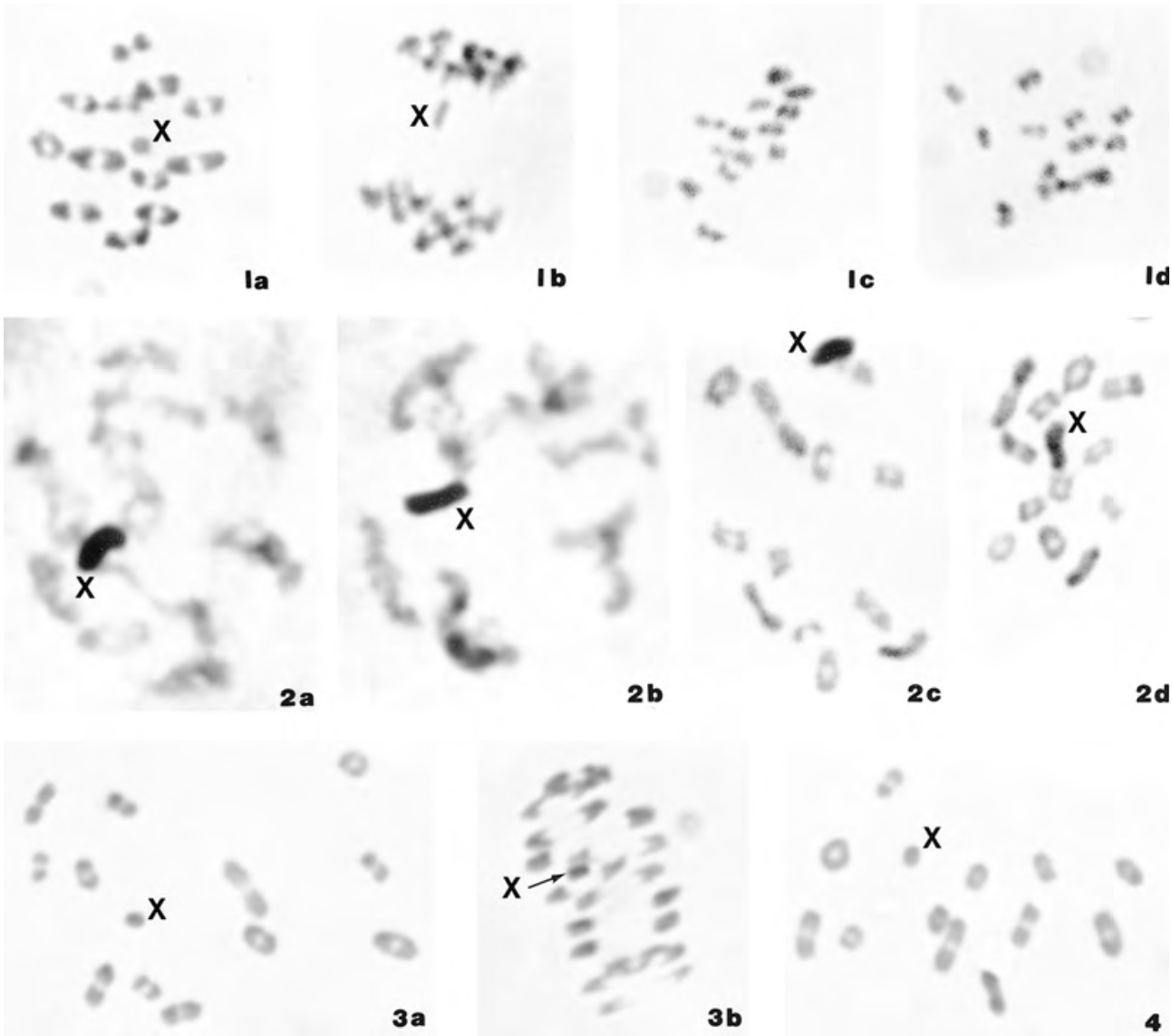
Six males were studied. The male diploid karyotype was 2n = 25 (24 + X). Males had two follicles in each testis. The follicles were elongate and tubiform with a slender apical end. Three zones of differentiation were observed inside the follicle: spermatocyte cysts, bundles of spermatids and mature sperm were aligned in one row.

Cells in MI were available for analysis. MI showed 12 bivalents and the univalent X-chromosome (Fig. 7). Bivalents were comparatively small and evenly sized, each with one terminal chiasma.

Trioza sp. 2

Seven males were studied. The male diploid karyotype was 2n = 25 (24 + X). Males had two follicles in each testis. The follicles were elongate and tubiform with a slender apical end. Three zones of differentiation were observed inside the follicle: spermatocyte cysts, bundles of spermatids and mature sperm were aligned in several poorly defined rows.

Cells at MI were available for analysis. MI demonstrated 12 autosomal bivalents and the univalent X-chromosome (Fig. 8). Bivalents were comparatively small and evenly sized, each with one terminal chiasma.



Figs 1–4. Chromosomes. **(1a–d)** *Acizzia loranthacae*. **(1a)** Metaphase I; **(1b)** anaphase I; **(1c,d)** metaphase II. **(2a–d)** *Acizzia acaciaebaileyanae*. **(2a,b)** Diplotene; **(2c,d)** diakinesis/metaphase I. **(3a,b)** *Acizzia* sp. 1. **(3a)** Metaphase I; **(3b)** anaphase I. **(4)** *Acizzia* sp. 2, metaphase I. All figs to same scale.

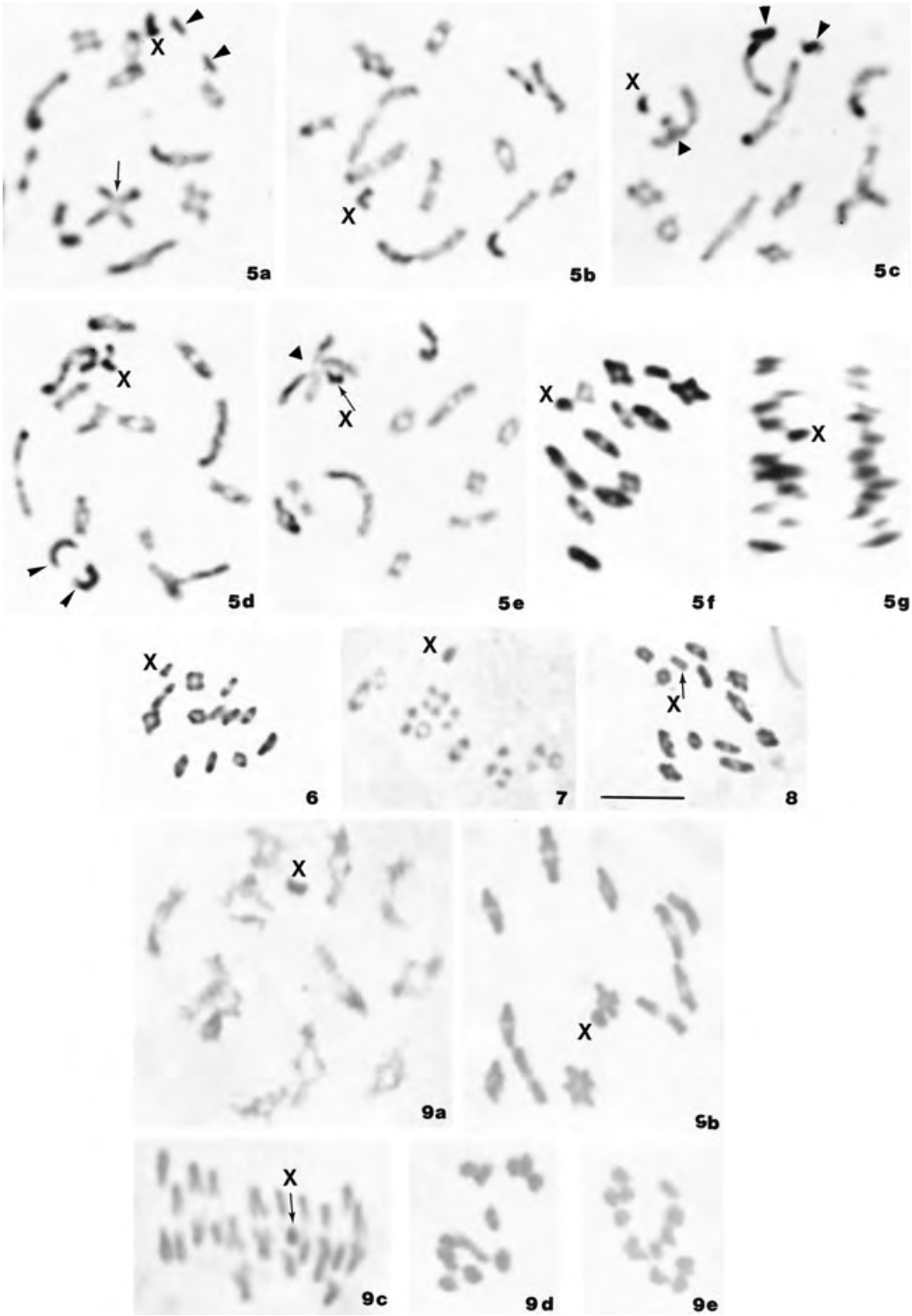
Trioza sp. 3

Six males were studied. Male diploid karyotype was 2n = 25 (24 + X). Males had two follicles in each testis. The follicles were elongate and tubiform with a slender apical end. Within the follicles the spermatocyte cysts and bundles of spermatids and mature sperm were aligned in one row.

Cells in diplotene-diakinesis, in MI, in AI and in MII were available for analysis. In diplotene-diakinesis, 12 autosomal bivalents and heteropycnotic X univalent were visible (Fig. 9a). In MI, bivalents were comparatively evenly sized, each with one terminal or subterminal chiasma (Fig. 9b). The X was close in size to one of the middle half-bivalents. In AI the sex chromosome turned towards one of the sister nuclei (Fig. 9c); as a result there appeared to be two MII, those with 12 autosomes and those with 12 autosomes and the X (Fig. 9d,e).

Schedotrioza apicobystra Taylor, *S. distorta* Taylor and *S. multitudinea* (Maskell)

Five, six and four males were studied for each of the species, respectively. Karyotypes of the aforementioned species could not be determined. Males had two follicles in each testis in all three species examined. The follicles were elongate and tubiform with slender apical ends. Within the follicle spermatocyte cysts, bundles of spermatids, and bundles of mature sperms were aligned in one row.



Figs 5–9. Chromosomes. **(5a–g)** *Protyora sterculiae*. **(5a,b)** Diakinesis, arrow indicates interstitial chiasma; **(5c–e)** diakinesis with chromosomal aberrations; triangles indicate translocations, arrow heads indicate univalents; **(5f)** metaphase I; **(5 g)** anaphase I. **(6)** *Aacanthocnema dobsoni,* metaphase I. **(7)** *Trioza* sp. 1, metaphase I. **(8)** *Trioza* sp. 2, metaphase I. **(9a–e)** *Trioza* sp. 3. **(9a)** Diplotene/diakinesis; **(9b)** metaphase I; **(9c)** anaphase I; **(9d,e)** metaphase II. Scale in Fig. 8 = 10 μm.

DISCUSSION

All available classifications and phylogenies of the Psylloidea are based on the external morphological characters. Because of the diversity of the Psylloidea there are numerous taxonomic and phylogenetic problems (Becker-Migdisova 1973; White & Hodkinson 1985; Burckhardt 1987; Gegechkori & Loginova 1990; Klimaszewski 1993). Gℓowacka and Klimaszewski (1968, 1970) suggested that evolutionary changes of the anatomical structures have occurred at a lower rate compared with changes to external morphological characters. The male internal reproductive system was shown to be less differentiated than some external characters, and may be useful in systematic studies to construct relationships for the Psylloidea worldwide (Gℓowacka *et al*. 1995; Kuznetsova *et al*. 1995; Matcharashvili & Kuznetsova 1997; Maryańska-Nadachowska *et al*. 2001).

The present study, together with the recent work on the predominantly Australian Psyllidae: Spondyliaspidinae (Maryańska-Nadachowska *et al*. 2001), represents the only comprehensive karyological studies and descriptions of the male internal reproductive system for the Australian Psylloidea.

Including our new data, the karyotypes of approximately 125 species belonging to 51 genera of the Psylloidea have been determined (Kuznetsova *et al*. 1997a,b; Maryańska-Nadachowska & Gℓowacka 1997; Maryańska-Nadachowska & Yang 1997; Maryańska-Nadachowska *et al*. 2001). The only family not represented is the Phacopteronidae. In the present study the karyotypes of nine species assigned to the families Psyllidae, Carsidaridae and Triozidae were examined (Table 1). All species, including those from *Protyora* and *Aacanthocnema*, recorded here for the first time, had a karyotype in males of 2n = 25 (24 + X), which is consistent with the majority (approximately 70%) of the Psylloidea and most probably represents the ancestral character state for the group (Kuznetsova *et al*. 1995, 1997a,b).

Of the species included in the present study *Aacanthocnema dobsoni*, *Trioza* sp. 1 and *Trioza* sp. 2 had smaller chromosomes than the remaining six species, including *Trioza* sp. 3. In the genus *Trioza* Förster a number of the other species studied elsewhere also had comparatively small chromosomes (Kuznetsova *et al*. 1995, 1997a). The incidence of small chromosome size requires further study.

All species studied showed low chiasma frequency, having only one chiasma in each autosomal bivalent. Chiasmata were mainly terminal or subterminal. Low chiasma frequency has previously been reported for other Hemiptera; that is, in some families of the Auchenorrhyncha (Halkka 1964; Kuznetsova 1979).

The Psylloidea, like all other Hemiptera, display holokinetic chromosomes in which centromeric activity is diffused along the length of the chromosomes. If a holokinetic chromosome breaks, diffuse centromeric activity allows individual fragments to survive and move independently into daughter cells in subsequent divisions. (In the case of monokinetic chromosomes with localised centromeres any fragment without a centromere is lost.) We expect that in groups with holokinetic chromosomes, the chromosome aberrations are perpetuated in a population, resulting in increased variability in karyotypes across a particular taxonomic level. Aphids, for example, show high variability within subfamilies and tribes, indicating that chromosome numbers are not particularly useful in determining phylogenetic relationships at higher levels of classification. They are, with some notable exceptions where thelytokous reproduction contributes to karyotypic variability within parthenogenetic lines of single species, relatively stable at the generic level (Blackman 1980, 1987).

In Coccoidea and Auchenorrhyncha, chromosome numbers are quite stable at the higher taxonomic levels (Nur *et al*. 1987; Emelyanov & Kirillova 1992) and in some cases provide a good tool for taxonomic and phylogenetic studies (Kuznetsova 1986; Kuznetsova *et al.* 1998). Psylloids, too, show conservatism in chromosome numbers, with 2n = 24 + XX/XO recorded in the majority of species and superspecies taxa, although male diploid chromosome numbers as low as 7 have been recorded for some Australian Spondyliaspidinae (Maryańska-Nadachowska *et al*. 2001). Even so, there are some examples of minor karyotypic variability, in some instances at the generic level; for example in *Cardiaspina* Taylor and *Cryptoneossa* Taylor (Maryańska-Nadachowska *et al*. 2001).

Some unusual and aberrant patterns of meiosis have been described in different groups of insects with holokinetic chromosomes (Nur 1980; Tombesi & Papeshi 1993; Nokkala & Nokkala 1997). In Psylloidea meiosis of males takes place quite normally (Kuznetsova *et al*. 1997a). All chromosomes segregate reductionally in the first division and show an equational separation in the second division. In bivalents only one or, very rarely, two chiasmata occur, and this appears to be characteristic of holokinetic chromosomes (Halkka 1964). All species from the present study also demonstrated low chiasma frequency, having only one chiasma per bivalent. Chiasmata are mainly terminal or subterminal.

In one specimen of *Protyora sterculiae* (Carsidaridae) some meiotic abnormalities were observed. These were univalents and unusual chromosome translocations, but we failed to determine which chromosomes were involved. Chromosome translocations have been studied in detail for only two species of Psylloidea, *Cacopsylla sorbi* (L.) and *C. mali* (Schmidberger). In these, translocations have led to polymorphism of chromosome number and sex-chromosome constitution (Grozeva & Maryańska-Nadachowska 1995). A series of autosomal and X-autosomal translocations in the evolution of these species was suggested to be responsible for the rise of the neo X^1X^2Y sex chromosome type from an ancestral XO system.

Studies on the male internal reproductive system from all families of the Psylloidea, including the number of testicular follicles and arrangement of spermatocysts within the follicle, were reviewed recently (Gℓowacka *et al*. 1995). Testes consisting each of two follicles were found in 129 of 178 species examined, indicating the modality of this arrangement and the most probable ancestral state in the Psylloidea

(Kuznetsova *et al*. 1997a,b). Other species displayed testes each with one follicle (approx. 20%) and with three to five follicles (approx. 10%) of all specimens examined.

In the present study eight of 12 species studied had testes consisting of two follicles, seven of these species belonging to the Triozidae. The Australian triozid fauna currently consists three genera: the cosmopolitan *Trioza*, with free-living species on *Myoporum* and Casuarinaceae; the endemic genus *Aacanthocnema* free-living on Casuarinaceae; and the endemic genus *Schedotrioza*, which forms galls on *Eucalyptus* (Taylor 1990). Our data considered all three genera, *Aacanthocnema* and *Schedotrioza* having been examined for the first time. Evidence is consistent with the vast majority of all triozid species studied (G¢owacka *et al*. 1995; Maryańska-Nadachowska & G¢owacka 1997). The only exception is *Trichochermes walkeri* Förster from Poland, which has three follicles in each testis (G¢owacka & Klimaszewski 1968). With few exceptions in the Triozidae, spermatocysts, and bundles of spermatids and sperm are aligned in one row within the follicles.

Three of the four species of *Acizzia* that we studied had four follicles per testis, whereas males of *A. acaciaebaileyanae* had testes consisting each of two follicles. In two species of *Acizzia* studied previously (*A. uncatoides* (Ferris & Klyver) and *Acizzia* sp.) the testes consists of three follicles (G¢owacka *et al*. 1995). On the basis that most closely related species in the Psylloidea share the same testicular structure, the variability in the follicle number found in *Acizzia* is of taxonomic interest.

Males of *P. sterculiae* had one follicle in each testis, a character that is consistent with all species of the Carsidaridae-Carsidarinae studied, namely *Tenaphalara* Kuwayama, *Mesohomotoma* Kuwayama, and *Paracarsidara* Heslop-Harrison (G¢owacka *et al*. 1995). One further common character of the carsidarid species, including *P. sterculiae*, is that the spermatocysts and bundles of the spermatids inside their follicles are arranged in many poorly defined rows, whereas in most other Psylloidea they are aligned in one row.

The number of testicular follicles appears to constitute an important character of taxonomic and phylogenetic significance, not only for the Psylloidea but also for many other Hemipteran taxa (Pendergrast 1957; Wojciechowski 1977; Emelyanov & Kuznetsova 1983; Grozeva & Kuznetsova 1992).

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