

Variation in Sperm Formation Patterns in Jumping Plant-Lice (Hemiptera: Psylloidea): a Light Microscopic Study

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The patterns of sperm formation in sternorrhynchous jumping plant-lice are reviewed. To date information is available for 143 species belonging to 54 genera, 17 subfamilies and seven of the eight psylloid families (only Phacopteronidae is not represented). For the majority of the taxa (116 species, 39 genera, 10 subfamilies and the families Calophyidae, Carsidaridae and Liviidae) the data presented here is new and is based exclusively on studies using light microscopy. Five distinct patterns of chromatin reorganisation during metamorphosis of spermatids into spermatozoa are recognised, described and named here types I-V. Types I and III were previously known, types II, IV and V are described here for the first time for jumping plant-lice. The most widespread is type I which is found in every family representing the plesiomorphic condition of spermiogenesis in Psylloidea. Types III and V are autapomorphic for the Aphalarinae and Spondylaspidinae, respectively. Type IV was found only in two genera of Euphyllurinae and may represent a synapomorphy. Type II occurs in several unrelated subfamilies and is interpreted as a homoplasy. The patterns of sperm formation are stable within most of the examined subfamilies and can be used, to a certain extent, to elucidate phylogenetic relationships within Psylloidea.

Key words: Psyllids, Sternorrhyncha, spermiogenesis, evolution, systematics.

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Psyllids or jumping plant-lice (Sternorrhyncha: Psylloidea) are a relatively small group of hemipteran insects with about 3800 described and at least as many undescribed species worldwide (BURCKHARDT *et al.* 2014; D. BURCKHARDT, unpublished data). WHITE and HODKINSON (1985), in their seminal paper on the systematics of psyllids based mostly on morphological characters of immatures, introduced a classification with eight families (Aphalaridae, Calophyidae, Carsidaridae, Homotomidae, Phacopteronidae, Psyllidae, Spondylaspididae and Triozidae). This classification was tested in the last three decades by several authors who investigated many taxa using morphological adult and immature as well as molecular characters. White and Hodkinson's families were generally

supported with the exception of their Aphalaridae, Psyllidae, and Spondylaspididae which were shown to be polyphyletic (BURCKHARDT 1987a, b, 1991, 2005). Based on these results BURCKHARDT and OUVARD (2012) published a revised classification also comprising eight families of which five are similar to those of White and Hodkinson (Calophyidae, Carsidaridae, Homotomidae, Phacopteronidae, and Triozidae) but three are completely redefined (Aphalaridae, Liviidae, and Psyllidae).

Several attempts have been undertaken to study the systematics of Psylloidea using new characters, such as the number of seminal follicles (e.g. KLIMASZEWSKI 1972; KLIMASZEWSKI *et al.* 1974; GŁOWACKA *et al.* 1995; MARYAŃSKA-NADACHOWSKA *et al.* 2001a, b, c; KUZNETSOVA *et al.*

2012) and karyotypes (e.g. MARYAŃSKA-NADACHOWSKA 2002; LABINA *et al.* 2007). These characters were shown to be of some use in solving taxonomic problems at the suprageneric level.

Variation in sperm formation patterns within Psylloidea was investigated in a number of publications (LE MENN 1966a, b; KUZNETSOVA *et al.* 1997; TIAN *et al.* 2007). LE MENN (1966a, b) was the first to observe the remarkable, so-called “binuclear” male germ cells by electron microscopy in eight species of Homotomidae (*Homotoma ficus*), Psyllidae (*Arytaina genistae*, *Cacopsylla visci*, *Chamaepsylla hartigii*, *Psylla alni*, *P. buxi*) and Triozidae (*Bactericera femoralis*, *Trioza urticae*) corresponding to “Type I” as defined below. Later, KUZNETSOVA *et al.* (1997) discovered by light microscopy a different, also unusual type of sperm formation in ten species of the genera *Aphalara*, *Craspedolepta* and *Crastina* (Aphalaridae, Aphalarinae) corresponding to “Type III” as defined below. More recently, binuclear sperms were reported for *Acizzia jamatonica* (Psyllidae) and *Bharatiana septentrionalis* (Calophyidae) (TIAN *et al.* 2007) but the attribution to a particular sperm formation type is problematic.

In this paper we confirm the presence of the two previously described types of sperm formation and add another three discovered by light microscopy in a wide taxonomical range of Psylloidea. Furthermore, we plot the known types of sperm formation patterns on a cladogram reflecting the latest classification of Psylloidea by BURCKHARDT and OUVARD (2012) and discuss the phylogenetic implications.

Material and Methods

For nearly three decades, we have prepared hundreds of cytological preparations to study karyotypes and male meiosis of psyllids represented by a wide taxonomic range (e.g. MARYAŃSKA-NADACHOWSKA 2002; LABINA *et al.* 2007; KUZNETSOVA *et al.* 2012; NOKKALA *et al.* 2013). For this purpose, adult males were fixed in Carnoy fixative (96% ethanol and glacial acetic acid, 3:1) and refrigerated at 5°C in the laboratory until slides were made. Seminal follicles were extracted from adult specimens and squashed on the slide. The preparations were frozen using dry ice, the coverslips were removed with a razor blade, and the preparations were dehydrated in fresh Carnoy fixative for 20 min and air dried. Then they were subjected either to Schiff-Giems staining (GROZEVA & NOKKALA 1996) or to silver staining (HOWELL & BLACK 1980) or to C-banding (SUMNER 1972), as the case required.

In our present study, the same cytological preparations were used to study a post-meiotic phase of spermatogenesis, i.e. spermiogenesis. By light microscopy, we followed the progressive differentiation of the spermatid components and changes in chromatin organization during metamorphosis of spermatids into spermatozoa in males of 125 species belonging to 51 genera and 16 subfamilies of the families Aphalaridae, Calophyidae, Carsidaridae, Homotomidae, Liviidae, Psyllidae, and Triozidae. Observation and literature data are summarised in Table 1. We follow the classification by BURCKHARDT and OUVARD (2012). Voucher preparations are deposited at the Department of Experimental Zoology, Institute of Systematics and Evolution of Animals PAS in Kraków, Poland.

Table 1

Species studied and types of spermiogenesis

Taxon	Type of spermiogenesis	Collecting data	Indentification by	Reference
Aphalaridae				
Aphalarinae				
<i>Aphalara calthae</i> (Linnaeus, 1761)	binuclear sperm III	? Finland: near Turku – <i>Caltha palustre</i>	? S. Nokkala	LE MENN 1966a,b KUZNETSOVA <i>et al.</i> 1997
<i>Aphalara exilis</i> (Weber et Mohr, 1804)	III	Poland: Gorce Mts – <i>Rumex</i> sp.	E. Głowacka	KUZNETSOVA <i>et al.</i> 1997
<i>Aphalara maculipennis</i> Löw, 1886	III	Poland: west Beskidy Mts – <i>Polygonum</i> sp.	E. Głowacka	present paper
<i>Aphalara polygona</i> Foerster, 1848 ¹	III	Georgia: Kolkhida, Paliastomi Lake – <i>Polygonum</i> sp.	A. Gegechkori	KUZNETSOVA <i>et al.</i> 1997
<i>Craspedolepta bulgarica</i> Klimaszewski, 1961	III	Georgia: David Garedzhi – <i>Achillea</i> sp.	A. Gegechkori	KUZNETSOVA <i>et al.</i> 1997

Table 1 cont.				
<i>Craspedolepta flava</i> (Kuwayama, 1908)	III	Russia: Primorsky Krai, Khasansky District, near Kedrovaya Pad' Reserve – <i>Artemisia</i> spp.	E. Labina	present paper
<i>Craspedolepta flavipennis</i> (Foerster, 1848)	III	Poland: Kazimierz Dolny – <i>Chrysanthemum</i> sp.	E. Głowacka	present paper
<i>Craspedolepta kerzhneri</i> Loginova, 1963	III	Russia: Primorsky Krai, Khasansky District, near Kedrovaya Pad' Reserve – <i>Artemisia</i> spp.	E. Labina	present paper
<i>Craspedolepta latior</i> Wagner, 1944	III	Russia: Primorsky Krai, Khasansky District, near Kedrovaya Pad' Reserve – <i>Artemisia</i> spp.	E. Labina	present paper
<i>Craspedolepta lineolata</i> Loginova, 1962	III	Russia: Primorsky Krai, Vladivostok – <i>Artemisia</i> sp.	E. Labina	present paper
<i>Craspedolepta malachitica</i> (Dahlbom, 1851)	III	Poland: Mielnik – <i>Artemisia absinthium</i>	E. Głowacka	KUZNETSOVA <i>et al.</i> 1997
<i>Craspedolepta nebulosa</i> (Zetterstedt, 1828)	III	Poland: Gorce Mts – <i>Chamerion angustifolium</i>	E. Głowacka	KUZNETSOVA <i>et al.</i> 1997
<i>Craspedolepta nervosa</i> (Foerster, 1848)	III	Poland: Gorce Mts – <i>Achillea</i> sp.	E. Głowacka	KUZNETSOVA <i>et al.</i> 1997
<i>Craspedolepta omissa</i> Wagner, 1944	III	Poland: Gorce Mts – <i>Artemisia</i> sp.	E. Głowacka	KUZNETSOVA <i>et al.</i> 1997
<i>Craspedolepta sonchi</i> (Foerster, 1848)	III	Finland – <i>Leontodon autumnalis</i>	S. Nokkala	MARYAŃSKA-NA DACHOWSKA <i>et al.</i> 2001c
<i>Craspedolepta subpunctata</i> (Foerster, 1848)	III	Poland: Gorce Mts – <i>Chamerion angustifolium</i>	E. Głowacka	KUZNETSOVA <i>et al.</i> 1997
<i>Craspedolepta terminata</i> Loginova, 1962	III	Russia: Primorsky Krai, Khasansky District, near Kedrovaya Pad' Reserve; Khasansky District, Krabovy Peninsula – <i>Artemisia</i> spp.	E. Labina	present paper
<i>Craspedolepta topicalis</i> Loginova, 1962	III	Russia: Primorsky Krai, Khasansky District, near Kedrovaya Pad' Reserve; Ussuriysky District, Kraunovka – <i>Artemisia</i> spp.	E. Labina	present paper
<i>Craspedolepta villosa</i> Loginova, 1962	III	Russia: Altai Republic, Chemalsky District, Edigan Village – <i>Artemisia</i> sp.	E. Labina	present paper
<i>Crastina myricariae</i> Loginova, 1964	III	Georgia: Caucasus Mts, Hersureti, – <i>Myricaria bracteata</i>	A. Gegechkori	KUZNETSOVA <i>et al.</i> 1997
	III	Russia: Altai Republic, Chemalsky District, Edigan Village – <i>Tamarix</i> sp.	E. Labina	present paper
Pachyphyllinae				
<i>Pachyphylla</i> sp.	I	USA: Maryland, Beltsville – <i>Celtis tenuifolia</i>	M.-M. Yang	present paper
Rhinocolinae				
<i>Agonoscena cisti</i> (Puton, 1882)	II	Spain: Mallorca, Boquet Valley – <i>Pistacia lentiscus</i>	I.D. Hodkinson	present paper
	II	Spain: Cádiz prov., Sierra Blanquilla – under olive trees	E. Labina	present paper
<i>Agonoscena targionii</i> (Lichtenstein, 1874)	II	Spain: Mallorca, Boquet Valley – <i>Pistacia lentiscus</i>	I.D. Hodkinson	present paper
	II	Spain: Cádiz prov., Sierra Blanquilla – under olive trees	E. Labina	present paper
<i>Listronia varicicosta</i> (Hodkinson <i>et Hollis</i> , 1981)	II	Spain: Mallorca, Formentor – <i>Cistus albidus</i>	I.D. Hodkinson	present paper
<i>Rhinocola aceris</i> (Linnaeus, 1758)	II	Poland: Kraków – <i>Acer platanoides</i>	E. Głowacka	present paper
	II	Georgia: near Tbilisi – <i>A. platanoides</i>	A. Gegechkori	present paper
	II	Finland: Turku – <i>A. platanoides</i>	S. Nokkala	present paper
Spondyliaspinae				
<i>Anoeconeossa</i> sp. (<i>communis</i> group)	V	Australia: Adelaide, Urrbrae, Wait Campus – <i>Eucalyptus leucoxylon</i>	G.S. Taylor	present paper
<i>Anoeconeossa</i> sp. (<i>fuscipennis</i> group)	V	Australia: Adelaide, Urrbrae, Wait Campus – <i>Eucalyptus leucoxylon</i>	G.S. Taylor	present paper
<i>Anoeconeossa unicornuta</i> Taylor, 1987	V	Australia: Adelaide, Urrbrae, Wait Campus – <i>Eucalyptus leucoxylon</i>	G.S. Taylor	present paper

Table 1 cont.				
<i>Australopsylla</i> sp.	V	Australia: Strathalbyn-Goolwa – <i>Eucalyptus</i> sp.	G.S. Taylor	present paper
<i>Blastopsylla adnatariae</i> Taylor, 1985	V	Australia: Adelaide, Urrbrae, Wait Campus – <i>Eucalyptus lehmannii</i>	G.S. Taylor	present paper
<i>Blastopsylla moorei</i> Taylor, 1985	V	Australia: Goolwa – <i>Melaleuca lanceolata</i>	G.S. Taylor	present paper
<i>Boreioglycaspis melaleucae</i> Moore, 1964	V	Australia: Queensland, Brisbane, Indooroopilly, CSIRO – <i>Melaleuca quinquenervia</i>	G.S. Taylor	present paper
<i>Cardiaspina albitextura</i> Taylor, 1962	V	Australia: Goolwa – <i>Eucalytus camaldulensis</i>	G.S. Taylor	present paper
<i>Cardiaspina retator</i> Taylor, 1962	V	Australia: Ambleside, near Hahndorf – <i>Eucalytus camaldulensis</i>	G.S. Taylor	present paper
<i>Creiis</i> sp.	V	Australia: Urrbrae, Wait Campus – <i>Eucalyptus leucoxydon</i>	G.S. Taylor	present paper
<i>Cryptoneossa triangula</i> Taylor, 1990	V	Australia: Urrbrae, Wait Campus – <i>Angophora floribunda</i>	G.S. Taylor	present paper
<i>Ctenarytaina eucalypti</i> (Maskell, 1890)	V	Ethiopia: <i>Eucalyptus</i> sp.	E. Labina	present paper
	V	Portugal: Madeira – <i>Eucalyptus</i> sp.	E. Labina	present paper
<i>Glycaspis brimblecombei</i> Moore, 1964	V	Australia: Ambleside, near Hahndorf – <i>Eucalytus camaldulensis</i>	G.S. Taylor	present paper
<i>Hyalinaspis</i> sp.	V	Australia	G.S. Taylor	present paper
<i>Platyobria lewisi</i> Taylor, 1987	V	Australia: Ambleside, near Hahndorf – <i>Eucalytus camaldulensis</i>	G.S. Taylor	present paper
<i>Spondylaspis plicatuloides</i> (Froggatt, 1900)	V	Australia: Adelaide, Urrbrae, Wait Campus – <i>Eucalyptus microcarpa</i>	G.S. Taylor	present paper
Calophyidae				
Calophyinae				
<i>Calophya nigripennis</i> Riley, 1885	I	USA: Maryland	M.-M. Yang	present paper
<i>Calophya schini</i> Tuthill, 1959	I	USA: California, Alameda Co., Berkeley, UC Campus – <i>Schinus Molle</i>	P.G. da Silva as <i>C. rubra</i>	present paper
	I	South Africa: near Cape Town	E. Głowacka	present paper
Mastigimatinæ				
<i>Bharatiana septentrionalis</i> Yang & Li, 1983	binuclear sperm	China	?	TIAN <i>et al.</i> 2007
Carsidaridae				
<i>Protyora sterculiae</i> (Froggatt, 1901)	I	Australia: Clare – <i>Brachychiton</i> sp.	G.S. Taylor	present paper
<i>Tenaphalara acutipennis</i> Kuwayama, 1908	I	Taiwan – <i>Bombax ceiba</i>	Ch.-T. Yang	present paper
Homotomidae				
Dynopsyllinae				
<i>Dynopsylla pinnativena</i> (Enderlein, 1914)	I	Taiwan – <i>Ficus nervosa</i>	Ch.-T. Yang	present paper
Homotominae				
<i>Homotoma ficus</i> (Linnaeus, 1758)	binuclear sperm	?	?	LE MENN 1966b
	I	Croatia: Makarska	E. Głowacka	present paper
	I	Italy: Roma – <i>Ficus carica</i>	E. Głowacka	present paper
	I	Portugal: Madeira – <i>Ficus carica</i>	E. Labina	present paper
Macrohomotominae				
Edenini				
<i>Mycopsylla fici</i> (Tryon, 1895)	II	Australia: New South Wales, Sidney – <i>Ficus</i> sp.	E. Głowacka	present paper
Macrohomotomini				
<i>Macrohomotoma gladiata</i> Kuwayama, 1908	I	Taiwan – <i>Ficus retusa</i>	Ch.-T. Yang	present paper
Liviidae				
Euphyllurinae				
<i>Diaphorina acokantherae</i> (Petty, 1924)	I	South Africa	E. Głowacka	present paper
<i>Diaphorina</i> cf. <i>chobauti</i> Puton, 1898	I	Israel – <i>Convolvulus</i> sp.	D. Burckhardt	present paper
<i>Diaphorina helichrysi</i> Capener, 1970	I	South Africa: Fonre	E. Głowacka	present paper
<i>Diaphorina lamproptera</i> Burckhardt, 1981	I	Israel – <i>Zygophyllum</i> sp.	D. Burckhardt	present paper

Table 1 cont.				
<i>Diaphorina loranthe</i> Capener, 1973	I	South Africa: Agnes Mine,	E. Głowacka	present paper
<i>Diaphorina petteyi</i> Capener, 1970	I	South Africa: Cape Town	E. Głowacka	present paper
<i>Diaphorina putonii</i> Löw, 1879	I	Portugal: Castro Marim-Vila Real de Santo António	E. Labina	present paper
' <i>Paurocephala</i> ' ² <i>bicarinata</i> Pettey, 1924	IV	South Africa	E. Głowacka	present paper
' <i>Paurocephala</i> ' <i>hottentotti</i> Pettey, 1933	IV	South Africa	E. Głowacka	present paper
' <i>Paurocephala</i> ' sp.	IV	South Africa	E. Głowacka	present paper
<i>Peripsyllopsis speciosa</i> (Capener, 1973)	IV	South Africa: Fonre – <i>Combretum</i>	E. Głowacka	present paper
Liviinae Löw, 1879				
<i>Caramatoscena speciosa</i> (Flor, 1961)	I	Finland: Turku – <i>Populus generosa</i>	S. Nokkala	present paper
<i>Paurocephala chonchaiensis</i> Boselli, 1929	I or II	Taiwan – <i>Ficus beechayana</i> , <i>F. pumila</i>	Ch.-T. Yang	present paper
<i>Paurocephala trematos</i> Yang, Yang et Chao, 1986	I or II	Taiwan: – <i>Trema orientalis</i>	Ch.-T. Yang	present paper
Psyllidae				
Acizziinae				
<i>Acizzia acaciaebaileyanae</i> (Froggatt, 1901)	I	Australia: Adelaide, Urrbrae, Wait Campus – <i>Acacia baileyana</i>	G.S. Taylor	present paper
<i>Acizzia jamatonica</i> (Kuwayama, 1908)	binuclear sperm	China	?	TIAN <i>et al.</i> 2007
<i>Acizzia uncatoides</i> (Ferris & Klyver, 1932)	I	Italy: Liguria, Taggia – <i>Acacia pycnantha</i>	C. Conci	present paper
	I	South Africa	E. Głowacka	present paper
Ciriacreminae				
<i>Ciriacremum capense</i> Enderlein, 1923	I	South Africa	E. Głowacka	present paper
<i>Heteropsylla cubana</i> Crawford, 1914	I	Taiwan – <i>Oryza sativa</i>	Ch.-T. Yang	KUZNETSOVA <i>et al.</i> , 1997
Macrocorsinae				
<i>Colophorina</i> sp.	I	South Africa	E. Głowacka	present paper
Psyllinae				
<i>Arytaina genistae</i> (Latreille, 1804)	binuclear sperm I	?	?	LE MENN, 1966b;
		Poland: Pińczów – <i>Cytisus scorparius</i>	E. Głowacka	present paper
<i>Arytaina maculata</i> (Löw, 1886)	I	Italia: Sicily	E. Głowacka	present paper
<i>Arytainilla barbagalloi</i> Rapisarda, 1986	I	Italia: Sicily, Calabria	E. Głowacka	present paper
<i>Arytainilla cytisi</i> (Puton, 1876)	I	Spain: Avila prov., Sierra de Candelario, San Martín del Pimpollar	E. Głowacka, E. Labina	present paper
<i>Arytainilla spartiophila</i> (Foerster, 1848)	I I	Spain: Cáceres prov., Puerto de Tornavacas	E. Głowacka	present paper
		Spain: Avila prov., Hoyos del Espino	E. Labina	present paper
<i>Arytinis umbonata</i> (Loginova, 1976)	I	Portugal: Madeira	E. Labina	present paper
<i>Baeopelma foersteri</i> (Flor, 1861)	I I	Finland: near Turku	S. Nokkala	present paper
		Poland: near Kraków – <i>Alnus</i> sp.	E. Głowacka	present paper
<i>Baeopelma colorata</i> (Löw, 1888)	I I	Georgia	A. Gegechkori	present paper
		Bulgaria: near Sofia	E. Głowacka	present paper
<i>Cacopsylla crataegi</i> (Schrank, 1801)	I	Georgia: near Tbilisi, Kodzhori – <i>Crataegus orientalis</i>	A. Gegechkori	KUZNETSOVA <i>et al.</i> 1997
<i>Cacopsylla fraudatrix</i> Labina & Kuznetsova, 2012	I	Poland: Bieszczady Mts, Połonina Caryńska, Wielka Rawka, and Tarnica ridges – <i>Vaccinium myrtillus</i>	E. Labina	present paper
<i>Cacopsylla ginnalı</i> (Kononova & Loginova 1985) ³	I	Russia: Primorsky Krai, Khasansky District, Gvosdevo Village, and Ussuriysky District, Kraunovka – <i>Acer ginnala</i>	E. Labina	present paper
<i>Cacopsylla hippophaes</i> (Foerster, 1848)	I I	The Netherlands – <i>Hippophae rhamnoides</i>	I.H. Woudstra	present paper
		Finland: near Turku	S. Nokkala	present paper

Table 1 cont.				
<i>Cacopsylla mali</i> (Schmidberber, 1836)	I	Poland: Kraków – <i>Malus</i> sp.	E. Głowacka	present paper
<i>Cacopsylla palmeni</i> (Löw, 1882)	I	Finland – <i>Salix</i> sp.	S. Nokkala	present paper
<i>Cacopsylla parvipennis</i> (Löw, 1877)	I	Poland: Mielnik – <i>Salix rosmarinifolia</i>	E. Głowacka	present paper
<i>Cacopsylla permixta</i> Burckhardt et Hodkinson, 1986	I	Georgia: David Garekhi – <i>Pyrus salicifolia</i>	A. Gegechkori	KUZNETSOVA <i>et al.</i> 1997
<i>Cacopsylla pruni</i> (Scopoli, 1763)	I	Poland: Kraków – <i>Prunus</i> sp.	E. Głowacka	present paper
⁴ <i>Cacopsylla pseudosieboldiani</i> (Konovalova & Loginova 1985)	I	Russia: Primorsky Krai, Khasansky District, near Kedrovaya Pad' Reserve – <i>Acer pseudosieboldianum</i>	E. Labina	present paper
<i>Cacopsylla pulchra</i> (Zetterstedt, 1840)	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Cacopsylla pyri</i> (Linnaeus, 1758)	I	Poland: Lipie Śląskie – <i>Pyrus communis</i>	E. Głowacka	present paper
<i>Cacopsylla pyricola</i> (Foerster, 1848)	I	Poland: Kraków – <i>Pyrus</i> sp.	E. Głowacka	present paper
<i>Cacopsylla saliceti</i> (Foerster, 1848)	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Cacopsylla sorbi</i> (Linnaeus, 1767)	I	The Netherlands – <i>Sorbus</i> sp.	I.H. Woudstra	present paper
	I	Finland: Twarmine – <i>Sorbus</i> sp.	E. Głowacka	present paper
<i>Cacopsylla ulmi</i> (Foerster, 1848)	I	Finland: near Turku – <i>Ulmus</i> sp.	S. Nokkala	present paper
	I	Poland: Niepołomice – <i>Ulmus</i> sp.	E. Głowacka	present paper
<i>Cacopsylla visci</i> (Curtis, 1835)	binuclear sperm	?	?	LE MENN 1966b
<i>Cacopsylla zaicevi</i> (Šulc, 1915)	I	Russia: Altai Republic, Chemalsky District, Edigan Village – <i>Salix</i> sp.	E. Labina	present paper
<i>Cacopsylla zetterstedti</i> (Thomson, 1877)	I	Poland: Mielnik – <i>Hippophae rhamnoides</i>	I.D. Hodkinson	present paper
<i>Chamaepsylla hartigii</i> (Flor, 1961)	binuclear sperm	?	?	LE MENN 1966b
	I	Finland – <i>Betula</i> sp.	S. Nokkala	present paper
<i>Cyamophila caraganae</i> (Loginova, 1964)	I	Georgia: David Garekhi – <i>Caragana grandifolia</i>	A. Gegechkori	KUZNETSOVA <i>et al.</i> 1997
<i>Cyamophila medicaginis</i> (Andrianova, 1952)	I	Russia: Altai Republic, Chemalsky District, Edigan Village	E. Labina	present paper
<i>Cyamophiliopsis fasciata</i> (Löw, 1881)	I	Georgia: near Tbilisi – <i>Spiraea hypericifolia</i>	A. Gegechkori	KUZNETSOVA <i>et al.</i> 1997 (as <i>Psylla</i>);
	I	Russia: Altai Republic, Chemalsky District, Edigan Village – <i>Spiraea</i> sp.	E. Labina	present paper
<i>Livilla magna</i> Hodkinson et Hollis, 1987	I	Italia: Sicily	E. Głowacka	present paper
<i>Livilla nervosa</i> Hodkinson et Hollis, 1987	I	Portugal: Madeira	E. Labina	present paper
<i>Livilla pyrenaea</i> (Mink, 1859)	I	Spain: Malaga prov., Sierra de Oreganal; Cádiz prov., Sierra del Niño	E. Głowacka	present paper
<i>Livilla radiata</i> (Foerster, 1848)	I	Poland: Gorce Mts	E. Głowacka	present paper
	I	Spain: Almeria prov., Sierra de Alhamilla	E. Labina	present paper
<i>Livilla spectabilis</i> (Flor, 1861)	I	Italia: Sicily	E. Głowacka	present paper
<i>Livilla variegata</i> (Löw, 1881)	I	Italy	E. Głowacka	present paper
<i>Psylla alni</i> (Linnaeus, 1758)	binuclear sperm	?	?	LE MENN, 1966b
	I	Poland: Mielnik – <i>Alnus</i> sp.	E. Głowacka	present paper
	I	Spain: Avila prov., Solana de Bejar – <i>Alnus</i>	E. Labina	present paper
<i>Psylla betulae</i> (Linnaeus, 1758)	I	Finland: Täktom near Hanko – <i>Betula verrucosa</i> , <i>B. pubescens</i>	E. Głowacka	present paper
<i>Psylla buxi</i> (Linnaeus, 1758)	binuclear sperm	?	?	LE MENN 1966b;
	I	USA: Maryland	M.-M. Yang	present paper
<i>Psylla fusca</i> (Zetterstedt, 1828)	I	Poland: Katowice – <i>Alnus incana</i>	E. Głowacka	present paper
Triozidae Löw, 1879				
<i>Bactericera albiventris</i> (Foerster, 1848)	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Bactericera curvatineris</i> (Foerster, 1848)	I	Finland: Turku – <i>Salix</i> spp.	S. Nokkala	present paper

Table 1 cont.				
<i>Bactericera femoralis</i> (Foerster, 1848)	binuclear sperm I	?	?	LE MENN 1966b
<i>Bactericera maura</i> (Foerster, 1848)	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Bactericera nigricornis</i> (Foerster, 1848)	I	The Netherlands: – <i>Salix</i> sp. Russia: Primorsky Krai, Ussuriysky District, Kraunovka – <i>Artemisia</i> sp.; Altai Republic, Chemalsky District, Edigan Village	I.H. Woudstra E. Labina	present paper
<i>Bactericera salicivora</i> (Reuter, 1876)	I	Finland: Turku – <i>Salix</i> spp.	S. Nokkala	present paper
<i>Bactericera striola</i> (Flor, 1961)	I	Finland: Turku – <i>Salix</i> spp.	E. Głowacka	present paper
<i>Baeoalitrizus afrobsoletus</i> (Hollis, 1984)	I	South Africa: Cape Town	E. Głowacka	present paper
<i>Heterotrizoza chenopodii</i> (Reuter, 1876)	I	Finland: Turku – <i>Chenopodium album</i>	S. Nokkala	present paper
<i>Leptynoptera sulfurea</i> Crawford, 1919	I	Taiwan – <i>Calophyllum inophyllum</i>	Ch.-T. Yang	present paper
<i>Pauropsylla trichaeta</i> Pettey, 1924	I	South Africa: Cape Town	E. Głowacka	present paper
<i>Schedotrizoza apicobystra</i> Taylor, 1990	I	Australia: Bridgewater – <i>Eucalyptus cosmophylla</i>	G.S. Taylor	present paper
<i>Schedotrizoza multitudinea</i> (Maskell, 1898)	I	Australia: Mylor – <i>Eucalyptus obliqua</i>	G.S. Taylor	present paper
<i>Trichohermes grandis</i> Loginova, 1965	I	Russia: Primorsky Krai, Arsenyev	E. Labina	present paper
<i>Trichohermes walkeri</i> (Foerster, 1848)	I	Bulgaria: Melnik – <i>Rhamnus cathartica</i>	E. Głowacka	present paper
<i>Trioza abdominalis</i> Flor, 1961	I	Poland: Gorce Mts – <i>Salix</i> sp.	E. Głowacka	present paper
<i>Trioza agrophila</i> Löw, 1888	I	Russia: Altai Republic, Chemalsky District, Edigan Village	E. Labina	present paper
<i>Trioza alacris</i> Flor, 1861	I	Italy: Sicily	E. Głowacka	present paper
<i>Trioza carvalhoi</i> Hollis, 1984	I	South Africa	E. Głowacka	present paper
<i>Trioza cirsii</i> Löw, 1881	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Trioza dispar</i> Löw, 1878	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Trioza elaeagni</i> Scott, 1880	I	Portugal: Madeira	E. Labina	present paper
<i>Trioza eleutherococci</i> Konovalova, 1980	I	Russia: Primorsky Krai, Khasansky District, near Kedrovaya Pad' Reserve – <i>Eleutherococcus</i> sp.	E. Labina	present paper
<i>Trioza eugeniae</i> Froggart, 1901	I	USA: California, Long Beach, Alamada Street – <i>Syzygium</i> sp.	P.G. da Silva	present paper
<i>Trioza flavipennis</i> Foerster, 1848	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Trioza fletcheri</i> Crawford, 1912	I	India – <i>Terminalia termentosa</i>	A. Raman	present paper
<i>Trioza ilicina</i> (De Stefani Perez, 1901)	I	Spain: Mallorca – <i>Quercus ilex</i>	I.D. Hodkinson	present paper
<i>Trioza munda</i> Foerster, 1848	I	Poland: Gorce Mts,	E. Głowacka	present paper
<i>Trioza remota</i> Foerster, 1848	I	The Netherlands – <i>Quercus</i> sp.	I.H. Woudstra	present paper
<i>Trioza rumicis</i> Löw, 1880	I	Georgia: Tbilisi – <i>Rumex acetosella</i>	A. Gegechkori	KUZNETSOVA <i>et al.</i> , 1997
<i>Trioza senecionis</i> (Scopoli, 1763)	I	Poland: Gorce Mts	E. Głowacka	present paper
<i>Trioza urticae</i> (Linnaeus, 1758)	binuclear sperm I	?	?	LE MENN, 1966a
		Poland: Mielnik – <i>Urtica dioica</i>	E. Głowacka	present paper

¹Probably *A. freji* Burckhardt & Lauterer, 1997

²This and the following two species belong to an undescribed Afrotropical genus associated with Proteaceae (D. BURCKHARDT, unpublished data).

³*Cacopsylla ginnali* (Konovalova & Loginova 1985) comb. nov. from *Psylla*. *C. ginnali* is closely related to *C. abieti* (Kuwayama, 1908), *C. lineatipennis* (Kwon, 1983) and *C. liricapita* Li, 2011, all associated with *Acer ginnala* and members of *Cacopsylla*. For this reason *P. ginnali* is transferred here to *Cacopsylla*. *C. ginnali* is probably a junior synonym of *C. lineatipennis* but relevant type material has to be examined before the species is formally synonymised. The name 'ginnali', if derived from 'ginnala', the species epithet of the host plant should, correctly formed, be 'ginnalae'. According to the International Code of Zoological Nomenclature article 32.5 this is, however, not considered as incorrect original spelling and the spelling 'ginnali' has to be accepted.

⁴*Cacopsylla pseudosieboldiani* (Konovalova & Loginova 1985) comb. nov. from *Psylla*. *C. pseudosieboldiani* is congeneric with *C. abieti* and *C. ginnali*, two species also associated with *Acer*. For this reason *P. pseudosieboldiani* is transferred here to *Cacopsylla*.

Results

Our study reveals the presence of five distinctive types of sperm formation in males among the 125 examined psyllid species. The types referred to as “Type I” to “Type V” differ from one another in the mode of chromatin reorganization during metamorphosis of spermatids into spermatozoa.

Type I (Fig. 1a-f)

At the very beginning of spermatid maturation (post-telophasic cells), the chromosomes lose their integrity and associate; a large mass of chro-

matin subsequently concentrates at one pole of the nucleus (Fig. 1a). As the nucleus elongates (Fig. 1b,c), two tails (nuclear prolongations) are produced extending along the flagellum. The tails are slightly different in length and all the chromatin mass (as a heteropycnotic body) is present in the distal part of the shorter tale. The longer tail shows no evidence of DNA (Fig. 1d-f).

Type II (Fig. 2a-e)

As in Type I, at the very beginning of spermiogenesis the chromosomes lose their integrity and associate; a large mass of chromatin subsequently concentrates

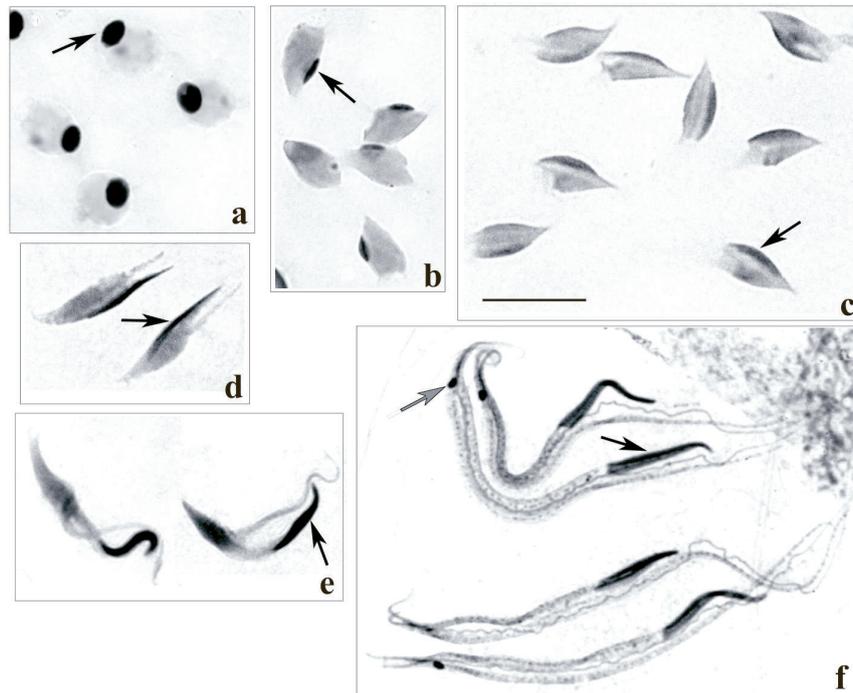


Fig. 1. Spermiogenesis of Type I with consecutive stages of sperm formation. Black arrows indicate chromatin bodies inside the nuclei (for explanation, see Results). Grey arrow indicates basal body. a – *Chamaepsylla hartigii*, b – *Diaphorina helichrysi*, c, d – *Acizzia uncatoides*, d – *Arytainilla cytisi*, f – *Bactericera striola*. Bar = 10 μ m.

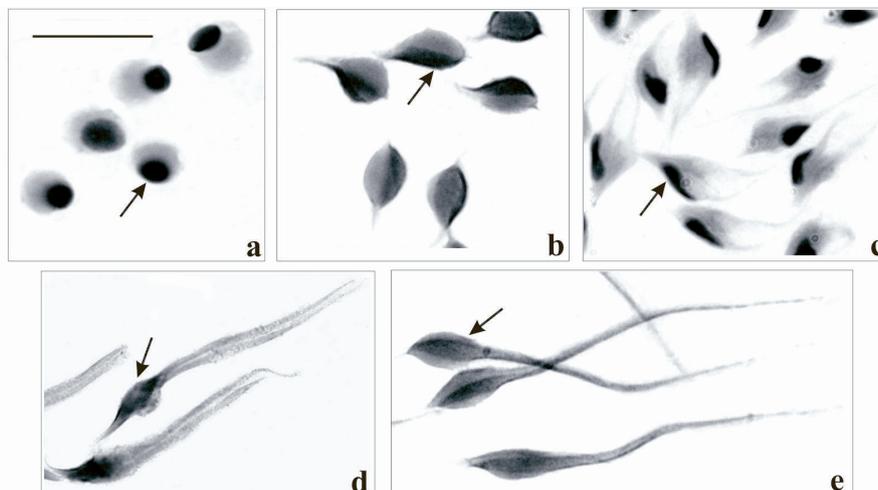


Fig. 2. Spermiogenesis of Type II with consecutive stages of sperm formation. Black arrows indicate chromatin bodies inside the nuclei. a, b, d, e – *Rhinocola aceris*, c – *Agonoscyta cisti*. Bar = 10 μ m.

at one pole of the nucleus (Fig. 2a). As the nucleus elongates, two cytoplasmic tails are produced extending along the flagellum (Fig. 2b,c). Contrary to Type I, the chromatin mass (as a heteropycnotic body) remains in the sperm head instead of moving into the tail (Fig. 2d,e). Types I and II are so similar that it is impossible to attribute with certainty some species (*Paurocephala chonchaiensis* and *P. trematos*, Liviidae; Table 1) to one of the two types.

Type III (Fig. 3a-f)

This type differs distinctly from the two types above. At the very beginning of spermogenesis

the chromosomes lose their integrity and associate; a large mass of chromatin subsequently divides into the two heteropycnotic bodies which concentrate at the opposite lateral parts of the nucleus (Fig. 3a,b). As the nucleus elongates, two cytoplasmic tails are produced extending along the flagellum. The chromatin masses (as two heteropycnotic bodies) elongate in parallel with the nucleus and each moves to one of the tails (Fig. 3c-e). Afterwards, each of the bodies disintegrates and separate chromatin units are distributed throughout the tail's length being highly condensed and easy to count at this stage. The units show a tandem (end-to-end) arrangement and their number is ap-

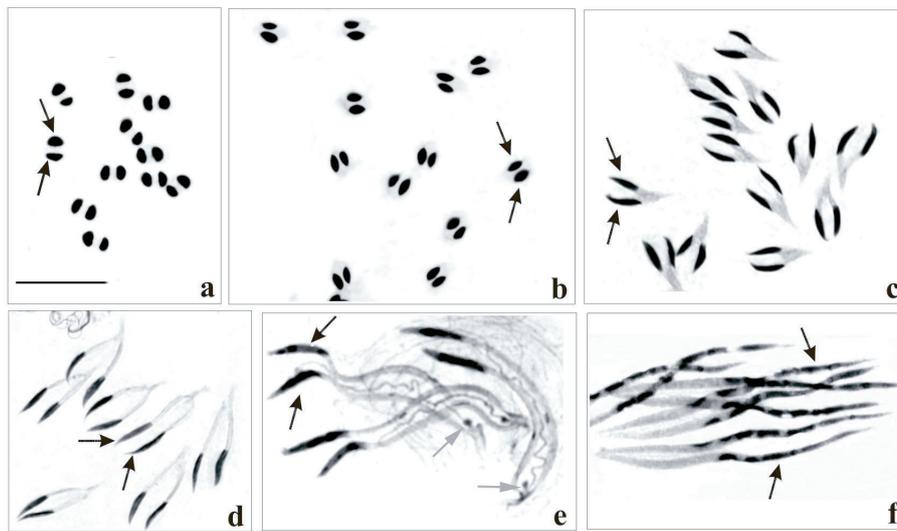


Fig. 3. Spermogenesis of Type III with consecutive stages of sperm formation. Black arrows indicate chromatin bodies inside the nuclei. Grey arrow indicate basal body. a-d – *Aphalara polygona*, e – *Aphalara calthae*, f – *Craspedolepta topicalis*. Bar = 10 μm .

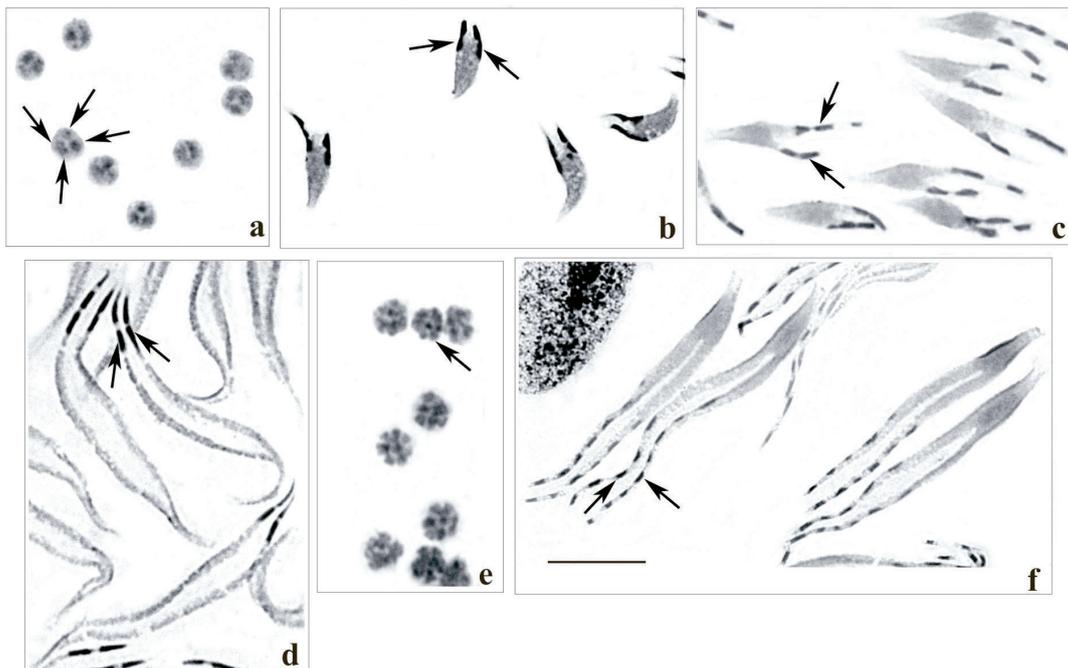


Fig. 4. Spermogenesis of Type IV with consecutive stages of sperm formation (a-d – species with low chromosome number; e & f – species with high chromosome number). Black arrows indicate chromatin bodies inside the nuclei. a-d – *Peripsyllopsis speciosa*, e – *Paurocephala hottentoti*, f – *Paurocephala* sp. Bar = 10 μm .

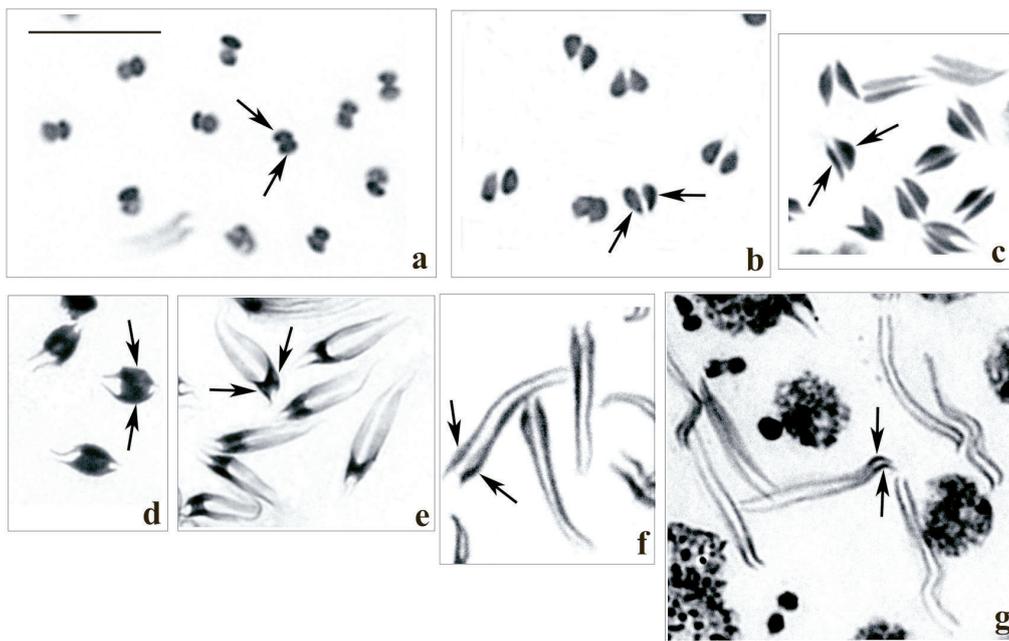


Fig. 5. Spermiogenesis of Type V with consecutive stages of sperm formation. Black arrows indicate chromatin bodies inside the nuclei. a – *Anoeconeossa unicornuta*, b – *Cryptoneossa* cf. *triangula*, c – *Blastopsylla moorei*, d & e – *Cardiaspina albitextura*, f – *Anoeconeossa* sp. (communis group), g – *Creiis*. Bar = 10 μ m.

proximately consistent with the haploid chromosome set of a species (Fig. 3f). At a later stage, the tails further elongate, the chromosomes associate again and form two heteropycnotic bodies each positioned at the end of a tail.

Type IV (Fig. 4a-f)

This type is similar to Type III but differs clearly at the initial stage of spermiogenesis. At this stage, the chromosomes maintain their integrity in the spermatid nucleus and appear as separate chromatin units distributed throughout the whole nucleus. The number of chromatin units is approximately consistent with the number of chromosomes in the haploid set of a species, e.g. in *Peripsyllopsis speciosa* with $n = 4 + X/0$ (Fig. 4a) and in '*Paurocephala hottentotti*' with $n = 12 + X/0$ (Fig. 4e). At a later stage, the nucleus elongates and the cytoplasmic tails are produced. The chromosomes are divided into the two groups and show a tandem arrangement along each tail, being easy to count at this stage (Fig. 4b-d, f). Later, the tails elongate further, the chromosomes associate again and form a heteropycnotic band at the end of each tail.

Type V (Fig. 5a-g)

As in Type III, at the beginning of spermiogenesis all the chromosomes unite into two heteropycnotic bodies. The spermatids are very small in Type V and the chromatin bodies are therefore po-

sitioned very close to each other in the nucleus (Fig. 5a-b). The nucleus elongates and two cytoplasmic tails are produced. Gradually the heteropycnotic bodies elongate in parallel with the nucleus being from then on observed as two bands expanded along the entire lengths of each tail (Fig. 5c-g).

Discussion

Spermiogenesis is a highly regulated and extremely complex process by which post-meiotic male germ cells differentiate into mature spermatozoa. This process involves remarkable changes in cell morphology and chromatin organization during spermatid differentiation. References on insect spermiogenesis, mainly on the fine structure of spermatozoa, are numerous in studies using the electron microscope, suggesting that these characters may be potentially informative in phylogenetic analyses (see e.g. JAMIESON 1987; JAMIESON *et al.* 1999). Evidence for Psylloidea is, however, scarce and limited to just a few studies carried out either with electron microscopy (LE MENN 1966a, b; DALAI 1979) or light microscopy (KUZNETSOVA *et al.* 1997; TIAN *et al.* 2007; present study).

By electron microscopy, LE MENN (1966a, b) revealed the unique nuclear structure of spermatids and mature spermatozoa in eight species of Homotomidae, Psyllidae and Triozidae (Table 1). In spermatids, a large mass of Feulgen-positive

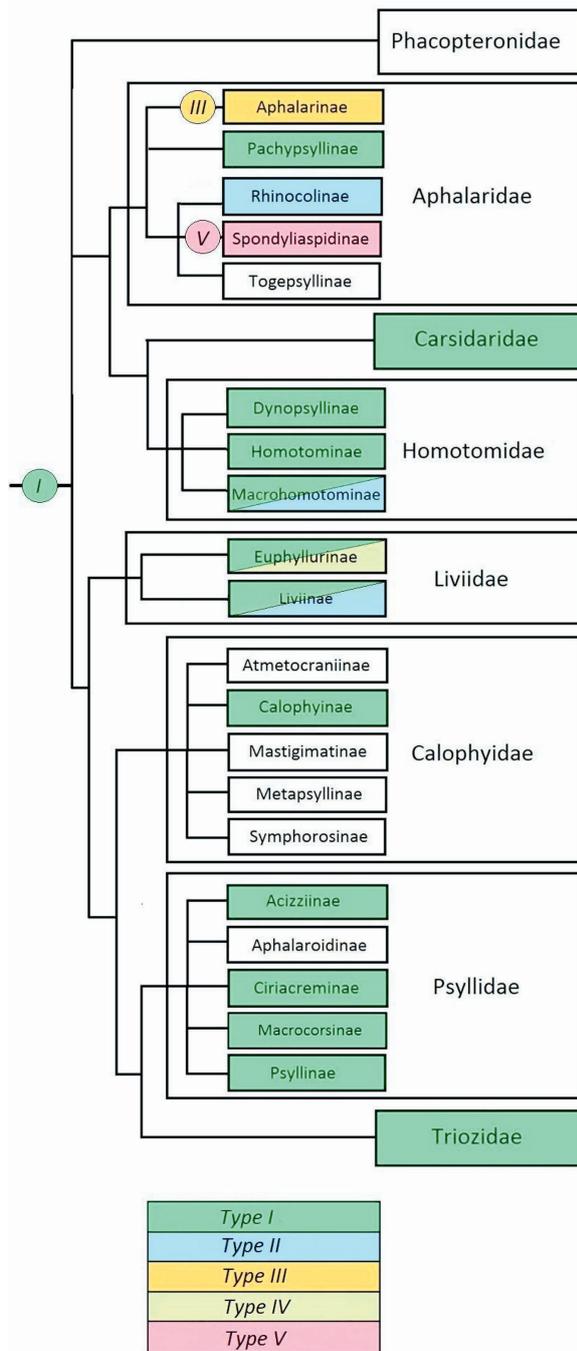


Fig. 6. Types of spermiogenesis mapped onto a cladogram representing the hypothesised phylogenetic relationships of Psylloidea according to BURCKHARDT and OUVARD (2012).

chromatin was shown to concentrate at one pole of the nucleus; the remainder of the nucleus shows no trace of DNA; the mass of chromatin is subsequently carried to the tip of only one of the nuclear prolongations (tails). This pattern referred to by LE MENN as “binuclear” (i.e. as showing a “divided nucleus”) corresponds to the Type I in our classification.

Surprisingly, this remarkable sperm pattern, not previously known in any insect, “has largely es-

aped attention in the literature” (JAMIESON 1987: 159). With light microscopy KUZNETSOVA *et al.* (1997) found in ten species of Aphalarinae (Aphalaridae) a different, also unusual type of sperm formation which they named the “binuclear” type (Type III according to our classification). In these species, the chromatin mass was found to break down into two portions in the spermatid nucleus and each of the DNA masses subsequently enters one of the two nuclear tails. TIAN *et al.* (2007) described a kind of binuclear sperm in *Bharatiana septentrionalis* (Calophyiidae) and *Acizzia jamatonica* (Psyllidae). In these species, a second spermatocyte was shown to form binuclear spermatozoa as a result of cytokinesis failure.

The present light microscopic study carried out on 125 psyllid species representing 51 genera and seven families (Table 1) revealed the presence of five types of post-meiotic chromatin reorganization in males. The variation observed at the morphological level is most likely correlated with the molecular reorganization of the chromatin that occurs in spermatid nuclei. Table 1 summarises the data on spermiogenesis available for 143 species of 54 genera, 17 subfamilies and seven families (only Phacopteronidae is not represented). *B. septentrionalis* and *A. jamatonica* were not examined by us and the information is taken from Fig. 1i in TIAN *et al.* (2007). At present it is not possible to decide whether the binuclear spermatozoa in these species represent Type I, Type III or a new type. Apart from these two species, the variation in sperm formation is limited to the five types listed above.

For exploring evolutionary patterns we mapped the five types of sperm formation on the cladogram illustrating the hypothesised phylogenetic relationships of psyllid families and subfamilies by BURCKHARDT and OUVARD (2012) (Fig. 6). Type I, found in 93 species of 31 genera (not counting *Paurocephala* with two studied species; see Table I), occurs in 13 subfamilies and all the families studied. It is the only type in the Triozidae and Carsidaridae. The data on Carsidaridae are still very scarce; those on Triozidae available for 32 species of 8 genera are slightly more representative although the Triozidae comprise well over 1000 described species. The exclusive presence of Type I was also documented in the following subfamilies: Pachypsyllinae (1 species/1 genus; Aphalaridae), Dynopsyllinae and Homotominae (2/2; Homotomidae), Calophyinae (2/1; Calophyiidae), as well as Acizziinae, Ciriacreminae, Macrocorsinae and Psyllinae (46/14; Psyllidae). Type I also occurs in *Macrohomotoma* (1 species; Homotomidae, Macrohomotominae), *Diaphorina* (7; Liviidae, Euphyllurinae) and *Camartoscena* (1; Liviidae, Liviinae).

The chromatin organization and transformations in Type II closely resemble those of Type I but clearly differ in that the whole DNA mass remains in the sperm head rather than moving into a tail as in Type I (see Results). Type II is found in Aphalaridae where it occurs in all members of the Rhinocolinae (4 species/3 genera), as well as in *Mycoposylla* (1/1; Homotomidae). The occurrence of Type II in phylogenetically distant taxa suggests that there is no common evolutionary origin of this type and that the underlying molecular mechanism is either different in the above three groups or convergent.

Type III is restricted to the Aphalarinae (20 species/3 genera; Aphalaridae). The main difference between Type III and Types I and II is that the chromatin mass breaks down into two portions which are subsequently carried to the tips of both cytoplasmic prolongations. With the present data Type III can be interpreted as an autapomorphy of the Aphalarinae, however, only three of the 16 currently recognised genera have been examined. According to the cladistic analysis of BURCKHARDT and QUEIROZ (2013) *Aphalara* and *Craspedolepta* are closely related, but *Crastina* only distantly, representing only a small fraction of taxonomic diversity of the subfamily.

Type IV is restricted to some members of Euphyllurinae (4 species/2 genera; Liviidae), i.e. one species of *Peripsyllopsis* and three species of an undescribed genus which contains two described and at least a dozen undescribed species in the Afrotropical region associated with Proteaceae (D. BURCKHARDT & D. HOLLIS, in preparation). Whether Type IV represents a synapomorphy for a monophyletic clade within Euphyllurinae should be tested with other genera such as the Palearctic *Psyllopsis* or the New World *Katacephala*, *Notophorina* and *Tuthillia*, a group of genera associated with Myrtaceae and other families.

Type V is restricted to the predominantly Australian Spondylaspidinae where it occurs in all examined taxa (16 species/12 genera; Aphalaridae). The 12 studied genera represent half of known Spondylaspidinae genera (BURCKHARDT & OUVARD 2012). The monophyly of Spondylaspidinae is well supported by a series of morphological characters (BURCKHARDT 1991). Type V spermatogenesis, the very small spermatid nuclei, the low chromosome numbers and testes consisting of only two follicles (MARYAŃSKA-NADACHOWSKA *et al.* 2001a) represent additional potential autapomorphies of the subfamily.

As discussed above, the main shared feature of Types III, IV and V is that the chromatin in spermatids undergoes, in one way or another, division into a number of chromatin blocks in spermatids and subsequently lands in both cytoplasmic tails.

Based on a statistic correlation between the number of these blocks and haploid chromosome number of a species, the blocks correspond to chromosomes. The disposition of chromosomes in sperms, i.e. whether they are arranged randomly or they occupy specific positions in a sperm nucleus, has been the subject of many studies over several decades (e.g. HUGHES-SCHRADER 1946; INOUE & SATO 1962; TAYLOR 1964). From the evidence of some species studied, in particular of '*Paurocephala*' *hottentotti* and *Peripsyllopsis speciosa* (Fig. 4a & e), it is concluded that the chromosomes of psyllids are arranged in a defined order in the sperm nucleus. This finding supports the hypothesis that specific chromosome arrangement is a general feature of animal sperm (WATSON *et al.* 1996).

Within Psylloidea, there are two main chromatin reorganisation pathways during metamorphosis of spermatids into spermatozoa represented by Types III, IV and V on the one hand and by Types I and II on the other hand. Type I has the widest distribution over the higher-level taxa (at the subfamily level) followed by Type II (Fig. 6). Ancestral state reconstruction suggests that Type I is ancestral within Psylloidea. It follows that Type II evolved four times independently (once each in Aphalaridae and Homotomidae, respectively and twice in Liviidae).

Concluding remarks

Our light microscopic study shows that in Psylloidea spermatids undergo substantial morphological changes as they transform into mature sperm, and the type of chromatin organization and sperm formation greatly differ between the species examined. Within Psylloidea, five types are recognized. Type I most likely represents a plesiomorphic condition while the remaining Types II-V are derived traits. Types III and V represent autapomorphies supporting the monophyly of the Aphalarinae and Spondylaspidinae, respectively. Type IV may also constitute a synapomorphy grouping some genera within the Euphyllurinae but more taxa have to be examined to support this suggestion. Type II, finally, represents a homoplasy. In summary, among the five types of spermiogenesis, two are phylogenetically significant, giving additional support for the monophyly of two of the best defined subfamilies of Psylloidea, and one perhaps shows phylogenetic signal. Thus, the pattern of spermiogenesis can be used for resolving taxonomic questions and inferring phylogenetic relationships within Psylloidea, even if in a limited way.

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