Protsenko, O., Kovalenko, P., Protsenko, Yu., & Kozeretska, I. (2026). Reproductive endosymbiotic bacteria of Antarctic springtails: on the verge of new discoveries?
Ukrainian Antarctic Journal, *24*(1), 87–99.
https://doi.org/10.33275/1727-7485.1.2026.760

Reproductive endosymbiotic bacteria of Antarctic springtails: on the verge of new discoveries?

Oleksandra Protsenko[1, 2, *], **Pavlo Kovalenko**[2, 3], **Yurii Protsenko**[1, 4], **Iryna Kozeretska**[2]

[1] Taras Shevchenko National University of Kyiv, Kyiv, 01601, Ukraine
[2] State Institution National Antarctic Scientific Center, Ministry of Education and Science of Ukraine, Kyiv, 01601, Ukraine
[3] Institute for Evolutionary Ecology, National Academy of Sciences of Ukraine, Kyiv, 03143, Ukraine
[4] Pyriatyn National Nature Park, Pyriatyn, 37000, Ukraine

*** Corresponding author:** protsenko.olexandra@gmail.com

Abstract. Endosymbiotic bacteria infect a vast number of invertebrate representatives from diverse taxa. This study reviews the results of identifying endosymbiotic bacteria (specifically the genera *Wolbachia*, *Cardinium*, *Rickettsia*, *Arsenophonus* and *Spiroplasma*) that are capable of potentially influencing the reproductive strategies of the host organism in members of the Collembola fauna of the Antarctic region. Outside Antarctica, these bacteria have an important role in forming the adaptive mechanisms and population structures of arthropods in response to changing environmental conditions. This study analyses the species diversity of Antarctic Collembola and conducts a retrospective search for available data on the infection of species found in and beyond the Antarctic region by endosymbiotic bacteria. It was established that these bacteria infect springtail species, including those that may occur in Antarctica (*Folsomia candida*, *Megalothorax minimus*, *Mesaphorura macrochaeta*, and *Parisotoma notabilis*). The ecology and physiology of the region's arthropods have already been extensively studied. However, there is currently no information available in the scientific literature indicating the presence of relevant endosymbiotic associations in Antarctic springtails. The identified lack of data may indicate either the potential isolation of local populations or the existence of environmental conditions in which infection of Antarctic springtails by bacteria of the genera *Wolbachia*, *Cardinium*, *Rickettsia*, *Arsenophonus*, and *Spiroplasma* is not possible for various reasons. At the same time, more extensive molecular genetic screening using modern sequencing technologies is required to provide a definitive answer regarding the possible infection of Antarctic springtail species by endosymbiotic bacteria. The analysis of the published data highlights a promising direction for further studies of symbiotic microorganisms associated with Antarctic organisms, particularly springtails.

Keywords: *Arsenophonus*, *Cardinium*, Collembola, *Rickettsia*, *Spiroplasma*, *Wolbachia*

1 Introduction

Microorganisms play a crucial role in the functioning of macroorganisms and can facilitate their adaptation to harsh environmental conditions (McFall-Ngai et al., 2013). The role of bacteria in the life of invertebrates can be very diverse. For example, they (e.g., *Buchnera*, *Lactobacillus*, *Serratia*, *Staphylococcus*, *Ishikawaella*, various Firmicutes and Bacteroidetes members, *etc.*) can provide invertebrate hosts with necessary nutrients in case the insect uses a nutrient-poor substrate for

food (Douglas, 2015; Chabanol & Gendrin, 2024; Kaltenpoth et al., 2025). Some of them (*e.g.*, *Buchnera*, *Citrobacter*, *Hamiltonella*, *Pseudomonas*, *Regiella*, *Serratia*, *Sphingomonas*, *etc.*) can help metabolise various toxic substances, including secondary plant metabolites, pesticides, and environmental toxins (Mondal et al., 2023; Chabanol & Gendrin, 2024; Haider et al., 2025). It has been shown that bacteria (*e.g.*, *Anoxybacillus*, *Meiothermus*, *Pseudomonas*, etc.) can help adapt to survival in cold conditions by changing the behaviour and physiology of invertebrates (Castrillo et al., 2001; Senula et al., 2022; Morgan-Richards et al., 2023; Buschi et al., 2024). They also provide immune protection to hosts against other bacteria and viruses (Haider et al., 2025).

Among microorganisms, some are inherited through the maternal line and can manipulate the host's reproduction, and provide it with a number of advantages, including at low temperatures (Serga et al., 2024). At the same time, it has been shown that endosymbiotic bacteria more often infect invertebrates in warm regions of the planet (Corbin et al., 2017).

However, recently, Kovalenko et al. (2025) used 515F and 806R barcode universal primers to the V3-V4 region of bacterial 16S rRNA sequence and detected *Wolbachia* in the only insect endemic to Antarctica, *Belgica antarctica* Jacobs, 1900 (Chironomidae), in 5 out of 33 tested samples from Galindez Island (Wilhelm Archipelago). This is the first confirmed detection of infection with this endosymbiont in representatives of the invertebrate fauna of terrestrial ecosystems of Antarctica, as previous attempts to detect it in various organisms including mites (Holmes et al., 2019), insects (Holmes et al., 2019; Maistrenko et al., 2023; Brayley et al., 2025a), tardigrades (Vecchi et al., 2018; Mioduchowska et al., 2021; McQueen et al., 2022), nematodes (McQueen et al., 2022), and springtails (Rodrigues et al., 2023) from this region have been unsuccessful (reviewed by Serga et al., 2024).

In addition, Kovalenko et al. (2025) detected, at low abundance, two more known endosymbiotic bacteria of invertebrates in *B. antarctica* from Galindez Island (Antarctica): *Rickettsia* and *Cardinium*. At the same time, Brayley et al. (2025a; 2025b) have detected a high abundance of *Rickettsia* in another insect, closely related to the genus *Belgica*, *Eretmoptera murphyi* Schäffer, 1914 (Chironomidae), from Signy Island (South Orkney Islands, Subantarctic).

In general, infection of invertebrates and springtails in particular in Antarctica remains poorly understood. In this work, we analysed the data to identify endosymbiotic bacteria in springtails in Antarctica.

2 Endosymbionts – reproductive parasites of invertebrates

Endosymbiotic bacteria (*i.e.*, bacteria that have symbiotic relationships with the host organism and exist inside it within or outside its cells; Casem, 2016) that are capable of regulating the reproduction of Arthropoda include representatives of the five genera from different groups: *Rickettsia*, *Wolbachia* (Alphaproteobacteria: Rickettsiaceae), *Arsenophonus* (Gammaproteobacteria: Morganellaceae), *Spiroplasma* (Mollicutes: Spiroplasmataceae), and *Cardinium* (Cytophagia: Amoebophilaceae) (Duron et al., 2008; Massey & Newton, 2022).

2.1 *Wolbachia*

Wolbachia, in particular, the most-studied species, *Wolbachia pipientis* Hertig, 1936, is an obligate intracellular symbiont in invertebrates that is mainly maternally transmitted (transovarial) and capable of manipulating the reproductive processes of its hosts (Werren et al., 2008; Kaur et al., 2021). There is also evidence that the bacterium can be transmitted through codivergence, hybrid introgression, and horizontal transfer (Baldo et al., 2008; Raychoudhury et al., 2009).

It is predominantly localised in reproductive tissues, but can also be present in somatic cells (Dobson et al., 1999; Pietri et al., 2016). *Wolbachia* has been identified in a wide range of invertebrate groups (Weinert et al., 2015; Jolley et al., 2018;

Charlesworth et al., 2019; Mioduchowska et al., 2023). In various organisms, it can cause effects such as feminisation, cytoplasmic incompatibility, parthenogenesis, and male killing (O'Neill et al., 1997; Werren et al., 2008; Mioduchowska et al., 2023).

2.2 *Rickettsia*

Rickettsia is an intracellular symbiont that can infect various groups of arthropods, including insects, mites, and spiders – about 24% species (Weinert et al., 2009). Its strains are capable of killing infected male embryos in some lady beetles, *e.g.*, *Adalia decempunctata* (Linnaeus, 1758) (Coccinellidae) (von der Schulenburg et al., 2001) and the leaf-mining buprestids, *e.g.*, *Brachys tessellatus* (Fabricius, 1801) (Buprestidae) (Lawson et al., 2001). They are also the cause of thelytokous parthenogenesis (in which mothers produce only daughters from unfertilised eggs) in a parasitoid wasp (Giorgini et al., 2010).

Presumably, the temperature effects of *Rickettsia*, particularly on host survival, are species-specific, as in some cases infection with this endosymbiont increases resistance to changes in environmental temperature (Brumin et al., 2011), whereas in others it decreases it (Socolovschi et al., 2012).

To date, there is evidence of the presence of *Rickettsia* in two invertebrate species in Antarctica: in low abundance in the endemic, gonochoristic *B. antarctica* (Kovalenko et al., 2025) in the Antarctic region and in very high abundance in the invasive to this region, parthenogenetic *E. murphyi* (Brayley et al., 2025a; 2025b) in the subantarctic region.

2.3 *Cardinium*

Candidatus Cardinium hertigii Zchori-Fein et al., 2004 (the only known species of the genus to date) is an obligate intracellular bacterium that is maternally transmitted and infects approximately 13% of arthropod species (Weinert et al., 2015). *Cardinium* strains induce at least three reproductive manipulations: parthenogenesis, feminisation, and cytoplasmic incompatibility, as well as affecting other host fitness traits (Stouthamer et al., 2019; Kaya, 2022; Mathieson et al., 2025).

There is evidence that *Cardinium* infection can contribute to longer developmental time and reduced total fecundity (Haghshenas-Gorgabi et al., 2023). It is also shown that temperature can influence the phenotypic effects of *Cardinium* on the host (Doremus et al., 2019).

To date, only one preliminary study has detected this endosymbiont in Antarctic invertebrates, specifically in low abundance, in the insect *B. antarctica* (Kovalenko et al., 2025).

2.4 *Arsenophonus*

Arsenophonus is a genus of Gram-negative bacteria that participates in a variety of symbiotic relationships with approximately 5% of arthropod species (Duron et al., 2008). These relationships range from the probable pathogenicity (*Arsenophonus apicola* in honey bees (Nadal-Jiménez et al., 2023)), through reproductive parasitism (*Arsenophonus nasoniae* Gherna et al., 1991 in *Nasonia* wasps) to mutualism (*Candidatus* Arsenophonus arthropodicus Dale et al., 2006 and *Candidatus* Arsenophonus lipopteni Nováková et al., 2016 in Hippoboscidae flies). This bacterium also causes male killing in the offspring of *Nasonia vitripennis* (Walker, 1836) (Pteromalidae) wasps (Nadal-Jiménez et al., 2023). Interestingly, arthropods serve as vectors for the transmission of *Arsenophonus* to plants (Bressan et al., 2012).

The effects of temperature on interactions between *Arsenophonus* bacteria and their hosts, as well as their possible presence in Antarctica, remain unstudied. In the few works (*e.g.*, Maistrenko et al., 2023; Brayley et al., 2025b; Kovalenko et al., 2025) devoted to the study of the terrestrial arthropod microbiota of this continent, there is no evidence of their presence.

2.5 *Spiroplasma*

Many species of *Spiroplasma* have been isolated from a wide range of hosts, mainly arthropods (Bové, 1997; Regassa & Gasparich, 2006; Bolacos et al.,

2015). It is currently known that from 7 to over 11% of species from different groups of arthropods can be infected with this bacterium (Duron et al., 2008; Kakizawa et al., 2022).

In their hosts, *Spiroplasma* most often reproduce in the intestine, but some pathogenic species of *Spiroplasma* are found in the hemolymph, ovaries, fat body, hypodermis, or salivary glands (Regassa & Gasparich, 2006; Masson et al., 2018; Blow & Douglas, 2019; Garcia-Arraez et al., 2019). If bacteria attach to the midgut epithelial cells, no apparent negative effect on the host is observed (Regassa & Gasparich, 2006). While the pathogenicity of *Spiroplasma* in insect hosts is usually associated with the ability to penetrate host tissues beyond the midgut. For example, *Spiroplasma melliferum* Clark et al., 1985 and *S. apis* Mouches et al., 1984 are pathogens of honey bees. They cross the insect intestinal barrier and reach the hemolymph, where they actively reproduce and kill the host (Rivera et al., 2013).

Another route of infection and transmission is transovarial, resulting in the killing of male offspring in infected females (Harumoto et al., 2014; Arai et al., 2022). The most thoroughly studied example to date is *Spiroplasma poulsonii* Williamson et al., 1999, which was isolated from the Neotropical species *Drosophila willistoni* Sturtevant, 1916 (Drosophilidae). In its extreme form, *S. poulsonii* infection can kill all male offspring in infected females (Regassa & Gasparich, 2006). Male killing by this bacterium has also been described in beetles of the Coccinellidae family: *Adalia bipunctata* (Linnaeus, 1758) (Hurst et al., 1999) and *Harmonia axyridis* (Pallas, 1773) (Regassa & Gasparich, 2006; Nakamura et al., 2006; Tsushima et al., 2015), as well as in butterflies of the Nymphalidae family, in particular *Danaus chrysippus* (Linnaeus, 1758) (Jiggins et al., 2000; Regassa & Gasparich, 2006).

It is also worth noting the possible mutualistic relationships of *Spiroplasma* with the host. It is known that it can provide resistance to certain members of the families Drosophilidae and Aphididae to fungal pathogens, as well as to parasitic nematodes and parasitoid wasps (Jaenike et al., 2010; Xie et al., 2010; Cockburn et al., 2013; Łukasik et al., 2013; Bolacos et al., 2015). It has also been established that *Spiroplasma kunkelii* Whitcomb et al., 1986 helps *Dalbulus maidis* (DeLong, 1923) (Cicadellidae) to survive in conditions of limited food resources during cold and drought (Ebbert & Nault, 1994).

In general, spiroplasmas grow in a wide range of positive temperatures; however, only a few strains retain the ability to grow at temperatures around +5 °C (Konai et al., 1996). This may explain why this endosymbiont has not been detected in Antarctic chironomid midges (Maistrenko et al., 2023; Kovalenko et al., 2025).

3 Springtails (Collembola)

Springtails or Collembola are small, primary wingless and intramaxillary arthropods belonging to the rank of class (www.collembola.org/taxa/collembo.htm). There are currently about 9 600 nominally extant species of springtails, with more than half of them described in the last 50 years. Most of these species have been recorded and described from the Holarctic region. Springtails are widespread in terrestrial environments but can also be found on the surface of standing pools of fresh or salt water, or even in subsurface coastal waters (Hopkin, 1997).

Collembola are recorded from all continents, including the High Arctic and Antarctic, and can live from arid desert areas to snowfields and permanent ice (Bellini et al., 2023). Most species, however, live in association with the soil, and within this environment they can be classified as: epedaphic (species that inhabit the above-ground surface, including the litter layer), hemiedaphic (taxa that can live both in the soil and on its surface), and euedaphic (organisms that live only within the soil) (Bellini et al., 2023). In edaphic environments, some species can also be found in birds' nests (van der Vegt & Bokhorst, 2024).

The distribution of different Collembola species is strongly dependent on environmental vari-

ables. At the regional scale, climate plays a key role by filtering for species adapted to different conditions (Bellini et al., 2023). Most Collembola depend on moist habitats within specific temperature ranges, but some are adapted to drought, extreme cold, complete absence of light, and other limiting conditions (Ávila-Jiménez & Coulson, 2011; Bellini et al., 2023).

With respect to collembolan biodiversity in the Arctic and Antarctic regions, marked differences are observed between the two biogeographic areas. To date, approximately 400 collembolan species have been found in the Arctic, the majority of which are of cosmopolitan or Palaearctic origin (Ávila-Jiménez & Coulson, 2011). Arctic collembolan populations exhibit low levels of genetic differentiation, consistent with postglacial colonisation of the region (Ávila-Jiménez & Coulson, 2011).

In contrast, collembolan biodiversity in Antarctica is comparatively lower and does not exceed 30 species on the continent (Chown & Convey, 2007), despite recent increases due to modern molecular and genetic methods (Convey et al., 2020). At the same time, the region with the largest number of them is the Western Antarctic Peninsula with adjacent islands – 20 species have been recorded there, but only a few are numerous (Protsenko et al., 2025). Even taking into account the slightly larger number of species distributed in the sub-Antarctic, it comprises approximately 160 springtail species (2.5 times fewer than in the Arctic) belonging to 60 genera and 15 families (Baird et al., 2019). The highest species richness is found in the genera *Cryptopygus* (Isotomidae) and *Friesea* (Neanuridae) (17 species each) (Baird et al., 2019). Many of these species are endemic to the region, and high levels of genetic divergence have been reported even among geographically proximate populations, indicating long-term isolation (Collins et al., 2019).

As in other invertebrates, several studies have described a diverse microbiome associated with collembolans (Czarnetzki & Tebbe, 2004; Agamennone et al., 2015; Bahrndorff et al., 2018; Zhu et al., 2018; Ding et al., 2019; Pathiraja et al., 2022; Hao et al., 2024), including Antarctica (Leo et al., 2021). Also, the presence of bacterial reproductive parasites in this group of Hexapoda was reported (Vandekerckhove et al., 1999; Czarnetzki & Tebbe, 2003; Timmermans et al., 2004; Frati et al., 2006; Pike & Kingcombe, 2009; Agamennone et al., 2015; Ma et al., 2017; Pilgrim et al., 2021; Kaya, 2022; Rodrigues et al., 2023; Timmermans et al., 2023).

4 Infection of springtails with bacterial reproductive parasites

4.1 *Wolbachia* in collembolan species

To date, the literature has reported *Wolbachia* in at least 17 determined springtail species across four orders: Entomobriomorpha, Poduromorpha, Neelipleona, and Symphypleona (Table). The largest screening study, encompassing 58 species and covering most regions of the world, including the polar ones, found an overall prevalence of 19% (Tanganelli et al., 2014; Rodrigues et al., 2023).

Interestingly, Antarctic samples included only one to three individuals (the exact number was not specified) of the collembolan *Cryptopygus sverdrupi* Lawrence, 1978 (Isotomidae) screened for the presence of *Wolbachia*, but no infection was detected (Rodrigues et al., 2023). In the same study, *Wolbachia* was identified in Arctic populations (Svalbard, Norway) of *Oligaphorura groenlandica* (Tullberg, 1876) (Onychiuridae). In contrast, *Wolbachia* was not detected in another species analysed from the same locality, *Megaphorura arctica* (T. Tullberg, 1877) (Onychiuridae) (Rodrigues et al., 2023). Notably, of these two species, only *O. groenlandica* is characterised by parthenogenetic reproduction (Rodrigues et al., 2023).

It should also be noted that of all the species listed in Table, only four, *Megalothorax minimus* V. Willem, 1900 (Neelidae), *Mesaphorura macrochaeta* Rusek, 1976 (Tullbergiidae), as well as *Folsomia candida* Willem, 1902, *Parisotoma notabilis* (Schäffer, 1896) (Isotomidae) occur in Antarctica according to the Register of Antarctic Species (RAS, 2026). However, no published data were found regarding investigations of *Wolbachia* in-

Table. Presence of *Wolbachia* in different Collembola species around the world. Species confirmed in Antarctica are in bold

No	Species	Family	Place of origin	References
		Order Entomobryomorpha		
1	***Folsomia candida* Willem, 1902**	Isotomidae	UK, France, China, The Netherlands, Germany (laboratory-cultivated "Berlin strain")	Vandekerckhove et al., 1999; Pike & Kingcombe, 2009; Agamennone et al., 2015; Ma et al., 2017
2	*Folsomia* sp.		France	Rodrigues et al., 2023
3	*Folsomides parvulus* Stach, 1922		China	Ma et al., 2017
4	*Hemisotoma cf thermophila* (Axelson, 1900)		France	Rodrigues et al., 2023
5	***Parisotoma notabilis* (Schäffer, 1896)**		France	Rodrigues et al., 2023
		Order Poduromorpha		
6	*Anurida maritima* (Guérin-Méneville, 1836)	Neanuridae	Netherlands	Rodrigues et al., 2023
7	*Oligaphorura groenlandica* (Tullberg, 1877)	Onychiuridae	Norway	Rodrigues et al., 2023
8	*Thalassaphorura houtanensis* Gao & Bu, 2014		China	Ma et al., 2017
9	*Podura aquatica* Linnaeus, 1758	Poduridae	Netherlands	Rodrigues et al., 2023
10	*Mesaphorura italica* (J. Rusek, 1971)	Tullbergiidae	Not specified	Czarnetzki & Tebbe, 2003
11	***Mesaphorura macrochaeta* Rusek, 1976**		Not specified	Czarnetzki & Tebbe, 2003; Timmermans et al., 2004
12	*Mesaphorura yosii* (J. Rusek, 1967)		China	Ma et al., 2017
13	*Mesaphorura* sp.		France	Rodrigues et al., 2023
14	*Paratullbergia callipygos* (Börner, 1902)		Not specified	Czarnetzki & Tebbe, 2003
		Order Neelipleona		
15	*Megalothorax incertus* C. Börner, 1903	Neelidae	China	Ma et al., 2017
16	*Megalothorax laevis* Denis, 1948		French Guinea	Rodrigues et al., 2023
17	***Megalothorax minimus* V. Willem, 1900**		France	Rodrigues et al., 2023
18	*Neelus koseli* L. Kovác & V. Papác, 2010		Slovakia	Rodrigues et al., 2023
		Order Symphypleona		
19	*Sphaeridia pumilis* (Krausbauer, 1898)	Sminthurididae	France	Rodrigues et al., 2023

fection in these or several other species collected in Antarctica (Serga et al., 2024). Nevertheless, given the rapid warming of the climate in the sixth continent region and surrounding areas (Wang et al., 2025), the bacteria can be expected to appear in invertebrates inhabiting these regions.

Overall, *Wolbachia* is predominantly associated with asexually reproducing collembolans and has been linked to the induction of parthenogenesis in this taxonomic group (Timmermans et al., 2023). Such results from polar regions are most likely explained by the long-standing isolation of Antarctic populations, while this is not typical for Arctic populations (Rodrigues et al., 2023). One cannot help but mention, among the possible reasons, the limited number of studies investigating *Wolbachia* infection in Antarctic springtail populations.

4.2 A rare case of infection of a collembolan species by *Spiroplasma*

As for *Spiroplasma*, it was found in the species *Anurida maritima* (Guérin-Méneville, 1836) (Neanuridae) by Timmermans et al. (2023). Moreover, the authors state that this is the first documented detection of infection with this endosymbiont in springtails.

Anurida maritima is characterised by the presence of sexual reproduction (Dallai et al., 1999). Also, according to Timmermans et al. (2023), it has a cosmopolitan distribution. Despite this, according to the Register of Antarctic Species (RAS, 2026) and the Global Biodiversity Information Facility database (GBIF, 2026), this species was not recorded in the Antarctic but is found in the Arctic (Svalbard, Norway). Unfortunately, Timmermans et al. (2023) do not specify in which localities *A. maritima* were collected for the study.

4.3 Restricted data for *Cardinium*, *Arsenophonus*, and *Rickettsia* infections

A possible association between *Entomobrya* sp. (Entomobryidae) and *Cardinium* has been reported in only a few works (Gupta et al., 2021; Kaya, 2022). However, the author noted that since the search for this endosymbiont was carried out in representatives of a single ecotope in microfauna samples from granaries in Turkey, this finding may reflect a temporary horizontal transfer of the bacterium between species. Thus, today it can be assumed that this endosymbiont is practically not identified in Collembola, so its search in species colonising the Antarctic and subantarctic regions currently appears unpromising.

Despite the fact that *Arsenophonus* is one of the richest and most widespread groups of symbiotic bacteria that infect arthropods, data on the infection of representatives of Hexapoda have not yet been found in the literature. Therefore, as in the case of *Cardinium*, it can be assumed that this endosymbiont is practically not identified in Collembola. Thus, its presence in species found in Antarctica and sub-Antarctica remains an open question.

Reports of *Rickettsia* in different Collembola species are limited and based on only a few studies. These bacteria have been reported in the species *Onychiurus sinensis* Stach, 1954 (Onychiuridae) (Frati et al., 2006). However, O. *sinensis* is not recorded in Antarctica (GBIF, 2026; RAS, 2026). In some cases, springtails were examined for *Rickettsia* without specifying the particular species analysed (*e.g.*, in Pilgrim et al., 2021).

4.4 Possibility of infection with multiple endosymbionts simultaneously

Today, it is also known that at least some springtails can be infected simultaneously with different types of reproductive parasitic bacteria.

The most well-described example is *A. maritima*. It has been found that representatives of this species are simultaneously hosts for two different genera of bacteria: *Wolbachia* and *Spiroplasma*. Interesting that in this case, *Wolbachia* belongs to supergroup A, which is unique for springtails (most other species are infected with supergroup E), and *Spiroplasma* is sister to the Citri-Chrysopicola-Mirum lineage (Timmermans et al., 2023).

At the same time, it is worth noting once again that *A. maritima* has not yet been identified in Antarctica.

In general, even outside the Antarctic context, it is still unclear how interactions between different bacterial species shape host reproduction, not to mention how frequently springtails are infected by multiple such species at once.

5 Conclusions

Therefore, today, the study of the prevalence of endosymbiotic reproductive parasite bacteria and, accordingly, their interactions with collembolans in Antarctic conditions is at an early stage and requires further research. If the presence of endosymbiotic bacteria in Antarctic collembolans is established, the question arises about their possible role in adaptation to the harsh conditions of existence on the sixth continent. In the event of a final failure to establish the corresponding bacterial group in Antarctic collembolans, it will be necessary to seek an explanation for their absence in the studied region, since in other parts of the planet these bacteria successfully colonise representatives of this invertebrate taxon.

Author contributions. O. P. Conceptualisation (supporting); formal analysis (equal); data curation (equal); writing – original draft (equal); writing – review and editing (equal). P. K. Conceptualisation (supporting); formal analysis (equal); data curation (equal); writing – original draft (equal); writing – review and editing (equal). Yu. P. Conceptualisation (supporting); formal analysis (equal); data curation (equal); writing – original draft (equal); writing – review and editing (equal). I. K. Conceptualisation (lead); validation (equal); writing – original draft (lead); writing – review and editing (equal); project administration (lead). All authors have read and approved the final version of the manuscript.

Funding. The current study was performed in the framework of the Ukrainian State Special-Purpose Research Program in Antarctica for 2011–2027.

Conflict of Interest. The authors have no conflicts of interest.

References

Agamennone, V., Jakupović, D., Weedon, J. T., Suring, W. J., van Straalen, N. M., Roelofs, D., & Röling, W. F. M. (2015). The microbiome of *Folsomia candida*: an assessment of bacterial diversity in a *Wolbachia*-containing animal. *FEMS Microbiology Ecology*, *91*(11), fiv128. https://doi.org/10.1093/femsec/fiv128

Arai, H., Inoue, M. N., & Kageyama, D. (2022). Male-killing mechanisms vary between *Spiroplasma* species. *Frontiers in Microbiology, 13*, 1075199. https://doi.org/10.3389/fmicb.2022.1075199

Ávila-Jiménez, M. L., & Coulson, S. J. (2011). A Holarctic biogeographical analysis of the Collembola (Arthropoda, Hexapoda) unravels recent post-glacial colonization patterns. *Insects, 2*(3), 273–296. https://doi.org/10.3390/insects2030273

Bahrndorff, S., de Jonge, N., Hansen, J. K., Lauritzen, J. M. S., Spanggaard, L. H., Sørensen, M. H., Yde, M., & Nielsen, J. L. (2018). Diversity and metabolic potential of the microbiota associated with a soil arthropod. *Scientific Reports, 8*(1), 2491. https://doi.org/10.1038/s41598-018-20967-0

Baird, H. P., Janion-Scheepers, C., Stevens, M. I., Leihy R. I., & Chown, S. L. (2019). The ecological biogeography of indigenous and introduced Antarctic springtails. *Journal of Biogeography, 46*(9), 1959–1973. https://doi.org/10.1111/jbi.13639

Baldo, L., Ayoub, N. A., Hayashi, C. Y., Russell, J. A., Stahlhut, J. K., & Werren, J. H. (2008). Insight into the routes of *Wolbachia* invasion: High levels of horizontal transfer in the spider genus *Agelenopsis* revealed by *Wolbachia* strain and mitochondrial DNA diversity. *Molecular Ecology, 17*(2), 557–569. https://doi.org/10.1111/j.1365-294X.2007.03608.x

Bellini, B. C., Weiner, W. M., & Winck, B. R. (2023). Systematics, ecology and taxonomy of Collembola: Introduction to the special issue. *Diversity, 15*(2), 221. https://doi.org/10.3390/d15020221

Blow, F., & Douglas, A. E. (2019). The hemolymph microbiome of insects. *Journal of Insect Physiology*, *115*, 33–39. https://doi.org/10.1016/j.jinsphys.2019.04.002

Bolacos, L. M., Servín-Garciduecas, L. E., & Martínez-Romero, E. (2015). Arthropod–*Spiroplasma* relationship in the genomic era. *FEMS Microbiology Ecology*, *91*(2), 1–8. https://doi.org/10.1093/femsec/fiu008

Bové, J. M. (1997). Spiroplasmas: Infectious agents of plants, arthropods and vertebrates. *Wiener Klinische Wochenschrift*, *109*(14–15), 604–612.

Brayley, O., Hayward, S., McCready, K., Liu, S., Chen, Y., Ullah, S., Teets, N., & Convey, P. (2025a).

Absence of *Wolbachia* in the sub-Antarctic midge, *Eretmoptera murphyi* (Diptera: Chironomidae). *Antarctic Science, 37*(4), 332–337. https://doi.org/10.1017/S0954102025000197

Brayley, O. D. M., McCready, K., Liu, S., Convey, P., Chen, Y., Ullah, S., Teets, N., & Hayward, S. A. L. (2025b). The microbiome of an invasive Antarctic insect, *Eretmoptera murphyi* (Diptera: Chironomidae), and its potential role in nutrient cycling. *Research Square*. https://doi.org/10.21203/rs.3.rs-7744438/v1

Bressan, A., Terlizzi, F., & Credi, R. (2012). Independent origins of vectored plant pathogenic bacteria from arthropod-associated *Arsenophonus* endosymbionts. *Microbial Ecology*, *63*(3), 628–638. https://doi.org/10.1007/s00248-011-9933-5

Brumin, M., Kontsedalov, S., & Ghanim, M. (2011). *Rickettsia* influences thermotolerance in the whitefly *Bemisia tabaci* B biotype. *Insect Science*, *18*(1), 57–66. https://doi.org/10.1111/j.1744-7917.2010.01396.x

Buschi, E., Dell'Anno, A., Tangherlini, M., Candela, M., Rampelli, S., Turroni, S., Palladino, G., Esposito, E., Martire, M. L., Musco, L., Stefanni, S., Munari, C., Fiori, J., Danovaro, R., & Corinaldesi, C. (2024). Resistance to freezing conditions of endemic Antarctic polychaetes is enhanced by cryoprotective proteins produced by their microbiome. *Science Advances, 10*(25), eadk9117. https://doi.org/10.1126/sciadv.adk9117

Casem, M. L. (2016). Cell Systems. In *Case Studies in Cell Biology* (pp. 345–371). Elsevier. https://doi.org/10.1016/B978-0-12-801394-6.00015-4

Castrillo, L. A., Lee, R. E. Jr., Wyman, J. A., Lee, M. R., & Rutherford, S. T. (2001). Field Persistence of Ice-Nucleating Bacteria in Overwintering Colorado Potato Beetles. *Biological Control*, *21*(1), 11–18. https://doi.org/10.1006/bcon.2000.0913

Chabanol, E., & Gendrin, M. (2024). Insects and microbes: Best friends from the nursery. *Current Opinion in Insect Science*, *66*, 101270. https://doi.org/10.1016/j.cois.2024.101270

Charlesworth, J., Weinert, L. A., Araujo, E. V., & Welch, J. J. (2019). *Wolbachia*, *Cardinium* and climate: An analysis of global data. *Biology Letters*, *15*(8), 20190273. https://doi.org/10.1098/rsbl.2019.0273

Chown, S. L., & Convey, P. (2007). Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1488), 2307–2331. https://doi.org/10.1098/rstb.2006.1949

Cockburn, S. N., Haselkorn, T. S., Hamilton, P. T., Landzberg, E., Jaenike, J., & Perlman, S. J. (2013). Dynamics of the continent-wide spread of a *Drosophila* defensive symbiont. *Ecology Letters*, *16*(5), 609–616. https://doi.org/10.1111/ele.12087

Collins, G. E., Hogg, I. D., Convey, P., Barnes, A. D., & McDonald, I. R. (2019). Spatial and temporal scales matter when assessing the species and genetic diversity of springtails (Collembola) in Antarctica. *Frontiers in Ecology and Evolution, 7*, 76. https://doi.org/10.3389/fevo.2019.00076

Convey, P., Biersma, E. M., Casanova-Katny, A., & Maturana, C. S. (2020). Refuges of Antarctic diversity. In *Past Antarctica* (pp. 181–200). Elsevier. https://doi.org/10.1016/B978-0-12-817925-3.00010-0

Corbin, C., Heyworth, E. R., Ferrari, J., & Hurst, J. D. D. (2017). Heritable symbionts in a world of varying temperature. *Heredity, 118*, 10–20. https://doi.org/10.1038/hdy.2016.71

Czarnetzki, A. B., & Tebbe, C. C. (2003). Detection and phylogenetic analysis of *Wolbachia* in Collembola. *Environmental Microbiology, 6*, 35–44. https://doi.org/10.1046/j.1462-2920.2003.00537.x

Czarnetzki, A. B., & Tebbe, C. C. (2004). Diversity of bacteria associated with Collembola – a cultivation-independent survey based on PCR-amplified 16S rRNA genes. *FEMS Microbiology Ecology*, *49*(2), 217–227. https://doi.org/10.1016/j.femsec.2004.03.007

Dallai, R., Fanciulli, P. P., & Frati, F. (1999). Chromosome elimination and sex determination in springtails (Insecta, Collembola). *The Journal of Experimental Zoology*, *285*(3), 215–225. https://doi.org/10.1002/(SICI)1097-010X(19991015)285:3<215::AID-JEZ4>3.0.CO;2-5

Ding, J., Zhu, D., Chen, Q.-L., Zheng, F., Wang, H.-T., & Zhu, Y.-G. (2019). Effects of long-term fertilization on the associated microbiota of soil collembolan. *Soil Biology and Biochemistry*, *130*, 141–149. https://doi.org/10.1016/j.soilbio.2018.12.015

Dobson, S. L., Bourtzis, K., Braig, H. R., Jones, B. F., Zhou, W., Rousset, F., & O'Neill, S. L. (1999). *Wolbachia* infections are distributed throughout insect somatic and germ line tissues. *Insect Biochemistry and Molecular Bio-logy*, *29*(2), 153–160. https://doi.org/10.1016/S0965-1748(98)00119-2

Doremus, M. R., Kelly, S. E., & Hunter, M. S. (2019). Exposure to opposing temperature extremes causes comparable effects on *Cardinium* density but contrasting effects on *Cardinium*-induced cytoplasmic incompatibility. *PLOS Pathogens*, *15*(8), e1008022. https://doi.org/10.1371/journal.ppat.1008022

Douglas, A. E. (2015). Multiorganismal insects: Diversity and function of resident microorganisms. *Annual Review of Entomology*, *60*, 17–34. https://doi.org/10.1146/annurev-ento-010814-020822

Duron, O., Bouchon, D., Boutin, S., Bellamy, L., Zhou, L., Engelstädter, J., & Hurst, G. D. (2008). The diversity of reproductive parasites among arthropods: Wolbachia do not walk alone. *BMC Biology*, *6*(1), 27. https://doi.org/10.1186/1741-7007-6-27

Ebbert, M. A., & Nault, L. R. (1994). Improved overwintering ability in *Dalbulus maidis* (Homoptera: Cicadellidae) vectors infected with *Spiroplasma kunkelii* (Mycoplasmatales: Spiroplasmataceae). *Environmental Entomology*, *23*(3), 634–644. https://doi.org/10.1093/ee/23.3.634

Frati, F., Negri, I., Fanciulli, P. P., Pellecchia, M., & Dallai, R. (2006). Ultrastructural and molecular identification of a new *Rickettsia* endosymbiont in the springtail *Onychiurus sinensis* (Hexapoda, Collembola). *Journal of Invertebrate Pathology, 93*(3), 150–156. https://doi.org/10.1016/j.jip.2006.07.002

Garcia-Arraez, M. G., Masson, F., Escobar, J. C. P., & Lemaitre, B. (2019). Functional analysis of RIP toxins from the *Drosophila* endosymbiont *Spiroplasma poulsonii*. *BMC Microbiology*, *19*(1), 46. https://doi.org/10.1186/s12866-019-1410-1

GBIF. (2026). *GBIF Occurrence Download*. Retrieved 29 January 2026, from https://doi.org/10.15468/dl.kesc38

Giorgini, M., Bernardo, U., Monti, M. M., Nappo, A. G., & Gebiola, M. (2010). *Rickettsia* symbionts cause parthenogenetic reproduction in the parasitoid wasp *Pnigalio soemius* (Hymenoptera: Eulophidae). *Applied and Environmental Microbiology, 76*(8). https://doi.org/10.1128/AEM.03154-09

Gupta, M., Kaur, R., Gupta, A., & Raychoudhury, R. (2021). Are ecological communities the seat of endosymbiont horizontal transfer and diversification? A case study with soil arthropod community. *Ecology and Evolution, 11*(21), 14490–14508. https://doi.org/10.1002/ece3.8108

Haghshenas-Gorgabi, N., Poorjavd, N., Khajehali, J., & Wybouw, N. (2023). *Cardinium* symbionts are pervasive in Iranian populations of the spider mite *Panonychus ulmi* despite inducing an infection cost and no demonstrable reproductive phenotypes when *Wolbachia* is a symbiotic partner. *Experimental and Applied Acarology*, *91*(3), 369–380. https://doi.org/10.1007/s10493-023-00840-0

Haider, K., Abbas, D., Galian, J., Ghafar, M. A., Kabir, K., Ijaz, M., Hussain M., Khan, K. A., Gramh, H. A., & Raza, A. (2025). The multifaceted roles of gut microbiota in insect physiology, metabolism, and environmental adaptation: Implications for pest management strategies. *World Journal of Microbiology and Biotechnology, 41,* 75. https://doi.org/10.1007/s11274-025-04288-9

Hao, C., de Jonge, N., Chen, T.-W., Gong, X., Xu, G., Wu, D., & Nielsen, J. L. (2024). Seasonal dynamics of microbiota in winter-adapted Collembola: Insights into symbiotic relationships and adaptation to low temperatures. *Applied Soil Ecology*, *202*, 105599. https://doi.org/10.1016/j.apsoil.2024.105599

Harumoto, T., Anbutsu, H., & Fukatsu, T. (2014). Male-killing *Spiroplasma* induces sex-specific cell death via host apoptotic pathway. *PLoS Pathogens, 10*(2), e1003956. https://doi.org/10.1371/journal.ppat.1003956

Holmes, C. J., Jennings, E. C., Gantz, J. D., Spacht, D., Spangler, A. A., Denlinger, D. L., Lee, R. E. Jr., Hamilton, T. L., & Benoit, J. B. (2019). The Antarctic mite, *Alaskozetes antarcticus*, shares bacterial microbiome community membership but not abundance between adults and tritonymphs. *Polar Biology, 42*(11), 2075–2085. https://doi.org/10.1007/s00300-019-02582-5

Hopkin, S. P. (1997). *Biology of the Springtails* (*Insecta: Collembola*). Oxford University Press. https://doi.org/10.1093/oso/9780198540847.001.0001

Hurst, G. D. D., von der Schulenburg, J. H., Majerus, T. M. O., Bertrand, D., Zakharov, I. A., Baungaard, J., Völkl, W., Stouthamer, R., & Majerus, M. E. N. (1999). Invasion of one insect species, *Adalia bipunctata*, by two different male-killing bacteria. *Insect Molecular Biology, 8*(1), 133–139. https://doi.org/10.1046/j.1365-2583.1999.810133.x

Jaenike, J., Unckless, R., Cockburn, S. N., Boelio, L. M., & Perlman, S. J. (2010). Adaptation via symbiosis: Recent spread of a *Drosophila* defensive symbiont. *Science*, *329*(5988), 212–215. https://doi.org/10.1126/science.1188235

Jiggins, F. M., Hurst, G. D. D., Jiggins, C. D., von der Schulenburg, J. H. G., & Majerus, M. E. N. (2000). The butterfly *Danaus chrysippus* is infected by a male-killing *Spiroplasma* bacterium. *Parasitology*, *120*(5), 439–446. https://doi.org/10.1017/S0031182099005867

Jolley, K. A., Bray, J. E., & Maiden, M. C. J. (2018). Open-access bacterial population genomics: BIGSdb software, the PubMLST.org website and their applications. *Wellcome Open Research, 3*, 124. https://doi.org/10.12688/wellcomeopenres.14826.1

Kakizawa, S., Hosokawa, T., Oguchi, K., Miyakoshi, K., & Fukatsu, T. (2022). *Spiroplasma* as facultative bacterial symbionts of stinkbugs. *Frontiers in Microbiology*, *13*, 1044771. https://doi.org/10.3389/fmicb.2022.1044771

Kaltenpoth, M., Flórez, L. V., Vigneron, A., Dirksen, P., & Engl, T. (2025). Origin and function of beneficial bacterial symbioses in insects. *Nature Reviews Microbiology, 23*, 551–567. https://doi.org/10.1038/s41579-025-01164-z

Kaur, R., Shropshire, J. D., Cross, K. L., Leigh, B., Mansueto, A. J., Stewart, V., Bordenstein, S. R., & Bordenstein, S. R. (2021). Living in the endosymbiotic world of *Wolbachia*: A centennial review. *Cell Host & Microbe*, *29*(6), 879–893. https://doi.org/10.1016/j.chom.2021.03.006

Kaya, T. (2022). Investigation of *Cardinium* endosymbiont in the micro-fauna of granaries and surroundings. *Plant Protection Bulletin, 62*(3), 29–36. https://doi.org/10.16955/bitkorb.1159274

Konai, M., Clark, E. A., Camp, M., Koeh, A. L., & Whitcomb, R. F. (1996). Temperature ranges, growth optima, and growth rates of *Spiroplasma* (Spiroplasmataceae, class Mollicutes) species. *Current Microbiology*, *32*(6), 314–319. https://doi.org/10.1007/s002849900056

Kovalenko, P., Pavlovska, M., Prekrasna-Kviatkovska, Y., Puhovkin, A., & Kozeretska, I. (2025). The microbiome of Antarctica's endemic chironomid midge: From general microbial community to endosymbiotic bacteria. *bioRxiv*. https://doi.org/10.64898/2025.12.13.694143

Lawson, E. T., Mousseau, T. A., Klaper, R., Hunter, M. D., & Werren, J. H. (2001). *Rickettsia* associated with male-killing in a buprestid beetle. *Heredity, 86*, 497–505. https://doi.org/10.1046/j.1365-2540.2001.00848.x

Leo, C., Nardi, F., Cucini, C., Frati, F., Convey, P., Weedon, J. T., Roelofs, D., & Carapelli, A. (2021). Evidence for strong environmental control on bacterial microbiomes of Antarctic springtails. *Scientific Reports*, *11*(1), 2973. https://doi.org/10.1038/s41598-021-82379-x

Łukasik, P., Guo, H., van Asch, M., Ferrari, J., & Godfray, H. C. J. (2013). Protection against a fungal pathogen conferred by the aphid facultative endosymbionts *Rickettsia* and *Spiroplasma* is expressed in multiple host genotypes and species and is not influenced by co-infection with another symbiont. *Journal of Evolutionary Biology*, *26*(12), 2654–2661. https://doi.org/10.1111/jeb.12260

Ma, Y., Chen, W.-J., Li, Z.-H., Zhang, F., Gao, Y., & Luan, Y.-X. (2017). Revisiting the phylogeny of *Wolbachia* in *Collembola*. *Ecology and Evolution, 7*(7), 2009–2017. https://doi.org/10.1002/ece3.2738

Maistrenko, O. M., Serga, S. V., Kovalenko, P. A., & Kozeretska, I. A. (2023). Bacteria associated with the Antarctic endemic insect *Belgica antarctica* Jacobs (Diptera Chironomidae). *Cytology and Genetics, 57*(3), 207–212. https://doi.org/10.3103/S0095452723030064

Massey, J. H., & Newton, I. L. G. (2022). Diversity and function of arthropod endosymbiont toxins. *Trends in Microbiology, 30*(2), 185–198. https://doi.org/10.1016/j.tim.2021.06.008

Masson, F., Calderon Copete, S., Schüpfer, F., Garcia-Arraez, G., & Lemaitre, B. (2018). *In vitro* culture of the insect endosymbiont *Spiroplasma poulsonii* highlights bacterial genes involved in host-symbiont interaction. *mBio*, *9*(2), https://doi.org/10.1128/mbio.00024-18

Mathieson, O. L., Schultz, D. L., Hunter, M. S., Kleiner, M., Schmitz-Esser, S., & Doremus, M. R. (2025). The ecology, evolution, and physiology of *Cardinium*: A widespread heritable endosymbiont of invertebrates. *FEMS Microbiology Reviews, 49*, fuaf031. https://doi.org/10.1093/femsre/fuaf031

McFall-Ngai, M., Hadfield, M. G., Bosch, T. C. G., Carey, H. V., Domazet-Lošo, T., Douglas, A. E., Dubilier, N., Eberl, G., Fukami, T., Gilbert, S. F., Hentschel, U., King, N., Kjelleberg, S., Knoll, A. H., Kremer, N., Mazmanian, S. K., Metcalf, J. K., Nealson, K., Pierce, N. E., ... & Wernegreen, J. J. (2013). Animals in a bacterial world, a new imperative for the life sciences. *Proceedings of the National Academy of Sciences of the United States of America, 110*(9), 3229–3236. https://doi.org/10.1073/pnas.1218525110

McQueen, J. P., Gattoni, K., Gendron, E. M. S., Schmidt, S. K., Sommers, P., & Porazinska, D. L. (2022). Host identity is the dominant factor in the assembly of nematode and tardigrade gut microbiomes in Antarctic Dry Valley streams. *Scientific Reports, 12*(1), 20118. https://doi.org/10.1038/s41598-022-24206-5

Mioduchowska, M., Konecka, E., Gołdyn, B., Pinceel, T., Brendonck, L., Lukić, D., Kaczmarek, Ł., Namiotko, T., Zając, K., Zając, T., Jastrzębski, J. P., & Bartoszek, K. (2023). Playing peekaboo with a master manipulator: metagenetic detection and phylogenetic analysis of *Wolbachia* supergroups in freshwater invertebrates. *International Journal of Molecular Sciences*, *24*(11), 9400. https://doi.org/10.3390/ijms24119400

Mioduchowska, M., Nitkiewicz, B., Roszkowska, M., Kačarević, U., Madanecki, P., Pinceel, T., Namiotko, T., Gołdyn, B., & Kaczmarek, Ł. (2021). Taxonomic classification of the bacterial endosymbiont *Wolbachia* based on next-generation sequencing: Is there molecular evidence for its presence in tardigrades? *Genome, 64*(10), 951–958. https://doi.org/10.1139/gen-2020-0036

Mondal, S., Somani, J., Roy, S., Babu, A., & Pandey, A. K. (2023). Insect microbial symbionts: Ecology, interactions, and biological significance. *Microorganisms, 11*(11), 2665. https://doi.org/10.3390/microorganisms11112665

Morgan-Richards, M., Marshall, C. J., Biggs, P. J., & Trewick, S. A. (2023). Insect freeze-tolerance Downunder: The microbial connection. *Insects, 14*(1), 89. https://doi.org/10.3390/insects14010089

Nadal-Jiménez, P., Parratt, S. R., Siozios, S., & Hurst, G. D. D. (2023). Isolation, culture and characterization of *Arsenophonus* symbionts from two insect species reveal loss of infectious transmission and extended host range. *Frontiers in Microbiology, 14*, 1089143. https://doi.org/10.3389/fmicb.2023.1089143

Nakamura, K., Miura, K., De Jong, P., & Ueno, H. (2006). Comparison of the incidence of sibling cannibalism between male-killing *Spiroplasma* infected and uninfected clutches of a predatory ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, *103*(2), 323–326. https://doi.org/10.14411/eje.2006.042

O'Neill, S. L., Hoffmann, A. A., & Werren, J. H. (Eds). (1997). *Influential Passengers: Inherited Microorganisms and Arthropod Reproduction*. Oxford University Press. https://doi.org/10.1093/oso/9780198577867.001.0001

Pathiraja, D., Wee, J., Cho, K., & Choi, I.-G. (2022). Soil environment reshapes microbiota of laboratory-maintained Collembola during host development. *Environmental Microbiome*, *17*(1), 16. https://doi.org/10.1186/s40793-022-00411-7

Pietri, J. E., DeBruhl, H., & Sullivan, W. (2016). The rich somatic life of *Wolbachia*. *MicrobiologyOpen*, *5*(6), 923–936. https://doi.org/10.1002/mbo3.390

Pike, N., & Kingcombe, R. (2009). Antibiotic treatment leads to the elimination of *Wolbachia* endosymbionts and sterility in the diplodiploid collembolan *Folsomia candida*. *BMC Biology, 7*, 54. https://doi.org/10.1186/1741-7007-7-54

Pilgrim, J., Thongprem, P., Davison, H. R., Siozios, S., Baylis, M., Zakharov, E. V., Ratnasingham, S., deWaard, J. R., Macadam, C. R., Smith, M. A., & Hurst, G. D. D. (2021). Torix *Rickettsia* are widespread in arthropods and reflect a neglected symbiosis. *GigaScience, 10*(3), giab021. https://doi.org/10.1093/gigascience/giab021

Protsenko, Y., Protsenko, O., Kovalenko, P., Parnikoza, I., Puhovkin, A., Svetlichny, L., Convey, P., & Kozeretska, I. (2025). New Collembola occurrence records from the western Antarctic Peninsula. *Ukrainian Antarctic Journal*, *23*(1(30), 64–89. https://doi.org/10.33275/1727-7485.1.2025.744

RAS (Eds.). (2026). *Register of Antarctic Species*. Accessed at https://ras.biodiversity.aq on 5 February 2026

Raychoudhury, R., Baldo, L., Oliveira, D. C. S. G., & Werren, J. H. (2009). Modes of acquisition of *Wolbachia*: Horizontal transfer, hybrid introgression, and codivergence in the *Nasonia* species complex. *Evolution*, *63*(1), 165–183. https://doi.org/10.1111/j.1558-5646.2008.00533.x

Regassa, L., & Gasparich, G. E. (2006). Spiroplasmas: Evolutionary relationships and biodiversity. *Frontiers in Bioscience, 11*(3), 2983–3002. https://doi.org/10.2741/2027

Rivera, A., Cedillo, L., Hernández, F., Romero, O., & Hernández, M. A. (2013). Spiroplasmas infectious agents of plants. *European Journal of Experimental Biology*, *3*(1), 583–591.

Rodrigues, J., Lefoulon, E., Gavotte, L., Perillat-Sanguinet, M., Makepeace, B., Martin, C., & D'Haese, C. A. (2023). *Wolbachia* springs eternal: symbiosis in Collembola is associated with host ecology. *Royal Society Open Science, 10*(5), 230288. https://doi.org/10.1098/rsos.230288

Senula, S. F., Scavetta, J. T., Mueller, U. G., Seal, J. N., & Kellner, K. (2022). Cold adaptations along a range limit in an obligate symbiosis. *Functional Ecology, 36*(9), 2267–2278. https://doi.org/10.1111/1365-2435.14120

Serga, S., Kovalenko, P. A., Maistrenko, O. M., Deconninck, G., Shevchenko, O., Iakovenko, N., Protsenko, Y., Susulovsky, A., Kaczmarek, Ł., Pavlovska, M., Convey, P., & Kozeretska, I. (2024). *Wolbachia* in Antarctic terrestrial invertebrates: Absent or undiscovered? *Environmental Microbiology Reports, 16*(6), e70040. https://doi.org/10.1111/1758-2229.70040

Socolovschi, C., Gaudart, J., Bitam, I., Huynh, T. P., Raoult, D., & Parola, P. (2012). Why are there so few *Rickettsia conorii conorii*-infected *Rhipicephalus sanguineus* ticks in the wild? *PLoS Neglected Tropical Diseases*, *6*(6), e1697. https://doi.org/10.1371/journal.pntd.0001697

Stouthamer, C. M., Kelly, S. E., Mann, E., Schmitz-Esser, S., & Hunter, M.S. (2019). Development of a multilocus sequence typing system helps reveal the evolution of *Cardinium hertigii*, a reproductive manipulator symbiont of insects. *BMC Microbiology, 19*, 266. https://doi.org/10.1186/s12866-019-1638-9

Tanganelli, V., Fanciulli, P. P., Nardi, F., & Frati, F. (2014). Molecular phylogenetic analysis of a novel strain from Neelipleona enriches *Wolbachia* diversity in soil biota. *Pedobiologia, 57*(1), 15–20. https://doi.org/10.1016/j.pedobi.2013.08.004

Timmermans, M. J. T. N., Mariën, J., Roelofs, D., Van Straalen, N. M., & Ellers, J. (2004). Evidence for multiple origins of *Wolbachia* infection in springtails. *Pedobiologia, 48*(5-6), 469–475. https://doi.org/10.1016/j.pedobi.2004.07.008

Timmermans, M. J. T. N., Prabha, H., & Kett, S. (2023). *Wolbachia* and *Spiroplasma* endosymbionts in the *Anurida maritima* (Collembola) species group. *Evolutionary Journal of the Linnean Society, 2*(1), kzad001. https://doi.org/10.1093/evolinnean/kzad001

Tsushima, Y., Nakamura, K., Tagami, Y., & Miura, K. (2015). Mating rates and the prevalence of male-killing *Spiroplasma* in *Harmonia axyridis* (Coleoptera: Coccinellidae). *Entomological Science*, *18*(2), 217–220. https://doi.org/10.1111/ens.12113

van der Vegt, W., & Bokhorst, S (2024). Bird traits and their nutrient impact on terrestrial invertebrate populations. *Polar Biology, 47*, 821–832. https://doi.org/10.1007/s00300-023-03161-5

Vandekerckhove, T. T. M., Watteyne, S., Willems, A., Swings, J. G., Mertens, J., & Gillis, M. (1999). Phylogenetic analysis of the 16S rDNA of the cytoplasmic bacterium *Wolbachia* from the novel host *Folsomia candida* (Hexapoda, Collembola) and its implications for wolbachial taxonomy. *FEMS Microbiology Letters*, *180*(2), 279–286. https://doi.org/10.1111/j.1574-6968.1999.tb08807.x

Vecchi, M., Newton, I. L. G., Cesari, M., Rebecchi, L., & Guidetti, R. (2018). The microbial community of tardigrades: Environmental influence and species specificity of microbiome structure and composition. *Microbial Ecology*, *76*(2), 467–481. https://doi.org/10.1007/s00248-017-1134-4

von der Schulenburg, J. H. G., Habig, M., Sloggett, J. J., Webberley, K. M., Bertrand, D., Hurst, G. D. D., & Majerus, M. E. N. (2001). Incidence of male-killing *Rickettsia* spp. (α-Proteobacteria) in the ten-spot ladybird beetle *Adalia decempunctata* L. (Coleoptera: Coccinellidae). *Applied and Environmental Microbiology, 67*(1), 270–277. https://doi.org/10.1128/AEM.67.1.270-277.2001

Wang, S., Li, G.-C., Zhang, Z.-H., Zhang, W.-Q., Wang, X., Chen, D., Chen, W., & Ding, M.-H. (2025). Recent warming trends in Antarctica revealed by multiple reanalysis. *Advances in Climate Change Research*, *16*(3), 447–459. https://doi.org/10.1016/j.accre.2025.03.003

Weinert, L. A., Araujo-Jnr, E. V., Ahmed, M. Z., & Welch, J. J. (2015). The incidence of bacterial endosymbionts in terrestrial arthropods. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1807), 20150249. https://doi.org/10.1098/rspb.2015.0249

Weinert, L. A., Werren, J. H., Aebi, A., Stone, G. N., & Jiggins, F. M. (2009). Evolution and diversity of *Rickettsia* bacteria. *BMC Biology, 7,* 6. https://doi.org/10.1186/1741-7007-7-6

Werren, J. H., Baldo, L., & Clark, M. E. (2008). *Wolbachia*: Master manipulators of invertebrate biology. *Nature Reviews Microbiology*, *6*(10), 741–751. https://doi.org/10.1038/nrmicro1969

Xie, J., Vilchez, I., & Mateos, M. (2010). *Spiroplasma* bacteria enhance survival of *Drosophila hydei* attacked by the parasitic wasp *Leptopilina heterotoma*. *PLOS ONE*, *5*(8), e12149. https://doi.org/10.1371/journal.pone.0012149

Zhu, D., Chen, Q.-L., An, X.-L., Yang, X.-R., Christie, P., Ke, X., Wu, L.-H., & Zhu, Y.-G. (2018). Exposure of soil collembolans to microplastics perturbs their gut microbiota and alters their isotopic composition. *Soil Biology and Biochemistry*, *116*, 302–310. https://doi.org/10.1016/j.soilbio.2017.10.027

Received: 6 February 2026
Accepted: 1 June 2026
Published: 3 July 2026

Репродуктивні ендосимбіотичні бактерії антарктичних ногохвісток: на порозі нових відкриттів?

Олександра Проценко[1, 2, *], Павло Коваленко[2, 3], Юрій Проценко[1, 4], Ірина Козерецька[2]

[1] Київський національний університет імені Тараса Шевченка, м. Київ, 01601, Україна
[2] Державна установа Національний антарктичний науковий центр, МОН України, м. Київ, 01601, Україна
[3] Державна установа «Інститут еволюційної екології НАН України», м. Київ, 03143, Україна
[4] Пирятинський національний природний парк, м. Пирятин, 37000, Україна

*** Автор для кореспонденції:** protsenko.olexandra@gmail.com

Реферат. Ендосимбіотичні бактерії інфікують величезну кількість безхребетних представників різноманітних таксонів. У цій роботі представлено огляд результатів щодо ідентифікації ендосимбіотичних бактерій (зокрема родів *Wolbachia*, *Cardinium*, *Rickettsia*, *Arsenophonus* та *Spiroplasma*), здатних потенційно впливати на репродуктивні стратегії організму-хазяїна у представників фауни Collembola Антарктичного регіону. Ці бактерії грають важливу роль у формуванні адаптаційних механізмів та популяційних структур членистоногих поза Антарктикою в мінливих умовах довкілля. У даній роботі проаналізовано видове різноманіття антарктичних колембол та проведено ретроспективний пошук відомостей про інфікування видів, які зустрічаються в цьому регіоні та поза ним, бактеріями-ендосимбіонтами. Встановлено, що дані бактерії інфікують представників ногохвісток, зокрема тих, які можуть зустрічатися в Антарктиці (*Folsomia candida, Megalothorax minimus, Mesaphorura macrochaeta*, *Parisotoma notabilis*). Екологія та фізіологія членистоногих регіону вже ґрунтовно вивчені. Втім, на сьогодні у доступних наукових джерелах відсутня інформація, яка б свідчила про наявність відповідних ендосимбіотичних асоціацій у колембол Антарктики. Виявлений дефіцит даних може вказувати як на потенційну ізольованість місцевих популяцій, так і на існування умов, за яких інфікування ногохвісток Антарктики бактеріями родів *Wolbachia*, *Cardinium*, *Rickettsia*, *Arsenophonus* та *Spiroplasma* неможливе в силу тих чи інших причин. Водночас потребується проведення більш масштабних молекулярно-генетичних скринінгів із застосуванням сучасних методів сиквенування з метою отримання остаточної відповіді з питання щодо можливого інфікування антарктичних видів ногохвісток ендосимбіотичними бактеріями. Проведений аналіз літературних даних окреслює перспективний напрям для подальших досліджень мікроорганізмів-симбіонтів антарктичних організмів, зокрема ногохвісток.

Ключові слова: *Arsenophonus*, *Cardinium*, Collembola, *Rickettsia*, *Spiroplasma*, *Wolbachia*