

The Distribution and Population Sex Ratio of *Cacopsylla myrtilli* (W.Wagner, 1947) (Hemiptera: Psylloidea)*

Eugenia S. LABINA, Seppo NOKKALA, Anna MARYAŃSKA-NADACHOWSKA
and Valentina G. KUZNETSOVA

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In *Cacopsylla myrtilli* (W. Wagner, 1947) bisexual populations, all-female populations and populations heavily biased towards females have been described. In the present paper all the available data on the distribution and population sex ratio of *C. myrtilli* are summarized. New data obtained by the authors are also presented. First records for Russia are described from Siberia and the southern part of the Far East.

Key words: Psylloidea, *Cacopsylla myrtilli*, parthenogenesis, zoogeography, population sex ratio.

Eugenia S. LABINA, Zoological Institute, Russian Academy of Sciences, Universitetskaya emb., 1, 199034 St. Petersburg, Russia.

E-mail: labina_e@mail.ru

Seppo NOKKALA, Laboratory of Genetics, Department of Biology, University of Turku, 20014 Turku, Finland.

E-mail: sepnok@utu.fi

Anna MARYAŃSKA-NADACHOWSKA, Department of Experimental Zoology, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, 31-016 Kraków, Poland.

E-mail: maryanska@isez.pan.krakow.pl

Valentina G. KUZNETSOVA, Zoological Institute, Russian Academy of Sciences, Universitetskaya St., 1, 199034 St. Petersburg, Russia.

E-mail: karyo@zin.ru

In several psyllid species (Hemiptera, Psylloidea) belonging to genera *Cacopsylla* Ossiannilsson, 1970, *Bactericera* Puton, 1876, *Trioza* Förster, 1848 and *Glycaspis* Moore, 1961, all-female populations have been described in addition to bisexual populations (HODKINSON 1983; GEGECHKORI 1985; MOORE 1970a, b). In the Palearctic, unisexual populations have been described in *T. abdominalis* Flor, 1961, *C. myrtilli* (W. Wagner, 1947) and *C. ledi* (Flor, 1961). Information on the sex ratio of populations is available mostly for holarctic species *Cacopsylla myrtilli* (LINNAVUORI 1951; LAUTERER 1963; KLIMASZEWSKI 1971; OSSIANNILSSON 1992; HODKINSON 1976, 1978, 1983, 2006; NOKKALA *et al.* 2008).

In *C. myrtilli* three types of populations are known: in some populations the ratio of females to males is approximately one to one, in others the

number of females is many times higher than the number of males, the third populations are all-female ones. Cytogenetic analysis has shown that in unisexual population females have apomictic meiosis and a triploid chromosome set (NOKKALA *et al.* 2008).

C. myrtilli is characterized by a holarctic, boreo-alpine distribution reaching Bulgaria (42°N) and north-eastern China (35°N) through mountain ranges. Being a narrow oligophage, *C. myrtilli* feeds on two species of the genus *Vaccinium*: bilberry (*V. myrtillus* L.) and bog bilberry (*V. uliginosum* L.).

C. myrtilli was described by WAGNER in 1947 from material obtained in Austria (Steiermark, Admont) which comprised almost exclusively females. The only male in the type series, as was later found (KLIMASZEWSKI 1963; OSSIANNILS-

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SON 1975), in fact belonged to another species *Psylla corcontum* Šulc, 1910. Parthenogenetic reproduction in *C. myrtilli* was suggested for the first time by LINNAVUORI (1951). Males of *C. myrtilli* were first reported from northeastern China (Shanxi Province) where three females and one male were found (KUWAYAMA & MIYATAKE 1971) and also from southeastern Poland (eastern spurs of the Carpathians, Bieszczady Mts) where a population with an approximately equal sex ratio was described (KLIMASZEWSKI 1971). The morphological description of males of *C. myrtilli* was made by OSSIANNILSSON (1975) on the basis of two specimens from the USSR (Karelia and Sverdlovsk Region). This author also reports a bisexual population of *C. myrtilli* found by HODKINSON in Canada. On the basis of specimens from that population HODKINSON (1976) described the subspecies *C. myrtilli canadensis*. Later in Alaska he found all-female populations of *C. m. canadensis* (HODKINSON 1978). No other locations of this subspecies were discovered. It can be assumed that its distribution is restricted to North America. Beginning from 1980, HODKINSON described a few more bisexual populations of *C. myrtilli*. One of these (Magadan Region) included odd males (HODKINSON & MACLEAN 1980; numbers of females and males are not indicated) and in two others (southern Norway, Telmark, Gudbrandsdalen; northern Sweden, Abisko) the sex ratio was approximately equal (HODKINSON 1983, 2006).

In this article all the data on the distribution and sex ratio of populations of *C. myrtilli* are summarized and briefly discussed. Several new discoveries of populations with different reproductive strategies are reported. Within the limits of Russia this species is reported for the first time for Siberia and the southern Far East. Such a review is of interest for the zoogeography of *C. myrtilli* and as a basis for further study on parthenogenesis in this species and psyllids as a whole.

Material and Methods

The authors conducted extensive collection of *C. myrtilli* in the regions of northwestern Russia (Karelia and Murmansk Region), Eastern Siberia (Irkutsk Region), Finland (east and north-east) and Poland (southeast, Bieszczady Mts). Scientific collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg) and University of Turku (Finland), collections of E.N. Rodchenkova and O.N. Kotenko from Karelia and collections of N.N. Vinokurov from Yakutia and A. Albrecht from Finland were also examined. The material was placed in 96% alcohol (for morphological and future molecular studies) and Carnoy

mixture consisting of 96% alcohol and glacial acetic acid at a ratio of 3:1 (for chromosome studies).

Results

Distribution of *Cacopsylla myrtilli* (see also Figs 1-3): The localities of first records are marked with an asterisk (*).

Canada: southwestern Alberta (Rocky Mountains, Kananaskis Valley) (HODKINSON 1976).

USA: widely distributed throughout Alaska (HODKINSON 1978; MACLEAN & HODKINSON 1980).

Norway: widely distributed throughout the south (OSSIANNILSSON 1992; HODKINSON 2006).

Sweden: widely distributed (OSSIANNILSSON 1952; HODKINSON 1983).

Finland: widely distributed (OSSIANNILSSON 1992; NOKKALA *et al.* 2008; present paper).

Germany: Baden-Württemberg (Northern Schwarzwald, Calw), Saxony (Chemnitz, Marienberg), Dresden (Dippoldeswalde) (LAUTERER 1976; BURCKHARDT 1983).

Switzerland: widely distributed (BURCKHARDT 1983).

Austria: Steiermark (Admont, Graz, Grazerhütte) (WAGNER 1947; WAGNER & FRANZ 1961).

Czech Republic: Karlovy Vary (Velký Kotel) and Olomouc District (Jeseniki Mountains) (LAUTERER 1963).

Slovakia: Zilina district (Belanské Tatras Mountains) (LAUTERER 1963).

Poland: provinces of Silesia (Sudety Mountains), and Lesser Poland (Tatra Mountains) (KLIMASZEWSKI, 1970), subcarpathians (Bieszczady Mountains) (KLIMASZEWSKI 1971).

Italy: autonomous region Trentino-Alto Adige (Bolzano Province (Trento)) (CONCI & TAMANINI 1989).

Bulgaria: Kyustendil Province (Borovets) (KLIMASZEWSKI 1970).

Ukraine: Transcarpathian Region (Polonina Rovna) (LOGINOVA 1964).

Russia: European part: Murmansk Region* (cities of Murmansk, Polyarnayi, Kola, Apatity, Kirovsk), Karelia (Cape Kartesh (OSSIANNILSSON 1975), Islands of the Keret' Archipelago*, Kem City*), Perm Region (city of Perm)*; Komi Republic (Kadzhherom station)*;

Urals: north of Sverdlovsk Region (Lozva River) (OSSIANNILSSON 1975);

Siberia*: Tyumen Region (Yamalo-Nenets Autonomous Area (Lake Varchaty)); southern Irkutsk

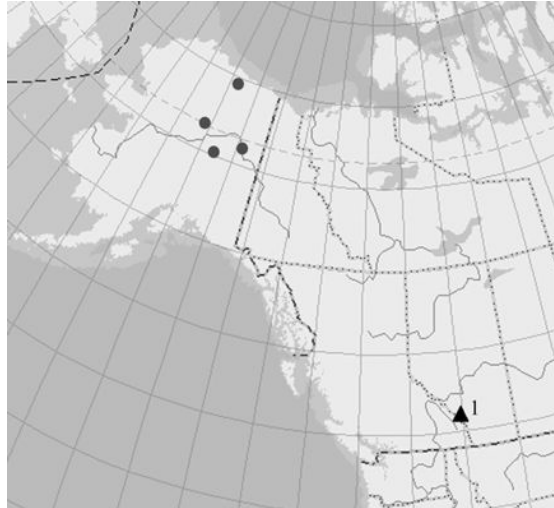


Fig. 1. Distribution of *C. myrtilli* in North America.

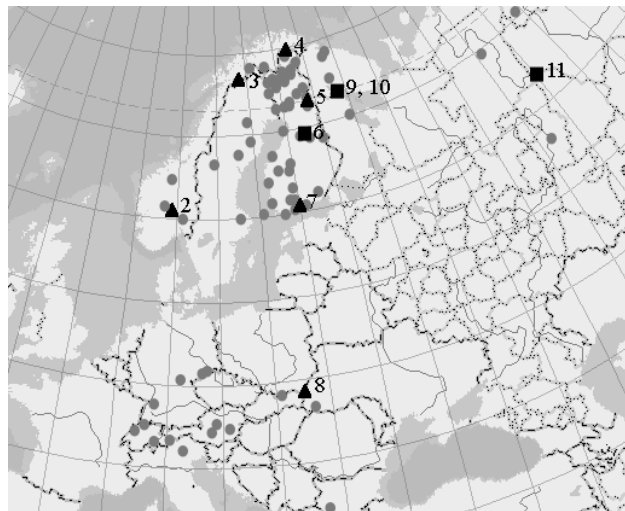


Fig. 2. Distribution of *C. myrtilli* in Europe and Western Siberia.

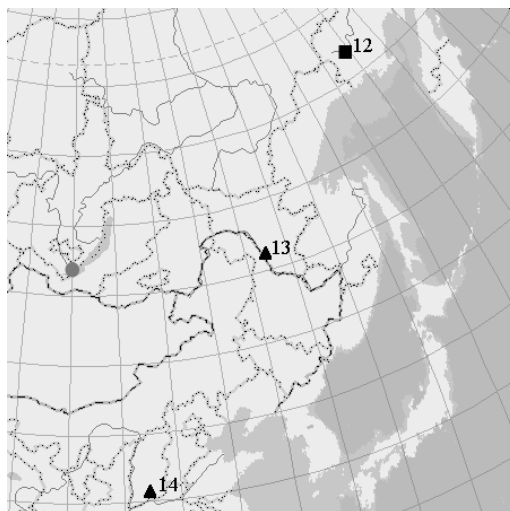


Fig. 3. Distribution of *C. myrtilli* in Eastern Siberia and in the Far East.

Figs 1-3 – symbols:

- – unisexual populations; ▲ – bisexual populations with equal or close to equal sex ratios (1-5, 7, 8, 13, 14);
- – female-biased bisexual populations (6, 9-12).

Table 1

Bisexual populations of *Cacopsylla myrtilli* with equal or close to equal sex ratio (1-5, 7, 8, 13, 14) and female-biased sex ratio (6, 9-12)

N ¹	Locality	Coordinates	Males and females number ²	Reference
North America				
1	Canada: Province Alberta, Rocky Mountains, Kananaskis Valley Barrier Mountain	51°39' N, 115°37' W	1:1	HODKINSON 1976
Europe				
2	Norway: Opplann, Gudbrandsdalen, Sjoa River	61°30' N, 9°20' E	1:1	HODKINSON 1983
3	Sweden: north of Norrbotten County, Abisko Village	68°21' N, 18°47' E	1:1	HODKINSON 2006
4	Finland: Lapland Province: Utsjoki Municipality	69°55' N, 27°01' E	3♂, 1♀	present paper
5	Oulu Province: Kuusamo Town	65°58' N, 29°11' E	6♂, 2♀	present paper
6	Paltamo Municipality	64°25' N, 27°50' E	2♂, 152♀ (1:75)	present paper
7	Southern Finland Province: Helsinki City, Sipoo Municipality	60°23' N, 25°16' E	6♂, 7♀	present paper
8	Poland: Subcarpatian Province, Bieszczady Mountains: Wielka Rawka, Polonina Caryńska, Tarnica	49°9' N, 22°28' E	1:1	KLIMASZEWSKI 1971
9	Russia: Karelia: Loukhi Region: Cape Kartesh	65°1' N, 32°31' E	1♂, 8♀	OSSIANNILSSON 1975
10	Islands of the Keret' Archipelago (Malyy Gorelyy, Bol'shoy Gorelyy and Sredniy Gorelyy)	66°17' N, 33°40' E	49♂, 2946♀ (1:60)	present paper
Asia				
11	Russia: Urals: Sverdlovsk Region, Lozva River, Khoekva Mountain	61°40' N, 59°46' E	1♂, 32♀	OSSIANNILSSON 1975
12	Far East: Magadan Region, Aborigen Mountain	62°58' N, 146°31' E	odd ♂	HODKINSON 1983
13	Amur Territory, Klimoutsy Village	51°27' N, 127°35' E	13♂, 57♀ (1:5)	present paper
14	China: Shanxi Province, Henglingguan Village	35°22' N, 111°36' E	1♂, 3♀	KUWAYAMA & MIYATAKE 1971

¹Numeric designations of the populations as in Figures 1-3.

²In all cases that the sex ratio is designated as 1:1, the latter is taken from the original papers. In other cases the number of males and females is provided with, on occasion, with a rough sex ratio in brackets.

Region (southwestern Baikal (Bol'shiye Koty settlement));

Far East: Magadan Region (Aborigen Station) (HODKINSON & MACLEAN 1980), Amur Territory* (Klimoutsy settlement).

China: southern Shanxi Province (KUWAYAMA & MIYATAKE 1971).

The species is reported for the first time for Siberia (Tyumen Region, Lake Varchaty and Irkutsk Region, southern extremity of Lake Baikal) (our collections) and the southern Far East (Amur Krai). In the latter case material stored in the collection of the Zoological Institute of the Russian Academy of Sciences (a total of 57 females and 13 males; collected by Zinovyev, 16.VI.1959) was

examined. For the first time four bisexual populations are reported from Finland: Utsjoki and Kuusamo (collection of Turku University), Paltamo (our collection) and Sipoo (Helsinki) (collection by A. Albrecht). More detailed information on the bisexual populations of *C. myrtilli* is given in Table 1.

Discussion

Distribution patterns of many psyllid species include false gaps because this group has been studied extremely unevenly. In particular, until the present study there were no data for Siberia. Knowledge of the distribution of *Cacopsylla myr-*

tilli is more complete as compared to other species but nevertheless still contains essential gaps that have been partially filled by this work (first indications for Siberia and southern Far East of Russia).

C. myrtilli is represented in the distribution range mainly by unisexual populations (Figs 1-3). The cytogenetic study of one of these populations from northeastern Finland has shown that females have an apomictic type of parthenogenesis in which meiosis is replaced by simple mitosis (recombination is absent) and a triploid chromosome set of $3n=39$ ($36+XXX$) (NOKKALA *et al.* 2008). It is easily recognized that this chromosome set is a triple haploid set of $n = 12 + X$ (diploid state: $2n = 24 + XX$), which is characteristic of the absolute majority of representatives of the genus *Cacopsylla* Ossianilsson, 1970 (MARYAŃSKA-NADACHOWSKA 2002).

Bisexual populations of *C. myrtilli* occur much less frequently (Figs 1-3) and are split into two categories (Table 1). In 9 populations the sex ratio is approximately 1:1 or is close to this (the number of females exceeds the number of males not more than 5 times). Until additional data are obtained the populations from Shanxi, Utsjoki and Kuusamo, represented by a small number of collected individuals (yet conforming to the given sex ratio), are tentatively included in this category. Although an equal ratio of males and females was reported for Bieszczady (KLIMASZEWSKI 1971), the situation with this population remains unclear. Materials from collections of Klimaszewski were lost; in any case we could not recover them from the collection of the University of Silesia (Katowice), in which the author was based. As *C. myrtilli* is one of the most difficult species for species diagnostics, we cannot exclude a mistake in the identification. This supposition is indirectly confirmed by the fact that from one hundred of specimens collected by us in 2008 from *Vaccinium myrtillus* in Bieszczady (in the locality indicated in the work by Klimaszewski) only one female was identified as *C. myrtilli*, whereas other individuals of both sexes belonged to *C. ledi* (Flor, 1961), morphologically very similar to *C. myrtilli*¹.

In several populations (Table 1) there is an abrupt shift in the sex ratio in favour of females (if representative material is available the number of females exceeds the number of males more than 30 times). In such populations the number of males is obviously insufficient to fertilize all females. It was assumed that such populations are mixed, some of the females reproduce amphimictically, whereas others parthenogenetically (NOKKALA *et al.* 2008). However, cytogenetic studies are needed to confirm this hypothesis.

Bisexual reproduction in multicellular organisms is a predominant strategy and undoubtedly ancestral in relation to parthenogenesis (WHITE 1973). In the opinion of KLIMASZEWSKI (1971) a bisexual population of *C. myrtilli* that survived during the last glacial advance in the mountains of Eastern Europe (presumably in Bieszczady in southeastern Poland, where he found the only then known bisexual population) further produced populations that spread throughout Europe and switched to parthenogenetic reproduction. This provided greater opportunities for survival in more rigorous conditions. Later however, bisexual populations were also discovered in Sweden, Norway, Finland, China and Russia (Table 1). Incidentally, Klimaszewski's hypothesis remains legitimate because fragmentary bisexual populations could have spread from one refugium presumably situated in East European mountains.

In species with a mixed reproductive strategy parthenogenetic forms often have a different distribution as compared to the bisexual populations (VANDEL 1928), a phenomenon currently known as "Vandel's rule of geographic parthenogenesis". According to this "rule" bisexual populations have restricted distribution ranges, whereas unisexual forms that have originated from them are characterized by wider distribution ranges and more pronounced ecological tolerance. They occur more frequently in "marginal" conditions: high latitudes and altitudes, regions with more severe climate, deserts, and on oceanic islands (SIMON *et al.* 2003; KEARNEY *et al.* 2006; AGUIN-POMPO *et al.* 2007).

In *C. myrtilli* the number of unisexual populations revealed exceeds many times the number of bisexual populations; their northern distribution boundaries are nearly the same, whereas unisexual populations are spread somewhat farther (7°) southwards (Figs 1-3). Populations with different reproductive strategies at first sight do not differ from each other also in the altitudinal constituent of the distribution: both occur in mountains and in lowlands. This problem, however, needs special consideration beyond the scope of the present article.

HODKINSON (2006) studied the sex ratio of populations of *C. myrtilli* along a transect near the large city of Abisko (Sweden) and concluded that a change in reproductive strategy of *C. myrtilli* is related to a change in habitat conditions. According to his observations populations under the forest canopy comprised females only, close to the forest boundary single males began to occur and above the forest boundary, in the zone of tundra vegetation, the ratio of males and females became approximately equal. In the opinion of Hodkinson, bisexual popu-

¹The identification was confirmed by D. Burckhardt.

lations are better adapted to more rigorous environmental conditions in open localities than parthenogenetic populations owing to the high level of genetic variation in the former (because sexual reproduction evokes diversity within populations).

Theoretically, unisexual lineages ought to have a higher potential for expansion into new territories and new biotopes as compared to bisexual populations because parthenogenetic females are characterized by higher fecundity and a single female may establish a new population (CUELLAR 1977). However, the evolutionary (ecological) advantage of parthenogenetic populations apparently is accounted for not by parthenogenesis as such, but by a multitude of factors: hybridization as the most frequent cause of the occurrence of parthenogenetic forms and polyploidy, which is frequently characteristic of parthenogenetic populations (LUNDMARK & SAURA 2006; HORANDL 2006). The success of parthenogenetic forms is however short-lived (SIMON *et al.* 2002). Prolonged clonal reproduction in a lineage not only leads to the accumulation of harmful mutations, but essentially restricts biodiversity (in unisexual populations the only source of variation is mutation) reducing the efficiency of selection, therefore parthenogenetic populations, as compared to bisexual populations, should have less of a chance of survival in changing environmental conditions.

The majority of known unisexual forms of insects are of polyphyletic origin (SIMON *et al.* 2003; STENBERG *et al.* 2003). It could be assumed that populations with odd males are a transitional stage from bisexuality to parthenogenesis. If this is true we have to acknowledge the polyphyletic origin of parthenogenetic populations of *C. myrtilli*. Thus, at present bisexual populations of this species are a source of new clones, which apparently are gradually dispersing into new regions of the Holarctic. At present the origin, history of divergence and dispersal of parthenogenetic lineages are studied successfully using cytogenetic and particularly molecular methods (DELMOTTE *et al.* 2003; KEARNEY *et al.* 2006; SCHWANDER & CRESPI 2009). Therefore further population studies of *C. myrtilli* should be conducted at the chromosome and molecular levels.

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