



Terrestrial nematodes from the Maritime Antarctic

Milka Elshishka[‡], Aleksandar Mladenov[‡], Stela Lazarova[‡], Vlada Peneva[‡]

[‡] Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113, Sofia, Bulgaria

Corresponding author: Milka Elshishka (melshishka@gmail.com)

Academic editor: Oleksandr Holovachov

Received: 16 Feb 2023 | Accepted: 29 Aug 2023 | Published: 14 Sep 2023

Citation: Elshishka M, Mladenov A, Lazarova S, Peneva V (2023) Terrestrial nematodes from the Maritime Antarctic. Biodiversity Data Journal 11: e102057. <https://doi.org/10.3897/BDJ.11.e102057>

Abstract

Background

Soil nematodes are one of the most important terrestrial faunal groups in Antarctica, as they are a major component of soil micro-food webs. Despite their crucial role in soil processes, knowledge of their species diversity and distribution is still incomplete. Taxonomic studies of Antarctic nematodes are fragmented, which prevents assessment of the degree of endemism and distribution of the species, as well as other aspects of biogeography.

New information

The present study is focused on the nematode fauna of one of the three Antarctic sub-regions, the Maritime Antarctic and summarises all findings published up to April 2023. A species list that includes 44 species, belonging to 21 genera, 16 families and eight orders is provided. A review of the literature on terrestrial nematodes inhabiting the Maritime Antarctic showed that the sites are unevenly studied. Three islands (Signy, King George and Livingston Islands) revealed highest species richness, probably due to the highest rates of research effort. Most species and four genera (*Antarctenchus*, *Pararhyssocolpus*, *Amblydorylaimus* and *Enchodeloides*) are endemic, proving that nematode fauna of the Maritime Antarctic is autochthonous and unique. Several groups of islands/sites have been revealed, based on their nematode fauna. The study showed that species with a limited

distribution prevailed, while only two species (*Plectus antarcticus* and *Coomansus gerlachei*) have been found in more than 50% of the sites. Based on the literature data, details on species localities, microhabitat distribution, plant associations and availability of DNA sequences are provided.

Keywords

endemics, distribution, DNA sequences, species

Introduction

Soil nematodes are one of the most important groups of the terrestrial fauna in Antarctica (Maslen and Convey 2006) as they are abundant, taxonomically and functionally diverse and occupy a central position in the soil micro-food webs (Adams et al. 2014) and may have an impact on nutrient cycling and carbon dioxide emission, when soils thaw for a longer period of the year under climate change (van den Hoogen et al. 2019). In the challenging environmental conditions of the Antarctic, their distribution is limited to ice-free areas, where they have evolved throughout millions of years of climatic fluctuations in refugia (Ebach et al. 2008, Convey et al. 2020, Stevens and Mackintosh 2023). The glaciations, long-term isolation, harsh climate and the patchy distribution of ice-free areas (present today where at least partially ice-free throughout repeated glacial maxima (Newman et al. 2009)) are the main factors affecting the Antarctic nematode fauna origin/genesis (i.e. the formation of fauna under the influence of multiple factors - historical, geographic and ecological) (Andrássy 1998, Convey and Peck 2019). In order to survive in the extreme environments, nematodes have developed exceptional cryptobiotic adaptations to manage freezing and desiccation stress (e.g. Pickup (1988), Wharton (1995), Treonis and Wall (2005), Kagoshima et al. (2019)).

Knowledge of the impact of climate change on nematode communities from extreme habitats and how they respond to these changes is insufficient (Freckman and Virginia 1997, Nielsen et al. 2011a). One of the main problems in predicting the effects of climate change in Antarctica is the limited knowledge on the diversity of terrestrial fauna, especially nematodes and the lack of comprehensive long-term studies (Gantait 2014). Data on species distribution and biogeography are not enough and the taxonomic information still remains confused or scarce (Andrássy 1998, Maslen and Convey 2006, Adams et al. 2014, Kagoshima et al. 2019). Nematodes possess high indicator potential for assessing various environmental changes in the soil environment because they are abundant, ubiquitous, utilise diverse trophic and live strategies and, thus, occupy key positions in soil micro-food webs (Neher 2001, Ferris et al. 2001, Neher 2010, Chauvin et al. 2020, Taylor et al. 2020, Ara Khanum et al. 2022, Du Preez et al. 2022). This highlights the need for research on the fauna of nematodes and their communities in extreme environments in view of the already occurring global change.

Antarctica represents three distinct climatic regions: the Sub-Antarctic, Maritime and Continental Antarctic (Holdgate 1977), with the Sub-Antarctic being the most favourable (mean air temperatures of most islands are low, but positive during the whole year), with the Continental Antarctic having the harshest conditions (the average monthly temperatures remain below freezing) (Convey 2017). The Continental Antarctic covers the territories of the continent, the Balleny Islands and the eastern side of the Antarctic Peninsula (Convey 2017). The Sub-Antarctic is the boundary zone that lies north of 56°S (Chown and Brooks 2019). The flora and fauna in this region are rather typical of temperate latitudes. In this paper, we focused on terrestrial nematodes from the Maritime Antarctic. This is a region with a strong influence of the Southern Ocean; it includes the western coast of the Antarctic Peninsula to ca. 72°S, the South Shetland, South Orkney and South Sandwich Islands and the isolated Bouvetøya and Peter I Øya (Convey 2006, Convey 2017). The Maritime Antarctic is characterised by more favourable conditions compared with the Continental Antarctic: mean air temperatures are positive for 1–4 months of the year (Convey 2017), the vegetation is predominantly cryptogamic (algae, mosses, liverworts, lichens); higher plants are represented by two species, *Deschampsia antarctica* Desv. (Poaceae) and *Colobanthus quitensis* Bartl. (Caryophyllaceae) (Greene 1970, Longton 1979, Smith 1984).

Studies on nematodes in the Maritime Antarctic started at the beginning of the 20th century, with the contribution of the Romanian biologist Emil Racoviță during the first scientific Antarctic expedition in winter (Andrássy 1998). This resulted in a description of the first Antarctic nematode species, *Mononchus gerlachei* (= *Coomansus gerlachei* (de Man 1904) Jairajpuri and Khan 1977), followed by three other species, *Plectus antarcticus* de Man 1904, *P. belgicae* de Man 1904 and *Dorylaimus* sp. Following these first data, targeted investigations on the terrestrial nematode fauna from this part of Antarctica started from the early 70s of the 20th century (Spaull 1972, Spaull 1973a, Spaull 1973b, Spaull 1973c, Loof 1975, Maslen 1979a, Maslen 1979b, Caldwell 1981, Maslen 1981, Spaull 1981, Pickup 1988, Shishida and Ohyama 1989, Tsalolikhin 1989, Pickup 1990, Janiec 1996, Peneva et al. 1996, Andrásy 1998, Peneva and Chipev 1999, Convey et al. 2000, Nedelchev and Peneva 2000, Peneva et al. 2002, Convey and Wynn-Williams 2002, Holovachov and Bostrom 2006, Maslen and Convey 2006, Nedelchev and Peneva 2007, Kito 2009, Peneva et al. 2009, Nielsen et al. 2011b, Velasco-Castrillón and Stevens 2014, Velasco-Castrillón et al. 2014a, Russell et al. 2014, Elshishka et al. 2015a, Elshishka et al. 2015b, Elshishka et al. 2017, Kagoshima et al. 2019, Newsham et al. 2020). Antarctic nematodes have been studied mainly in easy to access areas near to the research bases/stations; therefore, there are still many remote locations never sampled for nematodes which raise questions on how widespread the species are (Adams et al. 2014, Convey et al. 2020).

According to Andrásy (1998), numerous studies have reported species as new records with no morphological description making it impossible to confirm identifications, especially when the collected material is no longer available for subsequent examination. Further, this has an impact on the potential to assess fauna endemicity, which is critical for examining Antarctic biogeography within a global context (Andrásy 1998). There are numerous cases of misclassification and underestimation of the diversity for most microfaunal groups

in Antarctica, likely due to poor taxonomic resolution caused by insufficient sampling and their difficult identification (Adams et al. 2006, Iakovenko et al. 2015, Carapelli et al. 2017, Short et al. 2022, Collins et al. 2023), as well as the low degree of the development and application of molecular taxonomy.

In recent years, molecular studies have become more important in these marginal habitats, as a powerful toolkit to complement the traditional taxonomy, species identification and descriptions and to assess biodiversity and biogeography (Courtright et al. 2000, Velasco-Castrillón et al. 2014b, Elshishka et al. 2015b, Elshishka et al. 2017, Czechowski et al. 2017, Velasco-Castrillón et al. 2018, Kagoshima et al. 2019).

The integrative approach (combining morphological and molecular data) is an effective way to understand the scale of endemism, evolution and distribution of the Antarctic nematode fauna. However, the main problem of not linking molecular data with morphology still remains for the vast majority of Antarctic nematode species.

The present paper aims to summarise all records of nematode species occurrence in the Maritime Antarctic between the years of 1904 and April 2023 as a basis for further studies and to present a snapshot of nematode species diversity in this part of the Antarctic.

Materials and methods

The nematode species list has been composed, based on literature data and refers to the Maritime Antarctic. This list includes all species recovered in the Maritime Antarctic, as well as the islands and sites from where each species was reported, along with data on microhabitats and plant associations, accession numbers of published sequences in GenBank also included, if available. The type of microhabitat is reported as in the original paper, the scientific names of the plants being adapted according to the current systematics (Ochyra 1998). Geographical coordinates are presented additionally for each site if missing in the original paper. For the literature search, online bibliography search engine Google Scholar and the academic databases Scopus, Web of Science and CABI were used with search keywords “terrestrial nematode species*” and “Maritime Antarctic*”. We focused on studies reporting nematode species (see Holovachov (2014a)) from the Maritime Antarctic and omitted those that provide data only at the generic or family level.

Several papers recording multiple unidentified taxa at generic level (Maslen and Convey 2006, Nielsen et al. 2011b) probably contain many undescribed nematode species from those regions suggesting that the nematode diversity there might be underestimated to a great extent. Overall, nematodes from 37 sites (34 islands and three localities on the Antarctic Peninsula) are included in the review. The taxonomic position of the Antarctic species was presented according to the current nematode nomenclature. Classification follows Andrassy (2005), Andrassy (2007) and Andrassy (2009); only for order Plectida classification follows Holovachov (2014b). The analyses are based on species presence/absence data and Wizard > Matrix display function in PRIMER v.7.0 software (Clarke and Gorley 2015). The Matrix display wizard performs a sequence of sample and species

resemblance calculations and clustering and seriation steps resulting in a shade plot which visualises the species presence/absence data and sites similarity.

Checklist of terrestrial nematodes from the Maritime Antarctic

Order Dorylaimida

Family Nordiidae

Enchodeloides signyensis (Loof, 1975) Elshishka, Lazarova, Radoslavov, Hristov, Peneva, 2017

Nomenclature:

Enchodelus signyensis Loof, 1975

Family Qudsianematidae

Eudorylaimus coniceps Loof, 1975

Eudorylaimus pseudocarteri Loof, 1975

Eudorylaimus spaulli Loof, 1975

Eudorylaimus verrucosus Loof, 1975

Eudorylaimus cf. *carteri* Andrassy, 1959 (Bastian, 1865)

Family Pararhyssocolpidae

Pararhyssocolpus paradoxus (Loof, 1975) Elshishka, Lazarova, Radoslavov, Hristov, Peneva, 2015

Nomenclature:

Eudorylaimus paradoxus Loof, 1975|*Rhyssocolpus paradoxus* (Loof, 1975) Andrassy, 1986

Family Dorylaimidae

***Calcaridorylaimus signatus* (Loof, 1975) Andrásy, 1981**

Nomenclature:

Mesodorylaimus signatus Loof, 1975

***Mesodorylaimus antarcticus* Nedelchev and Peneva, 2000**

***Mesodorylaimus chipevi* Nedelchev and Peneva, 2000**

***Mesodorylaimus imperator* Loof, 1975**

***Mesodorylaimus masleni* Nedelchev and Peneva, 2000**

Family Aporcelaimidae

***Amblydorylaimus isokaryon* (Loof, 1975) Andrásy, 1998**

Nomenclature:

Eudorylaimus isokaryon Loof, 1975

Order Aphelenchida

Family Aphelenchoididae

***Aphelenchoides haguei* Maslen, 1979**

***Aphelenchoides vaghani* Maslen, 1979**

***Laimaphelenchus helicoma* (Maslen, 1979) Peneva and Chipev, 1999**

Nomenclature:

Aphelenchoides helicoma Maslen, 1979

Order Alaimida

Family Amphidelidae

Paramphidelus antarcticus Tsalolikhin, 1989

Order Monhysterida

Family Monhysteridae

Eumonhystera filiformis (Bastian, 1865) Andrásy, 1981

Eumonhystera vulgaris (de Man, 1880) Andrásy, 1981

Geomonhystera villosa (Bütschli, 1873) Andrásy, 1981

Order Plectida

Family Plectidae

Plectus antarcticus de Man, 1904

Plectus cf. *antarcticus* de Man, 1904

Plectus belgicae de Man, 1904

Plectus cf. *belgicae* de Man, 1904

Plectus insolens Andrásy, 1998

Plectus tolerans Andrásy, 1998

Plectus cf. *tolerans* Andrásy, 1998

Plectus meridianus Andrásy, 1998

Plectus cf. *meridianus* Andrásy, 1998

***Plectus armatus* Bütschli, 1873**

Nomenclature:

Ceratoplectus armatus (Bütschli, 1873) Andrásy, 1984

Order Tylenchida**Family Psilenchidae*****Antarctenchus hooperi* Spaul, 1972****Family Anguinidae*****Ditylenchus parcevivens* Andrásy, 1998****Order Rhabditida****Family Teratocephalidae*****Teratocephalus tilbrooki* Maslen, 1979*****Teratocephalus pseudolirellus* Maslen, 1979*****Teratocephalus rugosus* Maslen, 1979****Family Cephalobidae*****Acrobeloides arctowskii* Holovachov and Boström, 2006*****Cervidellus* cf. *vexilliger* (de Man, 1880) Thorne, 1937****Family Rhabditidae*****Cuticularia firmata* Andrásy, 1998*****Rhabditis krylovi* Tsalolikhin, 1989*****Rhabditis marina*-group**

Family Peloderidae

Pelodera teres-group

Pelodera strongyloides-group

Pelodera parateres-group

Order Mononchida

Family Mononchidae

Coomansus gerlachei (de Man, 1904) Jairajpuri and Khan, 1977

Nomenclature:

Mononchus gerlachei de Man, 1904|*Clarkus gerlachei* (de Man, 1904) Jairajpuri, 1970

Analysis

Results

To date, 44 species of terrestrial nematodes, belonging to 21 genera, 16 families and eight orders have been recorded in the Maritime Antarctic (Table 1, Fig. 1). Nematodes have been reported from 34 islands and three sites on the Antarctic Peninsula (Fig. 2). Several groups of islands/sites have been revealed, based on their nematode fauna. Those groups form a gradient from north (the group of Livingston, King George and Signy Islands) to south (the group of Adelaide, Charcot, Alexander, Leonie and Alameda Islands).

The order Dorylaimida is the best represented order in this Antarctic Region with five families, six genera and 13 species. The order Mononchida is represented by only one family (one genus and species).

The families Aphelenchoididae, Cephalobidae, Monhysteridae, Plectidae, Qudsianematidae, Peloderidae and Rhabditidae have a cosmopolitan distribution and, in the Maritime Antarctic, they are represented by one to two genera and two to ten species. The family Plectidae is the most diverse (10 species). Seven families (Amphidelidae, Anguinidae, Aporcelaimidae, Mononchidae, Nordiidae, Pararhyssocolpidae and Psilenchidae) are represented by only one species each.

Almost all species and four genera (*Antarctenchus*, *Pararhyssocolpus*, *Amblydorylaimus* and *Enchodeloides*) are endemic. Four species generally known as cosmopolitan are reported in some ecological studies in the Maritime Antarctic: *Eumonhystera vulgaris* (de Man 1880) Andr ssy (1981), *E. filiformis* (Bastian 1865) Andr ssy (1981), *Geomonhystera*

villosa (Bütschli 1873) Andrassy (1981) and *Plectus armatus* Bütschli 1873. Of these, a description and illustrations were provided only for *E. vulgaris* (Tsalolikhin 1989).

Table 1. Distribution of terrestrial nematodes in the Maritime Antarctic. * Taxonomic paper; ** Paper with molecular data; ***Paper with molecular and morphologica data Terrestrial reference sites (SIRS) at Signy Island for long-term monitoring of the various biotic and abiotic components of Antarctic moss-peat communities (for full descriptions, see Tilbrook (1973)). These sites no longer exist and no studies have been done since the late 1980s. SIRS 1 (<i>Polytrichastrum alpinum</i> (Hedwig), <i>Chorisodontium aciphyllum</i> (Hook. f. & Wilson) Broth. (60°43.5'S, 45°35.6'W)) SIRS 2 (<i>Sanionia uncinata</i> (Hedw.), <i>Warnstorfia sarmentosa</i> (Wahlenb.), <i>Warnstorfia laculosa</i> (Müll. Hal.), <i>Cephaloziella varians</i> (Gottsche) Steph. (60°43.7'S, 45°36'W)) ¹ Geographical coordinates according to original paper. ² Geographical coordinates additionally added.				
Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
<i>Enchodeloides signyensis</i>	Signy Island (type locality) ^{1,2} 60°43'S, 45°38'W	<i>Syntrichia filaris</i> (Müll. Hal.) (type habitat); <i>D. antarctica</i> ; <i>C. quitensis</i>		Loof (1975) *
				Maslen (1979b)
		SIRS 1; SIRS 2		Caldwell (1981)
		SIRS 1; SIRS 2		Maslen (1981)
	Alamode Island ^{1,2} 68°43'S, 67°32'W	<i>S. uncinata</i>		Loof (1975)*
				Maslen (1979b)
		Moss		Maslen and Convey (2006)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat		Maslen and Convey (2006)
	Alexander Island ¹ 71°52'40"S, 68°15'57"W			Convey and Wynn-Williams (2002)
	Blaiklock Island ^{1,2} 67°33'S, 67°00'W	<i>P. alpinum</i> , <i>Pohlia nutans</i> (Hedw.)		Loof (1975) *

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
				Maslen (1979b)
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Charcot Island ^{1,2} 69°45'S, 75°15'W	Soil, moss clumps, algae, various lichens		Convey et al. (2000)
		Moss, lichen, soil		Maslen and Convey (2006)
	Dream Island ² 64°44'0"S, 64°14'0"W	Moss mats with green algae		Shishida and Ohyama (1989)*
	Elephant Island ^{1,2} 61°10'S, 55°14'W	<i>D. antarctica</i> ; <i>Polytrichum</i> sp.		Loof (1975)*
				Maslen (1979b)
	Galindez Island ^{1,2} 65°15'S, 64°15'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	King George Island ¹ 62°09'32"S, 58°27'58"W	<i>D. antarctica</i> , <i>C. quitensis</i> , <i>Sanionia</i> sp., <i>S. filaris</i> , <i>Syntrichia magellanica</i> (Mont.)		Russell et al. (2014)
	King George Island ² 62°2'S, 58°21'W	Moist brown soil without vegetation, surrounded by moss	18S rDNA KY881720.1 28S rDNA KY881719.1	Elshishka et al. (2017)***
	Livingston Island ² 62°36'S, 60°30'W	<i>D. antarctica</i> ; <i>D. antarctica</i> + <i>S. uncinata</i> ; <i>D. antarctica</i> + <i>S. uncinata</i> + <i>C. quitensis</i> ; <i>P. alpinum</i> ; <i>S. uncinata</i> ; <i>Bryum</i> sp.; <i>Usnea</i> sp.+ <i>P. alpinum</i> ; <i>Cladonia</i> sp.+ <i>S. uncinata</i> + <i>P. alpinum</i> ; <i>Polytrichum juniperinum</i> Hedw.+ <i>S. uncinata</i> ; <i>S. uncinata</i> + <i>Bartramia patens</i> Brid.		Peneva et al. (2002)*
				Elshishka et al. (2015a)
		Moss; Soil under moss crust; Soil		Elshishka et al. (2017)*

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
<i>Eudorylaimus coniceps</i>	Signy Island (type locality) ^{1,2} 60°43'S, 45°38'W	<i>S. filaris</i> (type habitat); <i>Andreaea gainii</i> Card.; <i>C. quitensis</i> ; <i>W. laculosa</i> and <i>W. sarmentosa</i>		Loof (1975)*
		SIRS 1		Maslen (1979b)
		SIRS 2		Maslen (1981)
		<i>Andreaea</i> sp.		Pickup (1988)
				Wharton and Block (1993)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat		Maslen and Convey (2006)
	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	Charcot Island ^{1,2} 69°45'S, 75°15'W	Soil, moss clumps, algae, various lichens		Convey et al. (2000)
		Moss, lichen, soil		Maslen and Convey (2006)
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Elephant Island ^{1,2} 61°10'S, 55°14'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Emperor Island ^{1,2} 67°52'S, 68°43'W	<i>S. uncinata</i> and <i>Bryum pseudotriquetrum</i> (Hedw.)		Loof (1975)*
				Maslen (1979b)
	Guebriant Island ² 67°48'S, 68°25'W			Maslen (1979b)
	Halfmoon Island ¹ 62°35'45"S, 59°54'06"W			Russell et al. (2014)
	King George Island ² 62°2'S, 58°21'W	Mosses		Kito (2009)
	King George Island ¹ 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			Russell et al. (2014)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Leonie Island ² 67°36'S, 68°21'W	Mixture of soil, moss, lichen, liverworts, algae and cyanobacteria	18S rDNA LC457670.1 LC457669.1 LC457668.1 LC457667.1 LC457666.1 LC457665.1 LC457664.1 LC457663.1 LC457662.1 LC457647.1 LC457646.1 LC457645.1	Kagoshima et al. (2019) **
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>E. pseudocarteri</i>	Signy Island (type locality) ¹ 60°43'S, 45°38'W	<i>A. gainii</i> (type habitat); <i>W. laculosa</i> and <i>W. sarmentosa</i> ; <i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
		SIRS 1; SIRS 2		Maslen (1981)
		<i>Andreaea</i> sp.		Pickup (1988)
				Wharton and Block (1993)
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen		Maslen and Convey (2006)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat, freshwater		
	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	Charcot Island ^{1,2} 69°45'S, 75°15'W	Moss, lichen, soil		Maslen and Convey (2006)
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Elephant Island ^{1,2} 61°10'S, 55°14'W	<i>Polytrichum</i> sp.		Loof (1975)*
				Maslen (1979b)
	King George Island ² 62°2'S, 58°21'W	Puddle		Tsalolikhin (1989)*

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W			Russell et al. (2014)
	Livingston Island ¹ 62°39'14"S, 60°36'39"W			
<i>E. spaulii</i>	Alamode Island (type locality) ^{1,2} 68°43'S, 67°32'W	Soil around <i>S. uncinata</i> (type habitat)		Loof (1975)*
		Moss, lichen, soil, microbial mat		Maslen and Convey (2006)
				Maslen (1979b)
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen		Maslen and Convey (2006)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat		
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		
	Blaiklock Island ^{1,2} 67°33'S, 67°00'W	<i>P. alpinum</i> , <i>Pohlia nutans</i>		Loof (1975)*
				Maslen (1979b)
	Charcot Island ^{1,2} 69°45'S, 075°15'W	Soil, moss clumps, algae, various lichens		Convey et al. (2000)
		Moss, lichen, soil		Maslen and Convey (2006)
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Deception Island ² 62°58'37"S, 60°39'0"W			Maslen (1979b)
	Elephant Island ^{1,2} 61°10'S, 55°14'W	<i>D. antarctica</i> ; <i>Polytrichum</i> sp.		Loof (1975)*
				Maslen (1979b)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Limpet Island ^{1,2} 67°38'S, 68°19'W	<i>S. uncinata</i>		Loof (1975)*

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
				Maslen (1979b)
	Pourquoi pas Island ² 67°41'S, 67°28'W			Maslen (1979b)
	Signy Island ^{1,2} 60°43'S, 45°38'W	<i>S. filaris</i> <i>B. pseudotriquetrum</i> ; <i>D. antarctica</i> ; <i>W. laculosa</i> and <i>W. sarmentosa</i>		Loof (1975)*
				Wharton and Block (1993)
		<i>Andreaea</i> sp.		Pickup (1988)
				Maslen (1979b)
		SIRS 2		Maslen (1981)
<i>E. verrucosus</i>	Elephant Island (type locality) ^{1,2} 61°10'S, 55°14'W	<i>D. antarctica</i> (type habitat)		Loof (1975)*
				Maslen (1979b)
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen, soil, microbial mat		Maslen and Convey (2006)
	Signy Island ¹ 60°43'S, 45°38'W			Maslen (1979b)
		SIRS 1; SIRS 2		Maslen (1981)
				Wharton and Block (1993)
<i>Eudorylaimus</i> cf. <i>carteri</i>	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>Pararhysocolpus paradoxus</i>	Signy Island (type locality) ¹ 60°43'S, 45°38'W	<i>A. gainii</i> (type habitat); <i>S. filaris</i>		Loof (1975)*
				Maslen (1979b)
		SIRS 1; SIRS 2		Maslen (1981)
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen, soil, microbial mat		Maslen and Convey (2006)
	Adelaide Island ¹ 67°34.429'S, 68°07.284'W	<i>C. varians</i> and <i>S. uncinata</i>		Newsham et al. (2020)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Blaiklock Island ^{1,2} 67°33'S, 67°00'W			Maslen (1979b)
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Elephant Island ^{1,2} 61°10'S, 55°14'W	<i>S. uncinata</i>		Loof (1975)*
				Maslen (1979b)
	Galindez Island ^{1, 2} 65°15'S, 64°15'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Guebriant Island ² 67°48'S, 68°25'W			Maslen (1979b)
	Intercurrence Island ^{1,2} 63°55'S, 61°24'W	<i>Brachythecium</i> sp.		Loof (1975)*
				Maslen (1979b)
	King George Island ² 62°2'S, 58°21'W			Kito (2009)
		Soil	18S rDNA KM092521.1 28S rDNA KM092522.1	Elshishka et al. (2015b) ***
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			Russell et al. (2014)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Nelson Island ² 62°18'S, 59°3'W	Moss		Elshishka et al. (2015b)*
<i>Calcaridorylaimus signatus</i>	Signy Island (type locality) ¹ 60°43'S, 45°38'W	<i>S. filaris</i> (type habitat); <i>B. pseudotriquetrum</i> ; <i>C. quitensis</i> ; <i>D. antarctica</i> ; <i>Prasiola crispa</i> (Lightfoot)		Loof (1975)*
				Maslen (1979b)
		SIRS1		Caldwell (1981)
		SIRS 1; SIRS 2		Maslen (1981)
		Soil, moss, lichen, liverworts, algae and cyanobacteria	18S rDNA LC457654.1 LC457653.1 LC457652.1 LC457651.1 LC457650.1 LC457649.1 LC457648.1	Kagoshima et al. (2019) **
	Alamode Island ² 68°43'S, 67°32'W	Moss, lichen, soil		Maslen and Convey (2006)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat		
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		
	Anvers Island, Biscoe Point ² 64°49'6.85"S, 63°46'32.29"W	Soil around roots of <i>D. antarctica</i>		Shishida and Ohyama (1989)*
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Dream Island ² 64°44'0"S, 64°14'0"W	Moss mats with green algae		Shishida and Ohyama (1989)*
	Galindez Island ^{1,2} 65°15'S, 64°15'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
<i>Mesodorylaimus antarcticus</i>	Livingston Island (type locality) ¹ 62°39'22"S, 60°21'13"W	<i>Sanionia</i> sp. (type habitat); <i>D. antarctica</i> ; <i>D. antarctica</i> - <i>Polytrichum</i> sp.; A small moss tuft <i>Sanionia</i> sp.; A mix grass-moss spot <i>D. antarctica</i> + <i>Sanionia</i> sp.		Nedelchev and Peneva (2000)*
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W			Russell et al. (2014)
	Neko Harbour, Antarctic Peninsula ¹ 64°50'41"S, 62°31'53"W			
<i>M. chipevi</i>	Livingston Island (type locality) ¹ 62°34'48"S, 60°20'42"W	<i>D. antarctica</i> on the top of flat rock near sea (type habitat); Shallow soil with cover of green algae amongst grass on a rock; Small tuft of <i>D. antarctica</i> ; <i>Polytrichum</i> sp.+ <i>S. uncinata</i> + <i>D. antarctica</i> ; A mix grass-moss spot <i>D. antarctica</i> + <i>Sanionia</i> sp.; A large pure grass spot <i>D. antarctica</i>		Nedelchev and Peneva (2000)*
	Livingston Island ¹ 62°38'52"S, 60°22'24"W	<i>S. georgico-uncinata</i> Müll. Hal. + <i>D. antarctica</i>		Nedelchev and Peneva (2007)*
	King George Island ¹ 62°09'32"S, 58°27'58"W			Russell et al. (2014)
<i>M. imperator</i>	Emperor Island (type locality) ^{1,2} 67°52'S, 68°43'W	<i>S. uncinata</i> and <i>B. pseudotriquetrum</i> (type habitat)		Loof (1975)*
				Maslen (1979b)
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen, soil		Maslen and Convey (2006)
	Alamode Island ² 68°43'S, 67°32'W	Moss		
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, grass, lichen, soil, microbial mat, freshwater		
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Charcot Island ^{1,2} 69°45'S, 075°15'W	Soil, moss clumps, algae, various lichens		Convey et al. (2000)
	Cone Island ^{1,2} 67°41'S, 69°10'W	<i>S. uncinata</i>		Loof (1975)*

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
				Maslen (1979b)
	Killinbeck Island ² 67°34'S, 68°5'W	Moss, lichen, soil		Maslen and Convey (2006)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		
<i>M. masleni</i>	Livingston Island (type locality) ¹ 62°39'46"S, 60°23'29"W	A large area of <i>D. antarctica</i> (type habitat); A mix grass-moss spot <i>D. antarctica</i> + <i>Sanionia</i> sp.		Nedelchev and Peneva (2000)*
<i>Amblydorylaimus isokaryon</i>	Elephant Island (type locality) ^{1,2} 61°10'S, 55°14'W	<i>D. antarctica</i> (type habitat); <i>Polytrichum</i> sp.		Loof (1975)*
				Maslen (1979b)
	Galindez Island ^{1,2} 65°15'S, 64°15'W	<i>D. antarctica</i>		Loof (1975)*
				Maslen (1979b)
	Intercurrence Island ^{1,2} 63°55'S, 61°24'W	<i>Brachythecium</i> sp.		Loof (1975)*
				Maslen (1979b)
	King George Island ² 62°2'S, 58°21'W			Kito (2009)
		Soil		Elshishka et al. (2015b)*
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
		Grass spot (<i>D. antarctica</i>); a moss- grass (<i>D. antarctica</i> - <i>Polytrichum</i> sp.) community; <i>S. georgico-uncinata</i> and <i>D. antarctica</i> ; <i>C. quitensis</i> and <i>D. antarctica</i> , moss; <i>D. antarctica</i> and <i>C. quitensis</i>		Elshishka et al. (2015b)*
	Nelson Island ² 62°18'S, 59°3'W	Moss	18S rDNA KM092519.1 28S rDNA KM092520.1	Elshishka et al. (2015b) ***
<i>Aphelenchoides haguei</i>	Signy Island (type locality) ¹ 60°43'S, 45°38'W	SIRS 1 (type habitat); SIRS 2		Maslen (1979a)*
		SIRS 1; SIRS 2		Maslen (1981)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen		Maslen and Convey (2006)
	Adelaide Island ¹ 67°34.429'S, 68°07.284'W	<i>C. varians</i> and <i>S. uncinata</i>		Newsham et al. (2020)
	Alamode Island ² 68°43'S, 67°32'W	Moss		Maslen and Convey (2006)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat		
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		
	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	Deception Island ¹ 62°58'42"S, 60°33'29"W			
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			Russell et al. (2014)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Livingston Island ¹ 62°39'14"S, 60°36'39"W	Soil		Russell et al. (2014)
<i>A. vaughani</i>	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Signy Island (type locality) ¹ 60°43'S, 45°38'W	SIRS 1; SIRS 2		Maslen (1979a)*
		SIRS 1; SIRS 2		Maslen (1981)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
<i>Laimaphelenchus helicosoma</i>	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Signy Island (type locality) ¹ 60°43'S, 45°38'W	SIRS 1 (type habitat); SIRS 2		Maslen (1979a)*
		SIRS 1		Maslen (1981)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen		Maslen and Convey (2006)
	Adelaide Island ¹ 67°34.429'S, 68°07.284'W	<i>C. varians</i> and <i>S. uncinata</i>		Newsham et al. (2020)
	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	King George Island ¹ 62°09'32"S, 58°27'58"W 62°11'48"S, 58°59'28"W 62°11'50"S, 58°56'33"W			Russell et al. (2014)
	Livingston Island, ¹ 62°38'S, 60°20'W	Primitive soil around roots of <i>D. antarctica</i>		Peneva and Chipev (1999)*
<i>Paramphidelus antarcticus</i>	King George Island (type locality) ² 62°2'S, 58°21'W	Lichen (type habitat)		Tsalolikhin (1989)*
<i>Eumonhystera filiformis</i>	King George Island ¹ 62°09'S, 58°29'W	Thaw ponds, with the bottom inhabited by <i>W. sarmentosa</i>		Janiec (1996)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>E. vulgaris</i>	King George Island ¹ 62°09'S, 58°29'W	Puddle		Tsalolikhin (1989)*
		Moraine ponds, their shores are inhabited mainly by <i>S. uncinata</i> , <i>W. sarmentosa</i> and <i>B. pseudotriquetrum</i> ; Moss banks of <i>W. sarmentosa</i> and <i>W. laculosa</i> ; Thaw ponds, with the bottom inhabited by <i>W. sarmentosa</i> ; Nearshore ponds, colonised by <i>W. laculosa</i> and <i>W. sarmentosa</i>		Janiec (1996)
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			Russell et al. (2014)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>Geomonhystera villosa</i>	Coronation Island ^{1,2} 60°38'S, 45°35'W			Maslen (1979b)
	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Elephant Islan ^{1,2} 61°10'S, 55°14'W			Maslen (1979b)
	Galindez Island ^{1,2} 65°15'S, 64°15'W			
	Intercurrence Island ^{1,2} 63°55'S, 61°24'W			
	King George Island ¹ 62°09'S, 58°29'W	<i>W. sarmentosa</i> and <i>W. laculosa</i>		Janiec (1996)
	King George Island ¹ 62°11'48"S, 58°59'28"W 62°11'50"S, 58°56'33"W 62°11'53"S, 58°56'47"W			Russell et al. (2014)
	Livingston Island ¹ 62°39'14"S, 60°36'39"W			
	Neko Harbour, Antarctic Peninsula ¹ 64°50'41"S, 62°31'53"W			
	Signy Island ¹ 60°43'S, 45°38'W			Maslen (1979b)
		SIRS 1		Caldwell (1981)
		SIRS 1; SIRS 2		Maslen (1981)
		Mixture of soil, moss, lichen, liverworts, algae and cyanobacteria	18S rDNA LC457677.1 LC457676.1 LC457675.1 LC457674.1 LC457673.1 LC457672.1 LC457671.1	Kagoshima et al. (2019)
<i>Plectus antarcticus</i>	Danco Land coast, Beneden Head, Antarctic Peninsula (type locality) ² 64°46'S, 62°42'W	Freshwater algae (type habitat)		de Man (1904)*
				Maslen (1979b)
		Moss from rock		Andrássy (1998)*
	Adelaide Island ¹ 67°34'S, 68°07'W	Moss, lichen, soil, microbial mat		Maslen and Convey (2006)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
		<i>Cephaloziella varians</i> (Gottsche)	18S rDNA LC457559.1 LC457558.1 LC457557.1 LC457556.1 LC457555.1 LC457554.1	Kagoshima et al. (2019) **
	Adelaide Island ¹ 67°34.429'S, 68°07.284'W	<i>C. varians</i> and <i>S. uncinata</i>		Newsham et al. (2020)
	Alamode Island ² 68°43'S, 67°32'W			Spaull (1973a)
				Maslen (1979b)
		Moss		Maslen and Convey (2006)
	Alexander Island, ¹ 71°52'40"S, 68°15'57"W			Convey and Wynn-Williams (2002)
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat		Maslen and Convey (2006)
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		
	Avian Island ² 67°46"S, 68°54"W			Spaull (1973a)
	Blaiklock Island ^{1,2} 67°33'S, 67°00'W			Maslen (1979b)
	Charcot Island ^{1,2} 69°45'S, 075°15'W	Soil, moss clumps, algae, various lichens		Convey et al. (2000)
		Moss, lichen, soil		Maslen and Convey (2006)
	Cone Island ^{1,2} 67°41'S, 69°10'W			Maslen (1979b)
	Coronation Island ^{1,2} 60°38'S, 45°35'W			
	Deception Island ² 62°58'37"S, 60°39'0"W	Moss from basalt debris		Andrássy (1998)*
				Maslen (1979b)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Deception Island ¹ 62°58'43"S, 60°33'24"W	Only erratic patches of mosses, lichens and algae		Russell et al. (2014)
	Devil Island ¹ 63°47'54"S, 57°17'24"W	Soil substrates of the very sandy with embedded gravel		
	Elephant Island ^{1,2} 61°10'S, 55°14'W			Spaull (1973a)
				Maslen (1979b)
		<i>S. uncinata</i>		Andrássy (1998)*
	Emperor Island ² 67°52'S, 68°43'W			Spaull (1973a)
	Galindez Island ^{1,2} 65°15'S, 64°15'W			Maslen (1979b)
	Guebriant Island ² 67°48'S, 68°25'W			
	Intercurrence Island ^{1,2} 63°55'S, 61°24'W			Spaull (1973a)
				Maslen (1979b)
	Killingbeck Island ² 67°34'S, 68°5'W	Moss, lichen, soil		Maslen and Convey (2006)
	King George Island ² 62°2'S, 58°21'W	Soil around rhizosphere of grasses and under lichen		Tsalolikhin (1989)*
	King George Island ¹ 62°09'S, 58°29'W	Moraine ponds, their shores are inhabited mainly by <i>S. uncinata</i> , <i>W. sarmentosa</i> and <i>B. pseudotriquetrum</i> ; Moss banks of <i>W. sarmentosa</i> and <i>W. laculosa</i>		Janiec (1996)
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W	Mosses, lichens, <i>D. antarctica</i>		Russell et al. (2014)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Limpet Island ^{1,2} 67°38'S, 68°19'W			Maslen (1979b)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Pourquoui pas Island ² 67°41'S, 67°28'W			Maslen (1979b)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Signy Island ¹ 60°43'S, 45°38'W			Spaull (1973a)
				Spaull (1973b)
				Spaull (1973c)
				Maslen (1979b)
		SIRS 1; SIRS 2		Maslen (1981)
		SIRS1; SIRS2		Caldwell (1981)
		<i>Andreaea</i> sp.		Pickup (1988)
				Wharton and Block (1993)
<i>Plectus</i> cf. <i>antarcticus</i>	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Signy Island ² 60°43'S, 45°36'W	Mixture of soil, moss, lichen, liverworts, algae and cyanobacteria	18S rDNA LC457687.1 LC457686.1	Kagoshima et al. (2019)
<i>P. belgicae</i>	Cap Beneden, Danco Land, Antarctic Peninsula (type locality) ² 64°46"S, 62°42"W	Algae fresh water (type habitat)		de Man (1904)*
	Adelaide Island ¹ 67°34'S, 68°07'W	Moss, lichen, soil, microbial mat		Maslen and Convey (2006)
		<i>C. varians</i>	18S rDNA LC457565.1 LC457564.1 LC457563.1 LC457562.1 LC457561.1 LC457560.1	Kagoshima et al. (2019)
	Adelaide Island ¹ 67°34.429'S, 68°07.284'W	<i>C. varians</i> and <i>S. uncinata</i>		Newsham et al. (2020)
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Charcot Island ^{1, 2} 69°45'S, 075°15'W	Moss, lichen, soil		
	Elephant Island ^{1, 2} 61°10'S, 55°14'W	<i>P. juniperinum</i> ; <i>S. uncinata</i>		Andrássy (1998)*
	King George Island ² 62°2'S, 58°21'W	<i>B. pseudotriquetrum</i> and <i>Bartramia patens</i>	18S rDNA LC457638.1 LC457637.1 LC457636.1	Kagoshima et al. (2019)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Rhyolite Island, ² 69°40'S, 68°35'W	Moss, grass		Maslen and Convey (2006)
	Signy Island ² 60°43'S, 45°36'W	<i>Acrocladium</i> sp.; <i>Usnea</i> sp.; SIRS 2		Andrássy (1998)*
<i>Plectus</i> cf. <i>belgicae</i>	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	Deception Island ¹ 62°58'43"S, 60°33'24"W; 62°58'42"S, 60°33'29"W			
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			
	Livingston Island ¹ 62°39'14"S, 60°36'39"W			
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Petermann Island ¹ 65°10'29"S, 64°08'10"W			Russell et al. (2014)
<i>P. insolens</i>	Signy Island (type locality) ² 60°43'S, 45°36'W	Thin soil on rock covered with <i>Acrocladium</i> sp. (type habitat); roots of <i>D. antarctica</i>		Andrássy (1998)*
	Ardley Island ¹ 62°12'38"S, 58°56'40"W	Soils, <i>Sanionia</i> sp., <i>W. sarmentosa</i> and <i>Andreaea regularis</i> Müll. Hal.		Russell et al. (2014)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>P. tolerans</i>	Emperor Island (type locality) ² 67°52'S, 68°43'W	<i>S. uncinata</i> (type habitat)		Andrássy (1998)*
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		
	Charcot Island ^{1,2} 69°45'S, 075°15'W	Moss, lichen, soil		
	King George Island ² 62°2'S, 58°21'W			Kito (2009)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Rhyolite Island ² 69°40'S, 68°35'W	Moss, grass		Maslen and Convey (2006)
<i>Plectus</i> cf. <i>tolerans</i>	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			
	Livingston Island ¹ 62°39'14"S, 60°36'39"W			
<i>P. meridianus</i>	Terra Firma Island (type locality) ² 68°42'S, 67°32'W	Lichen (type habitat)		Andrássy (1998)*
	Emperor Island ² 67°52'S, 68°43'W	A carpet of <i>S. uncinata</i>		
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Signy Island ² 60°43'S, 45°36'W	Roots of <i>D. antarctica</i>		Andrássy (1998)*
<i>Plectus</i> cf. <i>meridianus</i>	Signy Island ² 60°43'S, 45°36'W	Soil, moss, lichen, liverworts, algae and cyanobacteria	18S rDNA LC457691.1 LC457690.1 LC457689.1 LC457688.1	Kagoshima et al. (2019)
<i>P. armatus</i>	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	Coronation Island ² 60°38'S, 45°35'W			Maslen (1979b)
	Elephant Island ² 61°10'S, 55°14'W			

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Galindez Island ² 65°15'S, 64°15'W			
	King George Island ¹ 62°11'48"S, 58°59'28"W			Russell et al. (2014)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Signy Island ¹ 60°43'S, 45°38'W	<i>D. antarctica</i> ; <i>C. quitensis</i> ; mosses		Spaull (1973b)
				Spaull (1973c)
				Maslen (1979b)
<i>Antarctenchus hooperi</i>	Signy Island (type locality) ^{1,2} 60°43'S, 45°38'W	<i>A. gainii</i> (type habitat); <i>Brachythecium</i> sp., <i>Calliergon</i> sp., <i>S. filaris</i> , <i>Grimmia antarctici</i> Card., <i>Ch. aciphyllum</i> , <i>P. juniperinum</i> and <i>D. antarctica</i>		Spaull (1972)*
		<i>Sanionia</i> sp.+ <i>Calliergon</i> sp.+ <i>Calliergidium</i> sp.; <i>Polytrichum</i> sp.; <i>Bryum</i> sp. + <i>Syntrichia</i> sp. + <i>Andreaea</i> sp.; <i>D. antarctica</i>		Spaull (1973a)
		<i>A. gainii</i> , <i>S. filaris</i> , <i>Calliergon-Calliergidium</i>		Spaull (1973b)
				Spaull (1973c)
				Maslen (1979b)
		SIRS 1; SIRS 2		Maslen (1981)
		<i>S. uncinata</i>		Caldwell (1981)
				Wharton and Block (1993)
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Spaull (1972)*
		<i>D. antarctica</i>		Spaull (1973a)
				Maslen (1979b)
<i>Ditylenchus parcevivens</i>	Signy Island (type locality) ² 60°43'S, 45°38'W	Fine silt (type habitat)		Andrássy (1998)*

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			Russell et al. (2014)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>Teratocephalus tilbrookii</i>	Signy Island (type locality) ^{1,2} 60°43'S, 45°38'W	SIRS 1 (type habitat); SIRS2		Maslen (1979a)*
		'Swamp' moss carpets		Maslen (1979b)
		SIRS 1; SIRS 2		Maslen (1981)
		<i>Andreaea</i> sp.		Pickup (1988)
				Wharton and Block (1993)
		<i>Usnea</i> sp.		Andrássy (1998)*
	Adelaide Island ² 67°15'S, 68°30'W	Moss, lichen		Maslen and Convey (2006)
	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	Charcot Island ^{1, 2} 69°45'S, 075°15'W	Moss, lichen, soil		Maslen and Convey (2006)
	Halfmoon Island ¹ 62°35'45"S, 59°54'06"W	Soil		Russell et al. (2014)
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W	Soil		
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
<i>T. pseudolirellus</i>	Signy Island (type locality) ¹ 60°43'S, 45°38'W	<i>S. filaris</i> (type habitat)		Maslen (1979a)*
	Alexander Island ² 71°0'0"S, 70°0'0"W	Moss, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Charcot Island ² 69°45'S, 075°15'W	Moss, lichen, soil		

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	King George Island ² 62°2'S, 58°21'W			Kito (2009)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>T. rugosus</i>	Signy Island (type locality) ² 60°43'S, 45°38'W	SIRS 1; SIRS 2		Maslen (1979a)*
				Maslen (1979b)
		SIRS 1; SIRS 2		Maslen (1981)
	Ardley Island ¹ 62°12'38"S, 58°56'40"W			Russell et al. (2014)
	Deception Island ¹ 62°58'42"S, 60°33'29"W			
	Devil Island ¹ 63°47'54"S, 57°17'24"W			
	Halfmoon Island ¹ 62°35'45"S, 59°54'06"W			
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'53"S, 58°56'47"W			
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
<i>Acrobeloides arctowski</i>	King George Island (type locality) ¹ 58°29'30"W, 61°05'S	Soil around roots of <i>D. antarctica</i> (type habitat)		Holovachov and Bostrom (2006)*
	King George Island ¹ 62°09'32"S, 58°27'58"W			Russell et al. (2014)
	Deception Island ¹ 62°58'43"S, 60°33'24"W; 62°58'42"S, 60°33'29"W	Soil devoid of vegetation or with <i>P. crista</i>		
<i>Cervidellus</i> cf. <i>vexilliger</i>	King George Island ¹ 62°09'32"S, 58°27'58"W			Russell et al. (2014)
<i>Cuticularia firmata</i>	Signy Island (type locality) ² 60°43'S, 45°36'W	Fine mud (type habitat); SIRS 2		Andrássy (1998)*
<i>Rhabditis krylovi</i>	King George Island (type locality) ² 62°2'S, 58°21'W	Flowing lake (type habitat)		Tsalolikhin (1989)*
<i>Rhabditis marina</i> -group	Deception Island ¹ 62°55'43"S, 60°40'48"W			Russell et al. (2014)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
<i>Pelodera teres</i> group	Deception Island ¹ 62°58'43"S, 60°33'24"W; 62°58'42"S, 60°33'29"W			Russell et al. (2014)
	Livingston Island ¹ 62°39'14"S, 60°36'39"W			
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Neko Harbour, Antarctic Peninsula ¹ 64°50'41"S, 62°31'53"W			Russell et al. (2014)
	Paulet Island ¹ 63°34'30"S, 55°46'59"W	Ornithogenic soils		
<i>Pelodera strongyloides</i> group	Devil Island ¹ 63°47'54"S, 57°17'24"W			Russell et al. (2014)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Livingston Island ¹ 62°39'14"S, 60°36'39"W			Russell et al. (2014)
	Neko Harbour, Antarctic Peninsula ¹ 64°51'45"S, 62°26'47"W; 64°50'41"S, 62°31'53"W			
<i>Pelodera parateres</i> group	Deception Island ¹ 62°58'42"S, 60°33'29"W			Russell et al. (2014)
	King George Island ¹ 62°09'32"S, 58°27'58"W			
<i>Coomansus gerlachei</i>	Danco Land coast, Beneden Head Antarctic Peninsula (type locality) ² 64°46"S, 62°42"W	Algae fresh water (type habitat)		de Man (1904)*
				Maslen (1979b)
				Andrássy (1998)*
	Caleta Cierva, Antarctic Peninsula ¹ 64°10'S, 60°57'W	Soil around roots of <i>D. antarctica</i>		Chaves (1990)*
	Antarctic Peninsula			Jiménez Guirado et al. (1998)*
	Adelaide Island ¹ 67°34.429'S, 68°07.284'W	<i>C. varians</i> and <i>S. uncinata</i>		Newsham et al. (2020)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Anchorage Island ² 67°36'14.01"S, 68°12'32.78"W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
	Anvers Island, Biscoe Point ² 64°49'6.85"S, 63°46'32.29"W	Soil around roots of <i>D. antarctica</i>		Shishida and Ohyama (1989)*
	Anvers Island, Old Palmer ² 64°45'48"S, 64°5'12"W	Moss mats		
	Avian Island ² 67°46"S, 68°54"W	<i>Sanionia</i> sp., <i>Bryum</i> sp.		Spaull (1973a)
				Maslen (1979b)
		<i>S. uncinata</i> , <i>B. pseudotriquetrum</i>		Spaull (1981)
	Coronation Island ^{1,2} 60°38'S, 45°35'W	<i>D. antarctica</i>		Spaull (1973a)
				Maslen (1979b)
	Charcot Island ^{1,2} 69°45'S, 75°15'W	Soil, moss clumps, algae, various lichens		Convey et al. (2000)
	Deception Island ² 62°58'37"S, 60°39'0"W	<i>Sanionia</i> sp.;		Spaull (1973a)
		<i>Polytrichum</i> sp.		Maslen (1979b)
		Melting snow moisten mosses in a shingle field		Andrássy (1998)*
	Dream Island ² 64°44'0"S, 64°14'0"W	Moss mats with green algae		Shishida and Ohyama (1989)*
	Elephant Island ^{1,2} 61°10'S, 55°14'W	<i>Brachythecium</i> sp.;		Spaull (1973a)
		<i>D. antarctica</i> ;		Maslen (1979b)
		<i>Sanionia</i> sp.		Spaull (1981)
	Galindez Island ^{1,2} 65°15'S, 64°15'W	<i>Brachythecium</i> sp.;		Spaull (1973a)
		<i>D. antarctica</i> ;		Maslen (1979b)
		<i>Bryum</i> sp.;		
		<i>Sanionia</i> sp. + <i>Pohlia</i> sp.		
				Maslen (1979b)

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
		<i>Brachythecium austrosalebrosus</i> (C. Muell.) Par.		Spaull (1981)
	Guebriant Island ² 67°48'S, 68°25'W	<i>Brachythecium</i> sp., <i>Bryum</i> sp., <i>Sanionia</i> sp.		Spaull (1973a)
				Maslen (1979b)
	Intercurrence Island ^{1,2} 63°55'S, 61°24'W	<i>Brachythecium</i> sp., <i>Bryum</i> sp., <i>Sanionia</i> sp.		Spaull (1973a)
				Maslen (1979b)
	Halfmoon Island ¹ 62°35'45"S, 59°54'06"W			Russell et al. (2014)
	King George Island ¹ 62°09'S, 58°29'W	Moraine ponds, their shores are inhabited mainly by <i>S. uncinata</i> , <i>W. sarmentosa</i> and <i>B. pseudotriquetrum</i>		Janiec (1996)
	Leonie Island ² 67°36'S, 68°21'W	Moss, grass, lichen, soil, microbial mat, freshwater		Maslen and Convey (2006)
		Mixture of soil, moss, lichen, liverworts, algae and cyanobacteria	18S rDNA LC457644.1 LC457643.1 LC457642.1 LC457641.1 LC457640.1 LC457639.1	Kagoshima et al. (2019) **
	Limpet Island ^{1,2} 67°38'S, 68°19'W	<i>Brachythecium</i> sp., <i>Bryum</i> sp., <i>Sanionia</i> sp.		Spaull (1973a)
				Maslen (1979b)
	King George Island ² 62°2'S, 58°21'W			Kito (2009)
	King George Island ¹ 62°09'32"S, 58°27'58"W; 62°11'48"S, 58°59'28"W; 62°11'50"S, 58°56'33"W; 62°11'53"S, 58°56'47"W			Russell et al. (2014)
	Litchfield Island ² 64°46'S, 64°6'W	Decaying moss mats with blue-green algae		Shishida and Ohyama (1989)*
	Livingston Island ² 62°36'S, 60°30'W	Soil under crisp of green algae; <i>D. antarctica</i> - <i>S. uncinata</i> ; <i>D. antarctica</i> , <i>P. alpinum</i>		Peneva et al. (1996)*

Nematode species	Locality / Coordinates	Microhabitat and plant species	DNA / Accession number in GenBank	Reference
	Livingston Island ¹ 62°39'14"S, 60°36'39"W			Russell et al. (2014)
	Livingston Island ² 62°36'S, 60°30'W			Elshishka et al. (2015a)
	Nelson Island ² 62°18'S, 59°3'W	Moss	18S rDNA KM092523.1 28S rDNA KM092524.1	Elshishka et al. (2015b)**
	Signy Island ^{1,2} 60°43'S, 45°38'W	<i>Sanionia</i> sp. + <i>Calliergon</i> sp. + <i>Calliergidium</i> sp.; <i>Polytrichum</i> sp.; <i>Bryum</i> sp. + <i>Syntrichia</i> sp. + <i>Andreaea</i> sp.; <i>D. antarctica</i>		Spaull (1973a)
				Spaull (1973b)
				Spaull (1973c)
				Maslen (1979b)
		<i>S. uncinata</i> and <i>W. sarmentosa</i>		Caldwell (1981)
		SIRS 1; SIRS 2		Maslen (1981)
		<i>P. crispa</i> from melt stream		Spaull (1981)
		<i>Sanionia</i> sp.		Pickup (1988)
		<i>P. crispa</i> ; <i>S. uncinata</i>		Pickup (1990)
		<i>Calliergon</i> sp.		Wharton and Block (1993)
		Mixture of soil, lichen, liverworts, algae and cyanobacteria	18S rDNA LC457661.1 LC457660.1 LC457659.1 LC457658.1 LC457657.1 LC457656.1 LC457655.1	Kagoshima et al. (2019) **

Most species (27) have limited distribution registered in up to five islands of the Maritime Antarctic. *Cuticularia firmata* Andr ssy 1998, *Cervidellus* cf. *vexilliger*, *Rhabditis krylovi* Tsalolikhin 1989, a species of the *Rhabditis marina*-group, *Mesodorylaimus masleni* Nedelchev and Peneva 2000, *Eudorylaimus* cf. *carteri* and *Plectus* cf. *meridianus* are recorded from one island only. Six species occurred in more than 30% of the sites (*C.*

In most of the literature sources, there are data on the microhabitats in which nematode species occurred. The nematodes have been recorded from various microhabitats: bare soil, microbial mats, moss, lichens and algae and soil around the two species of higher plants occurring in the Maritime Antarctic (Fig. 6).

The review of the literature related to terrestrial nematodes from the Maritime Antarctic showed that the different parts are unevenly studied and three islands, Livingston (31 species), King George (28 species) and Signy (25 species) exhibited the richest nematode fauna (Fig. 7). Signy Island is the best studied Antarctic island with 12 new species

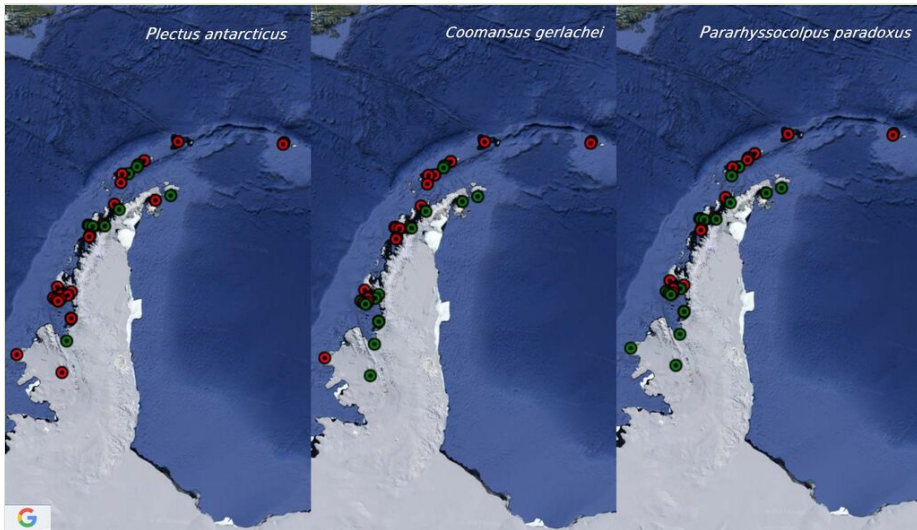


Figure 4. [doi](#)

Distribution of *P. antarcticus*, *C. gerlachei* and *Pararhyssocolpus paradoxus* in the Maritime Antarctic. In red are presented the sites with records of these species, in green are presented the sites with records of the other Antarctic terrestrial nematodes.

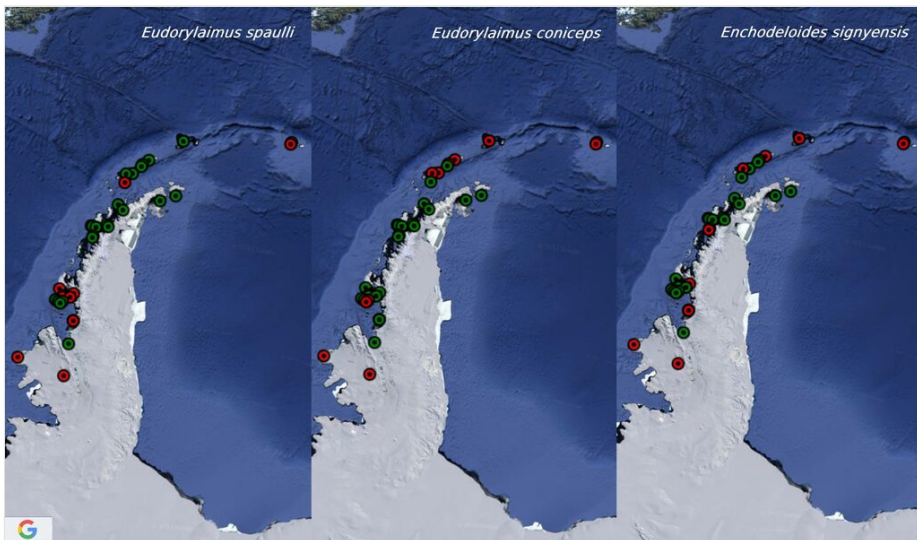


Figure 5. [doi](#)

Distribution of *Eudorylaimus spaulii*, *E. coniceps* and *Enchodeloides signyensis* in the Maritime Antarctic. In red are presented the sites with records of these species, in green are presented the sites with records of the other Antarctic terrestrial nematodes.

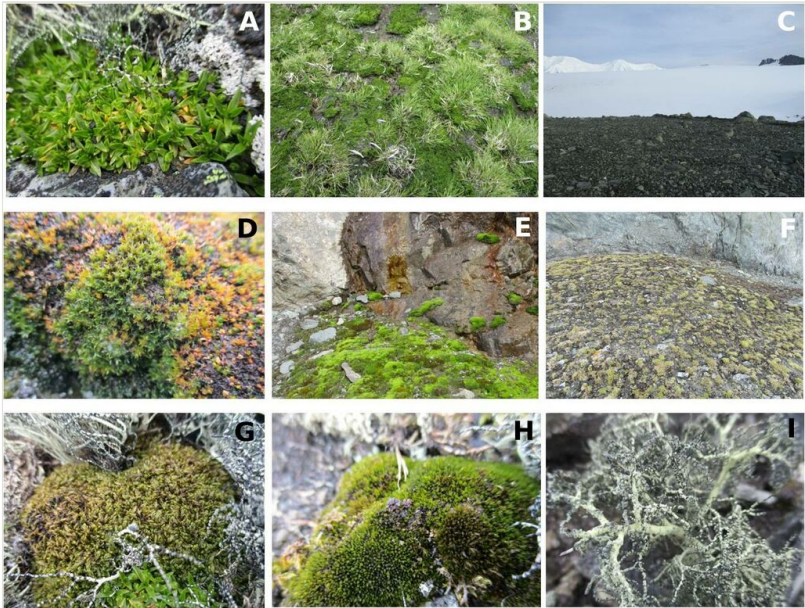


Figure 6. [doi](#)
Some microhabitats in the Maritime Antarctic. **A** *Colobanthus quitensis* **B** *Deschampsia antarctica* **C** Bare soil **D** *Syntrichia* sp. **E** *Bryum* sp. **F** *D. antarctica*, *C. quitensis*, mosses **G** *Sanionia* sp. **H** *Polytrichum* sp. **I** *Usnea* sp. Photographs by M. Elshishka (Livingston Island).

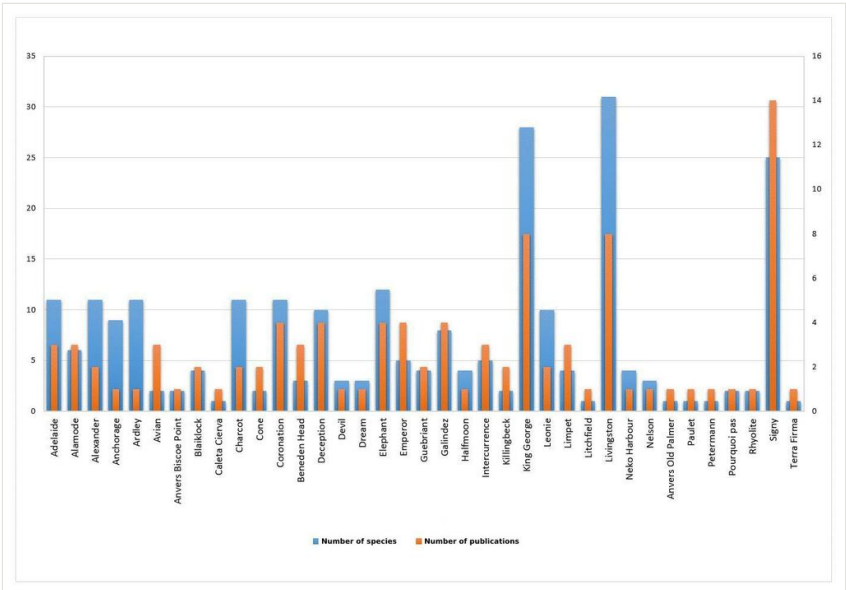


Figure 7. [doi](#)
Bar chart visualising the described species (left axis) and literature sources (right axis) per each island/site.

Discussion

Our knowledge of the nematode species diversity in the Maritime Antarctic is still insufficient and fragmented. The different study efforts at the various sites do not allow gaining a clear picture of trends in the diversity and distribution of nematode species in the target Antarctic Region. Yet, the analysis provided on the basis of species presence/absence data revealed several groups of sites with similar nematode fauna forming a latitudinal gradient (Fig. 1). The high level of endemism at both the species and genus level is a characteristic feature of the nematode fauna of the region as was mentioned above. This high degree of endemism can be explained by the long-term isolation and the harsh conditions of the region (Convey et al. 2008, Nielsen et al. 2011a). It has been suggested that the Antarctic terrestrial fauna might have survived glaciation in ice-free areas and some species might be remnants of the fauna of the Gondwana super-continent (Andrássy 1998, Maslen and Convey 2006, Chown and Convey 2016, Convey et al. 2020).

The physical isolation and harsh environment of Antarctic terrestrial ecosystems is the major reason for the difficult colonisation by non-native biota (Convey and Peck 2019). In recent decades, human visits and activities in the Antarctic have provided ways (e.g. cargo, vehicles, scientific equipment, fresh food, clothing, people) to overcome these barriers (Lee and Chown 2009, Hughes et al. 2010, Chwedorzewska et al. 2013, Adams et al. 2014). So far, the probability that introduced invertebrates will become established and spread is considered to be quite low; most of them are not able to complete the life cycle and establish a stable population outside the station (Chwedorzewska et al. 2013). Although these organisms cannot survive outside at present, they are potential colonisers, which could be established in the future following the climate warming (Convey and Peck 2019). The four cosmopolitan nematode taxa (*E. vulgaris*, *E. filiformis*, *G. villosa* and *P. armatus*) also reported from the Maritime Antarctic are considered to be of non-native origin by Andrássy (1998). Due to the absence or scarcity of data on the morphology of these species, at present, their origin cannot be confirmed. Future studies using an integrated taxonomic approach (i.e. simultaneous molecular and morphological characterisation) of materials obtained from pristine areas may help clarify their status. The gap in knowledge of nematode diversity, both in terms of taxonomy and distribution, is essential when assessing the introduction of non-native species. Nematode species richness in the Maritime Antarctic, which is underestimated (Nielsen et al. 2011b) may be compromised with increasing human impact in Antarctica.

The risk to Antarctic biodiversity is not limited to the transfer of alien species originating from other regions of Earth, but also concerns the transfer of native or endemic species from one part of Antarctica to another where they are not part of the indigenous biota (Convey 2008, Hughes et al. 2019, Hughes et al. 2020). This risk is greater because such species are likely to adapt well to the new location, unlike most non-native species that have been transferred to Antarctica from elsewhere (Convey 2015). The transfer of species across natural biogeographic boundaries can affect endemism in these areas. Antarctica is one of the few regions on the Planet where such boundaries still exist (Convey 2008). The nematode faunas of the Maritime and the Continental Antarctic are characterised by their

uniqueness, as no overlap at the species level of the two local faunas exists (Andrássy 1998, Maslen and Convey 2006, Convey et al. 2020). This is indicative of an ancient geographical divide between these areas (Andrássy and Gibson 2007) and led Chown and Convey (2006) to define the Gressitt Line, which is located across the base of the Antarctic Peninsula.

So far, there is no evidence for the transfer and establishment of nematode species from the Continental to the Maritime Antarctic. Some nematological reports have included data on the presence of species that are emblematic of the Continental Antarctic (*Plectus murrayi* Yeates 1970 and *P. frigophilus* Kirjanova 1958) in the Maritime part, without morphological data (see Velasco-Castrillón et al. (2014a)). In our study, these records are not included as they are most likely due to misidentification.

Regarding the biotope/microhabitat distribution of the species, the incomplete and insufficient data do not allow a definite conclusion, taking into account also the lack of research in the more inaccessible areas of the Antarctic Peninsula and the islands. Most likely the micro biotope distribution pattern is similar to that shown in the study of the nematode fauna of Cape Chelyuskin in the Arctic (Chernov et al. 1979), where species show very low biotopic associations and most of them inhabit all possible microhabitats (i.e. the majority of species are polytopic); this is also a characteristic feature of other groups of organisms in the polar regions (Chernov et al. 1979).

The major life strategy of organisms living in extreme environments is the development of tolerance and plasticity and not lack of competition and specialisation, which is typical of other biomes (Convey 1996, Chernov et al. 2011).

Comparing the two parts of the Antarctic shows that the nematode studies in the Maritime Antarctic are less represented, whereas investigations in the Continental Antarctic have been more intensive. However, the latter are primarily related to ecology (Adams et al. 2014, Velasco-Castrillón et al. 2014a, Velasco-Castrillón et al. 2018) and have identified to date 34 species of soil nematodes (Velasco-Castrillón et al. 2014a). The smaller number of species in the Continental Antarctic is associated with the harsher and more unfavourable environmental conditions. This zone includes ecosystems with the simplest terrestrial fauna on the Planet, where even nematodes are absent (Convey and McInnes 2005, Convey 2017).

The two opposite polar regions of the Earth are unevenly studied with respect to soil nematodes (Peneva et al. 2009, Holovachov 2014a). Despite the fewer taxonomic studies of terrestrial nematodes in the Arctic, 391 species have been recorded there (Holovachov 2014a). Key geographical and ecological features of both regions, such as geological history, climate, landscape, dispersal barriers and vegetation are responsible for the lower nematode diversity in the Antarctic than in the Arctic (Nielsen and Wall 2013).

Studies that include molecular data for the nematodes in the Maritime Antarctic are too rare to provide valuable information regarding nematode diversity, phylogenetics and endemism (Elshishka et al. 2015b, Elshishka et al. 2017, Kagoshima et al. 2019). The taxonomic

position of only three Antarctic dorylaimid species, *A. isokaryon*, *P. paradoxus* and *E. signyensis*, was reconsidered on the basis of morphological and molecular characteristics of 18S rDNA (SSU rDNA) and the D2-D3 expansion fragments of 28S rDNA (LSU rDNA) (Elshishka et al. 2015b, Elshishka et al. 2017) and two new endemic genera were proposed (*Pararhyssocolpus* and *Enchodeloides*).

To advance the understanding of phylogeny and phylogeography of Antarctic nematodes, studies are required of other genes with higher evolutionary rates than 18S rDNA, such as 28S rDNA, the internal transcribed spacer (ITS in the ribosomal RNA locus) or the mitochondrial cytochrome c oxidase subunit I (COI). These genes should be included in future taxonomic analyses of Antarctic nematodes (Kagoshima et al. 2019).

The application of integrated taxonomy and DNA barcoding will substantially assist in nematode diversity studies, phylogenetics and especially the recognition of cryptic species. Further, comprehensive molecular studies will provide valuable information on the patterns of species distribution and for gaining additional knowledge on evolutionary processes and biogeography of Antarctic nematodes.

The scant studies of polar regions, in particular of the Maritime Antarctic, demand more intensive sampling and research, especially in the territories that have so far remained unexplored, in order to give a clearer and more adequate view of species diversity and trends in their microhabitat and geographical distribution. Therefore, further efforts aiming at targeted and systematic integrative studies are needed.

Acknowledgements

This study was funded by the Programme for career development of young scientists, Bulgarian Academy of Sciences, the project №80-10-214, National Centre for Polar Studies, Sofia University "St. Kliment Ohridski" and ANIDIV4, Bulgarian Academy of Sciences. The authors are thankful to Prof. Aneta Kostadinova from the Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, for the critical reading of the manuscript and helpful suggestions.

References

- Adams BJ, Bardgett RD, Ayres E, Wall DH, Aislabie J, Bamforth S, Bargagli R, Cary C, Cavacini P, Connell L, Convey P, Fell JW, Frati F, Hogg ID, Newsham KK, O'Donnell A, Russell N, Seppelt RD, Stevens MI (2006) Diversity and distribution of Victoria Land biota. Soil Biology and Biochemistry 38: 3003-3018. <https://doi.org/10.1016/j.soilbio.2006.04.030>
- Adams BJ, Wall DH, Virginia RA, Broos E, Knox MA (2014) Ecological biogeography of the terrestrial nematodes of Victoria Land, Antarctica. ZooKeys 419: 29-71. <https://doi.org/10.3897/zookeys.419.7180>
- Andrássy I (1981) Revision of the order Monhysterida (Nematoda) inhabiting soil and waters. Opuscula Zoologica 17: 13-47.

- Andrassy I (1998) Nematodes in the Sixth continent. *Journal of Nematode Morphology and Systematics* 1: 107-186.
- Andrassy I (2005) Free-living nematodes of Hungary (Nematoda errantia), I. *Pedozoologica Hungarica* No. 3. Hungarian Natural History Museum, Budapest, 518 pp. [ISBN 9789637093906]
- Andrassy I (2007) Free-living nematodes of Hungary (Nematoda errantia), II. *Pedozoologica Hungarica*, No. 4. Hungarian Natural History Museum, Budapest, 496 pp. [ISBN 9789637093982]
- Andrassy I, Gibson J (2007) Nematodes from saline and freshwater lakes of the Vestfold Hills, East Antarctica, including the description of *Hypodontolaimus antarcticus* sp. n. *Polar Biology* 30: 669-678. <https://doi.org/10.1007/s00300-006-0224-4>
- Andrassy I (2009) Free-living nematodes of Hungary (Nematoda Errantia), III. *Pedozoologica Hungarica*, No 5. Hungarian Natural History Museum, Budapest, 608 pp. [ISBN 9789635085743]
- Ara Khanum T, Mehmood N, Khatoon N (2022) Nematodes as biological indicators of soil quality in the agroecosystems. *Nematodes - recent advances, management and new perspectives*. IntechOpen <https://doi.org/10.5772/intechopen.99745>
- Bastian HC (1865) Monograph on the Anguillulidae, or free nematoids, marine, land, and freshwater; with descriptions of 100 new species. *Transactions of the Linnean Society of London* 25: 73-184. <https://doi.org/10.1111/j.1096-3642.1865.tb00179.x>
- Bütschli O (1873) Beiträge zur Kenntnis der freilebenden Nematoden. *Nova Acta Academiae Nat Curios* 35 (5): 1-124.
- Caldwell JR (1981) The Signy Island terrestrial reference sites: XIII. Population dynamics of the nematode fauna. *British Antarctic Survey* 54: 33-46.
- Carapelli A, Convey P, Frati F, Spinsanti G, Fanciulli P (2017) Population genetics of three sympatric springtail species (Hexapoda: Collembola) from the South Shetland Islands: evidence for a common biogeographic pattern. *Biological Journal of the Linnean Society* 120 (4): 788-803. <https://doi.org/10.1093/biolinnean/blw004>
- Chauvin C, Trambolho M, Hedde M, Makowski D, C  r  monie H, Jimenez A, Villenave C (2020) Soil nematodes as indicators of heavy metal pollution: A meta-analysis. *Open Journal of Soil Science* 10 (12): 579-601. <https://doi.org/10.4236/ojss.2020.1012028>
- Chaves E (1990) Mononchida (Nematoda) from Argentina. *Nematologica* 36: 181-193. <https://doi.org/10.1163/002925990X00149>
- Chernov Y, Striganova R, Ananjeva I, Kuzmin L (1979) Animal world of the polar desert at Cape Chelyuskin. In: Aleksandrova VD, Matveyeva NV (Eds) In: *Arkticheskie Tundry i Polyarnye Pustyni Taimyra*. Nauka, 35–49 pp. [In Russian].
- Chernov Y, Matveeva N, Makarova O (2011) Polar deserts: At the limit of life. *Priroda* 9: 31-43. [In Russian].
- Chown S, Brooks C (2019) The State and Future of Antarctic Environments in a Global Context. *Annual Review of Environment and Resources* 44 (1): 1-30. <https://doi.org/10.1146/annurev-environ-101718-033236>
- Chown SL, Convey P (2006) Biogeography. In: Bergstrom DM, Convey P, Huiskes HL (Eds) *Biogeography: Trends in Antarctic terrestrial and limnetic ecosystems*. Springer Dordrecht, 55–70. https://doi.org/10.1007/1-4020-5277-4_4
- Chown SL, Convey P (2016) Antarctic entomology. *Annual Revue Entomology* 61 (1): 119-37. <https://doi.org/10.1146/annur>

- Chwedorzewska K, Korczak-Abshire M, Olech M, Lityńska-Zając M, Augustyniuk-Kram A (2013) Alien invertebrates transported accidentally to the Polish Antarctic Station in cargo and on fresh foods. *Polish Polar Research* 34 (1): 55-66. <https://doi.org/10.2478/popore-2013-0005>
- Clarke KR, Gorley RN (2015) PRIMER v7: User Manual/Tutorial. PRIMER-E Plymouth
- Collins G, Young M, Convey P, Chown S, Cary SC, Adams B, Wall D, Hogg I (2023) Biogeography and Genetic Diversity of Terrestrial Mites in the Ross Sea Region, Antarctica. *Genes* 14 (3). <https://doi.org/10.3390/genes14030606>
- Convey P (1996) The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. *Biological Reviews* 71 (2): 191-225. <https://doi.org/10.1111/j.1469-185x.1996.tb00747.x>
- Convey P, Smith RI, Peat HJ, Pugh PJ (2000) The terrestrial biota of Charcot Island, eastern Bellingshausen Sea, Antarctica: an example of extreme isolation. *Antarctic Science* 12: 406-413. <https://doi.org/10.1017/S095410200000047X>
- Convey P, Wynn-Williams D (2002) Antarctic soil nematode response to artificial climate amelioration. *European Journal of Soil Biology* 38: 255-259. [https://doi.org/10.1016/s1164-5563\(02\)01155-x](https://doi.org/10.1016/s1164-5563(02)01155-x)
- Convey P, McInnes S (2005) Exceptional tardigrade-dominated ecosystems in Ellsworth Land, Antarctica. *Ecology* 86 (2): 519-527. <https://doi.org/10.1890/04-0684>
- Convey P (2006) Antarctic terrestrial ecosystems: Responses to environmental change. *Polarforschung* 75: 101-111.
- Convey P (2008) Non-native species in Antarctic terrestrial and freshwater environments: presence, sources, impacts and predictions. In: Rogan-Finnemore M (Ed.) *Non-native species in the Antarctic*. Proceedings. Christchurch: Gateway Antarctica, 97-130 pp.
- Convey P, Gibson J, Hillenbrand D, Hodgson A, Pugh JA, Smellie L, Stevens I (2008) Antarctic terrestrial life - challenging the history of the frozen continent? *Biological Reviews* 83: 103-117. <https://doi.org/10.1111/j.1469-185X.2008.00034.x>
- Convey P (2015) Alien invasions. The impact of non-native species: changing the face of life on land in Antarctica? In: Liggett D, Storey B, Cook Y, Meduna V (Eds) *Exploring the last continent: an introduction to Antarctica*. Springer, Switzerland, 539-555 pp. https://doi.org/10.1007/978-3-319-18947-5_27
- Convey P (2017) Antarctic Ecosystems. Reference Module in Life Sciences <https://doi.org/10.1016/b978-0-12-809633-8.02182-8>
- Convey P, Peck LS (2019) Antarctic environmental change and biological responses. *Science Advances* 5 (11). <https://doi.org/10.1126/sciadv.aaz0888>
- Convey P, Biersma EM, Casanova-Katny A, Maturana CS (2020) Refuges of Antarctic diversity. In: Oliva M, Ruiz-Fernandez J (Eds) *Past Antarctica: Paleoclimatology and climate change*. Elsevier, 181-200 pp. <https://doi.org/10.1016/b978-0-12-817925-3.00010-0>
- Courtright EM, Wall DH, Virginia RA, Frisse LM, Vida JT, Thomas WK (2000) Nuclear and mitochondrial DNA sequence diversity in the Antarctic nematode *Scottinema lindsayae*. *Journal of Nematology* 32: 143-153.
- Czechowski P, J C, Cooper A, I S (2017) A primer to metabarcoding surveys of Antarctic terrestrial biodiversity. *Antarctic Science* 29: 3-15. <https://doi.org/10.1017/S0954102016000389>

- de Man JG (1880) Die einheimischen, frei in der reinen Erde und im süßen Wasser lebende Nematoden monographisch bearbeitet. Vorläufiger Bericht und descriptiv-systematischer Theil. Tijdschrift der Nederlandsche Dierkundige Vereeniging 5: 1-104.
- de Man JG (1904) Nematodes libres. Result. voyage S.Y Belgica, Zoology 55.
- Du Preez G, Daneel M, De Goede R, Du Toit MJ, Ferris H, Fourie H, Geisen S, Kakouli-Duarte T, Korthals G, Sánchez-Moreno S, Schmidt JH (2022) Nematode-based indices in soil ecology: Application, utility, and future directions. Soil Biology and Biochemistry 169 <https://doi.org/10.1016/j.soilbio.2022.108640>
- Ebach M, Pugh PJ, Convey P (2008) Surviving out in the cold: Antarctic endemic invertebrates and their refugia. Journal of Biogeography 35 (12): 2176-2186. <https://doi.org/10.1111/j.1365-2699.2008.01953.x>
- Elshishka M, Lazarova S, Peneva V (2015a) Terrestrial nematodes of Livingston Island, maritime Antarctica. In: Pimpirev Ch. & Chipev N. (Eds). Bulgarian Antarctic Research. A Synthesis. "St Kliment Ohridski" (BN:978-954-07-3939-7)320-334.
- Elshishka M, Lazarova S, Radoslavov G, Hristov P, Peneva V (2015b) New data on two remarkable antarctic species *Amblydorylaimus isokaryon* (Loof, 1975) Andrassy, 1998 and *Pararhysocolpus paradoxus* (Loof, 1975) gen. n., comb. n. (Nematoda, Dorylaimida). ZooKeys 511: 25-68. <https://doi.org/10.3897/zookeys.511.9793>
- Elshishka M, Lazarova S, Radoslavov G, Hristov P, Peneva V (2017) Biogeography and phylogenetic position of *Enchodeloides signyensis* (Loof, 1975) gen. n. comb. n. from Maritime Antarctic (Nematoda, Nordiidae). ZooKeys 697: 37-58. <https://doi.org/10.3897/zookeys.697.13770>
- Ferris H, Bongers T, de Goede RG (2001) A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied Soil Ecology 18 (1): 13-29. [https://doi.org/10.1016/s0929-1393\(01\)00152-4](https://doi.org/10.1016/s0929-1393(01)00152-4)
- Freckman DW, Virginia RA (1997) Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. Ecology 78: 363-369. <https://doi.org/10.1890/0012-9658>
- Gantait V (2014) Diversity of nematodes in Antarctica under changing climatic conditions. Journal of Crop and Weed 10 (2).
- Greene SW (1970) Studies in *Colobanthus quitensis* (Kunth) Bartl. And *Deschampsia antarctica* Desv. I Introduction. British Antarctic Survey Bulletin 23: 19-24.
- Holdgate MW (1977) Terrestrial Ecosystems in the Antarctic. Philosophical Transactions of the Royal Society B: Biological Sciences 279 (963): 5-25. <https://doi.org/10.1098/rstb.1977.0068>
- Holovachov O, Bostrom S (2006) Description of *Acrobeloides arctowski* sp. n. (Rhabditida: Cephalobidae) from King George Island, Antarctica. Russian Journal of Nematology 14: 51-56.
- Holovachov O (2014a) Nematodes from terrestrial and freshwater habitats in the Arctic. Biodiversity Data Journal 2: 1165. <https://doi.org/10.3897/BDJ.2.e1165>
- Holovachov O (2014b) Order Plectida Gadea, 1973. In: Schmidt-Rhaesa A (Ed.) Handbook of Zoology. Gastrotricha, Cycloneuralia, Gnathifera. Volume 2: Nematoda. De Gruyter <https://doi.org/10.1515/9783110274257.487>
- Hughes KA, Convey P, Maslen NR, Smith RIL (2010) Accidental transfer of non-native soil organisms into Antarctica on construction vehicles. Biological Invasions 12 (4): 875-891. <https://doi.org/10.1007/s10530-009-9508-2>

- Hughes KA, Convey P, Pertierra L, Vega G, Aragón P, Olalla-Tárraga M (2019) Human-mediated dispersal of terrestrial species between Antarctic biogeographic regions: A preliminary risk assessment. *Journal of Environmental Management* 232: 73-89. <https://doi.org/10.1016/j.jenvman.2018.10.095>
- Hughes KA, Pescott OL, Peyton J, Adriaens T, Cottier-Cook EJ, Key G, Rabitsch W, Tricarico E, Barnes DKA, Baxter N, Belchier M, Blake D, Convey P, Dawson W, Frohlich D, Gardiner LM, González-Moreno P, James R, Malumphy C, Martin S, Martinou AF, Minchin D, Monaco A, Moore N, Morley SA, Ross K, Shanklin J, Turvey K, Vaughan D, Vaux AGC, Werenkraut V, Winfield IJ, Roy HE (2020) Invasive non-native species likely to threaten biodiversity and ecosystems in the Antarctic Peninsula region. *Global Change Biology* 26 (4): 2702-2716. <https://doi.org/10.1111/gcb.14938>
- Iakovenko NS, Smykla J, Convey P, Kašparová E, Kozeretska IA, Trokhymets V, Dykyy I, Plewka M, Devetter M, Duriš Z, Janko K (2015) Antarctic bdelloid rotifers: diversity, endemism and evolution. *Hydrobiologia* 761 (1): 5-43. <https://doi.org/10.1007/s10750-015-2463-2>
- Jairajpuri MS, Khan WU (1977) Studies on Mononchida of India. IX. Further division of the genus *Clarkus* Jairajpuri, 1970 with proposal of *Coomansus* n. gen. and descriptions of two new species. *Nematologica* 23: 89-96. <https://doi.org/10.1163/187529270x00153>
- Janiec K (1996) The comparison of freshwater invertebrates of Spitsbergen (Arctic) and King George Island (Antarctic). *Polish Polar Research* 17: 173-202.
- Jiménez Guirado D, Wouts WM, Bello A (1998) Morphometric studies on *Coomansus* Jairajpuri & Khan, 1977 (Nematoda: Mononchida) and descriptions of two new species from the Subantarctic region. *Fundamental and Applied Nematology* 21: 527-546.
- Kagoshima H, Maslen R, Kito K, Imura S, Niki H, Convey P (2019) Integrated taxonomy combining morphological and molecular biological analyses of soil nematodes from maritime Antarctica. *Polar Biology* 42: 877-887. <https://doi.org/10.1007/s00300-019-02482-8>
- Kirjanova ES (1958) Antarkticheskie predstaviteli presnovodnykh nematod roda *Plectus* Bastian (Nematodes Plectidae). *Information Bulletin of the Soviet Antarctic Expedition* 3: 101-103.
- Kito K (2009) Taxonomical and ecological studies of free-living nematodes carried out in Antarctica as a cooperative research program of NIPR. *Sapporo Medical Journal* 78: 13-18.
- Lee JE, Chown SL (2009) Breaching the dispersal barrier to invasion: quantification and management. *Ecological Applications* 19 (7): 1944-1959. <https://doi.org/10.1890/08-2157.1>
- Longton RE (1979) Vegetation ecology and classification in the Antarctic zone. *Canadian Journal of Botany* 57 (20): 2264-2278. <https://doi.org/10.1139/b79-273>
- Loof PA (1975) Dorylaimoidea from some subantarctic islands. *Nematologica* 21: 219-255. <https://doi.org/10.1163/187529275X00581>
- Maslen NR (1979a) Six new nematode species from the maritime Antarctic. *Nematologica* 25 (3): 288-308. <https://doi.org/10.1163/187529279x00028>
- Maslen NR (1979b) Additions to the nematode fauna of the Antarctic Region with keys to taxa. *British Antarctic Survey Bulletin* 49: 207-229.
- Maslen NR (1981) The Signy Island terrestrial reference sites: XII. Population ecology of nematodes with additions to the fauna. *British Antarctic Survey Bulletin* 53: 57-75.

- Maslen NR, Convey P (2006) Nematode diversity and distribution in the southern maritime Antarctic - clues to history? *Soil Biology and Biochemistry* 38: 3141-3151. <https://doi.org/10.1016/j.soilbio.2005.12.007>
- Nedelchev S, Peneva V (2000) Description of three new species genus *Mesodorylaimus* Andr ssy 1959 (Nematoda, Dorylaimidae) in Livingston Island, Antarctic a notes *M. imperator* Loof 1975. *Russian Journal of Nematology* 8: 161-172.
- Nedelchev S, Peneva V (2007) Description of the male of *Mesodorylaimus chiievi* Nedelchev & Peneva, 2000 (Nematoda: Dorylaimidae) from Livingston Island, Antarctica. *Russian Journal of Nematology* 15: 75-77.
- Neher DA (2001) Role of nematodes in soil health and their use as indicators. *Journal of nematology* 33 (4): 161-8.
- Neher DA (2010) Ecology of plant and free-living nematodes in natural and agricultural soil. *Annual Review of Phytopathology* 48 (1): 371-394. <https://doi.org/10.1146/annurev-phyto-073009-114439>
- Newman L, Convey P, Gibson J, Linse K (2009) Antarctic Paleobiology: Glacial refugia and constraints on past ice-sheet reconstructions. *PAGES news* 17 (1): 22-24. <https://doi.org/10.22498/pages.17.1.22>
- Newsham K, Hall R, Maslen NR (2020) Experimental warming of bryophytes increases the population density of the nematode *Plectus belgic e* in maritime Antarctica. *Antarctic Science* 33 (2): 165-173. <https://doi.org/10.1017/s0954102020000528>
- Nielsen UN, Wall DH, Adams BJ, Virginia RA (2011a) Antarctic nematode communities: observed and predicted responses to climate change. *Polar Biology* 34: 1701-1711. <https://doi.org/10.1007/s00300-011-1021-2>
- Nielsen UN, Wall DH, Li G, Toro M, Adams BJ, Virginia RA (2011b) Nematode communities of Byers Peninsula, Livingston Island, maritime Antarctica. *Antarctic Science* 23 (4): 349-357. <https://doi.org/10.1017/s0954102011000174>
- Nielsen UN, Wall DH (2013) The future of soil invertebrate communities in polar regions: different climate change responses in the Arctic and Antarctic? *Ecology Letters* 16 (3): 409-419. <https://doi.org/10.1111/ele.12058>
- Ochyra R (1998) The moss flora of King George Island, Antarctica. *Polish Academy of Sciences* [ISBN 8385444602]
- Peneva V, Chihev N, Nedelchev S (1996) *Prionchulus punctatus* Cobb, 1917, a new record from Patagonia (Chile), with notes on other mononchids from Antarctic Regions. *Bulgarian Antarctic Research Life Sciences* 93-101.
- Peneva V, Chihev N (1999) *Laimaphelenchus helicossoma* (Maslen, 1979) n. comb. (Nematoda: Aphelenchida) from Livingston Island. In: Golemsky V, Chihev N (Eds). *Bulgarian Antarctic Research. Life Sciences. Pensoft. Sofia - Moscow* 2: 57-61.
- Peneva V, Lazarova S, Chihev N (2002) Description of the male of *Enchodelus* (Rotundus) signyensis Loof, 1975 (Nematoda, Nordidae) from Livingston Island, Antarctica, and notes on its morphology and distribution. In: Golemsky V, Chihev N (Eds) *Bulgarian Antarctic Research. Life Sciences. Vol.3. Pensoft, Sofia-Moscow*, 83-90 pp.
- Peneva V, Lazarova S, Elshishka M, Makarova O, Penev L (2009) Nematode assemblages of hair-grass (*Deschampsia* spp.) microhabitats from polar and alpine deserts in Arctic and Antarctic. In: Golovatch SI, Makarova OL, Babenko AB, Penev LD (Eds) *Species and communities in extreme environment. Pensoft Publishers & KMK Scientific Press, Sofia - Moscow*, 419-438 pp.

- Pickup J (1988) Ecophysiological studies of terrestrial free-living nematodes of Signy Island. *British Antarctic Survey Bulletin* 81: 77-81.
- Pickup J (1990) Seasonal variation in the cold-hardiness of a free-living predatory antarctic nematode, *Coomansus gerlachei* (Mononchidae). *Polar Biology* 10: 307-315. <https://doi.org/10.2307/2389345>
- Russell DJ, Hohberg K, Potapov M, Brückner A, Otte V, Christian A (2014) Native terrestrial invertebrate fauna from the northern Antarctic Peninsula: new records, state of current knowledge and ecological preferences - Summary of a German federal study. *Soil Organisms* 86: 1-58.
- Shishida Y, Ohyama Y (1989) A note on the terrestrial nematodes around Palmer Station, Antarctica (Extend abstract. Proceeding of the NIPR Symposium on Polar Biology 2: 223-224.
- Short KA, Sands CJ, McInnes SJ, Pisani D, Stevens MI, Convey P (2022) An ancient, Antarctic-specific species complex: large divergences between multiple Antarctic lineages of the tardigrade genus *Mesobiotus*. *Molecular Phylogenetics and Evolution* 170 <https://doi.org/10.1016/j.ympev.2022.107429>
- Smith RI (1984) Terrestrial plant biology of the sub-Antarctic and Antarctic. In: Laws RM (Ed.) *Antarctic ecology*. Vol. 1. Academic Press, 61-162 pp.
- Spaul VW (1972) *Antarctenchus hooperi*, gen., n. sp. (Nematoda: Dolichodoridae) from Signy Island, South Orkney Islands, with the erection of a new subfamily. *Nematologica* 18: 353-9. <https://doi.org/10.1163/187529272X00629>
- Spaul VW (1973a) Distribution of soil nematodes in the maritime Antarctic. *British Antarctic Survey Bulletin* 37: 1-6.
- Spaul VW (1973b) Qualitative and quantitative distribution of soil nematodes of Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* (33-34)177-184.
- Spaul VW (1973c) Distribution of nematode feeding group at Signy Island, South Orkney Islands, with an estimate of their biomass and oxygen consumption. *British Antarctic Survey Bulletin* 37: 21-32.
- Spaul VW (1981) Observations on *Coomansus gerlachei* (de Man) (Nematoda: Mononchidae), a predacious nematode from the Antarctic. *British Antarctic Survey Bulletin* (53)195-200.
- Stevens MI, Mackintosh AN (2023) Location, location, location: survival of Antarctic biota requires the best real estate. *Biological Letters* 19: 20220590. <https://doi.org/10.1098/rsbl.2022.0590>
- Taylor L, Phillips G, Bernard E, DeBruyn J (2020) Soil nematode functional diversity, successional patterns, and indicator taxa associated with vertebrate decomposition hotspots. *PLOS One* 15 (11). <https://doi.org/10.1371/journal.pone.0241777>
- Tilbrook PJ (1973) The Signy Island terrestrial reference sites: 1. An introduction. *British Antarctic Survey Bulletin* 33 & 34: 65-76.
- Treonis AM, Wall D (2005) Soil nematodes and desiccation survival in the extreme arid environment of the Antarctic dry valleys. *Integrative and Comparative Biology* 45 (5): 741-750. <https://doi.org/10.1093/icb/45.5.741>
- Tsalolikhin SJ (1989) Rare and new nematode species from Antarctica. *Trudi Zoologicheskogo Instituta Akademii Nauk, Leningrad* 194: 96-101. [In Russian].
- van den Hoogen J, Geisen S, Routh D, Ferris H, Traunsperger W, Wardle D, de Goede RM, Adams B, Ahmad W, Andriuzzi W, Bardgett R, Bonkowski M, Campos-Herrera R, Cares J, Caruso T, de Brito Caixeta L, Chen X, Costa S, Creamer R, Mauro da Cunha

- Castro J, Dam M, Djigal D, Escuer M, Griffiths B, Gutiérrez C, Hohberg K, Kalinkina D, Kardol P, Kergunteuil A, Korthals G, Krashevskaya V, Kudrin A, Li Q, Liang W, Magilton M, Marais M, Martín JAR, Matveeva E, Mayad EH, Mulder C, Mullin P, Neilson R, Nguyen TAD, Nielsen U, Okada H, Rius JEP, Pan K, Peneva V, Pellissier L, Carlos Pereira da Silva J, Pitteloud C, Powers T, Powers K, Quist C, Rasmann S, Moreno SS, Scheu S, Setälä H, Sushchuk A, Tiunov A, Trap J, van der Putten W, Vestergård M, Villenave C, Waeyenbergh L, Wall D, Wilschut R, Wright D, Yang J, Crowther TW (2019) Soil nematode abundance and functional group composition at a global scale. *Nature* 572 (7768): 194-198. <https://doi.org/10.1038/s41586-019-1418-6>
- Velasco-Castrillón A, Stevens M (2014) Morphological and molecular diversity at a regional scale: A step closer to understanding Antarctic nematode biogeography. *Soil Biology & Biochemistry* 70: 272-284. <https://doi.org/10.1016/j.soilbio.2013.12.016>
 - Velasco-Castrillón A, Gibson JE, Stevens M (2014a) A review of current Antarctic limno-terrestrial microfauna. *Polar Biology* 37 (10): 1517-1531. <https://doi.org/10.1007/s00300-014-1544-4>
 - Velasco-Castrillón A, Page TJ, Gibson JA, Stevens MI (2014b) Surprisingly high levels of biodiversity and endemism amongst Antarctic rotifers uncovered with mitochondrial DNA. *Biodiversity* 15: 130-142. <https://doi.org/10.1080/14888386.2014.930717>
 - Velasco-Castrillón A, Hawes I, Stevens M (2018) 100 years on: a re-evaluation of the first discovery of microfauna from Ross Island, Antarctica. *Antarctic Science* 30 (4): 209-219. <https://doi.org/10.1017/s095410201800007x>
 - Wharton DA, Block W (1993) Freezing tolerance in some Antarctic nematodes. *Functional Ecology* 7: 578-584. <https://doi.org/10.2307/2390134>
 - Wharton DA (1995) Cold tolerance strategies in nematodes. *Biological Reviews* 70 (1): 161-185. <https://doi.org/10.1111/j.1469-185x.1995.tb01442.x>
 - Yeates GW (1970) Two Terrestrial Nematodes from the McMurdo Sound Region Antarctica, with a note on *Anaplectus arenicola* Killick, 1964. *Journal of Helminthology* 44: 27-34. <https://doi.org/10.1017/S0022149X00021416>