Native terrestrial invertebrate fauna from the northern Antarctic Peninsula: new records, state of current knowledge and ecological preferences – Summary of a German federal study

David J. Russell[1*], Karin Hohberg[1], Mikhail Potapov[2], Alexander Bruckner[3], Volker Otte[1] and Axel Christian

[1] Senckenberg Museum of Natural History Görlitz, Postfach 300 154, 02806 Görlitz, Germany

[2] Moscow State Pedagogical University, M.Pirogovskaya 1, 119991 Moscow, Russia

[3] University of Natural Resources and Life Sciences, Gregor Mendel-Straße 33, 1180 Vienna, Austria

* Corresponding author, e-mail: david.russell@senckenberg.de

Abstract

The Antarctic terrestrial invertebrate fauna has been intensely studied during the last 120 years. However, due to their difficult accessibility, large regions of terrestrial Antarctica still remain to be investigated soil-zoologically. Some areas that have remained unstudied are now being increasingly visited by, i.e., Antarctic cruise-ship voyages. These sites are therefore becoming available for the expansion of Antarctic soil-zoological research. A study commissioned by the German Federal Environment Agency allowed the investigation of the edaphic fauna in ice-free areas along the routes of touristic cruise ships in the maritime Antarctic. A total of 13 localities around the northern Antarctic Peninsula were studied during the austral summers of 2009/2010 and 2010/2011, many of which had never been investigated regarding their edaphic fauna. Soil-substrate samples were taken and the Nematoda, Collembola and Acari extracted and identified. More than 320,000 individuals and almost 100 species were recorded. Nematoda represented the most individual- and species-rich taxonomic group, followed by Collembola (abundances) and actinedid mites (species richness). The recorded fauna was typical for Maritime Antarctica. Although previous authors consider Antarctic species to have a low habitat specificity and broad tolerance for different habitat conditions, in the present study many individual species showed significant relationships to specific habitat parameters (i.e., vegetation, soil organic matter, soil moisture). While no new endemic species were identified among the microarthropods (Collembola and Acari), several nematode taxa were found that are probably new to science. Previous knowledge regarding the distribution, ecology (i.e, microhabitat preferences, nutrient resources or life cycles) and partly also the taxonomy of the recorded species are reviewed.

1. Introduction

Terrestrial edaphic Antarctic faunal communities belong to the simplest on earth (Freckman & Virginia 1997, Convey et al. 2000b, Hogg et al. 2006). Many major taxonomical groups usually found in soils of temperate areas are missing in Antarctica, e.g., Lumbricidae or Diplopoda (Convey 2005, 2011). The endemic terrestrial invertebrate fauna consists solely of Diptera, Acari, Collembola, Nematoda, Rotifera, Tardigrada and Protozoa (Block 1984a, Hogg & Stevens 2002, Convey 2005). The Antarctic terrestrial soil flora and fauna is furthermore very species- and structurally poor throughout all occurring animal groups (Ryan et al. 1989, Sohlenius et al. 1995, Block & Starý 1996, Convey & Smith 1997, Freckman & Virginia 1997, Convey et al. 2000b, Convey 2005, 2011). Nonetheless, the abundances of species occurring in Antarctic ecosystems can at times be high (Ohyama & Hiruta 1995, Sohlenius et al. 1995, Caruso & Bargagli 2007, Sanyal & Hazra 2008,

Schulte et al. 2008, Sohlenius & Bostrom 2008), so that these simple biotic communities can be composed of few species in large populations. Furthermore, the functional diversity of Antarctic terrestrial habitats is very limited. Most Antarctic terrestrial invertebrates are most likely microbivorous or detritivorous, while true herbivores and predators play only a minor role (Convey et al. 2000b, Hogg et al. 2006, Tin et al. 2009).

The terrestrial micro- and mesofauna occurring in Antarctica are relatively well known due to the many, albeit often purely descriptive studies of the last 120 years (e.g., Michael 1895, Trägårdh 1908, Dalenius & Wilson 1958, Womersley & Strandtmann 1963, Wise 1964, 1971, Wallwork 1965, 1973, Hunter 1967a, Greenslade & Wise 1984, Somme 1986a,b, Usher & Booth 1986, Dastych 1989, Potapov 1991, Higashi & Sugawara 1992, Greenslade 1995, Block & Stary 1996, Andrássy 1998, 2008, McInnes & Pugh 1998, Convey et al. 2000a, Sanyal & Gupta 2005). Most studies have dealt with the species of specific taxonomic groups. The earliest collections of Collembola in Antarctica were made on August Island near the coast of the Antarctic Peninsula in 1898 (Willem 1901). In the first half of the 20th century, several European taxonomists dealt with Antarctic collections (Wahlgren 1906, Carpenter 1907, Salmon 1949, 1962 and other publications). During the last decade, several papers on the ecology and history of the distribution of Antarctic Collembola were published (Toricelli et al. 2010, Caruso et al. 2009b). Collembola of the maritime Antarctic, and particularly of the South Shetland Islands, have been studied intensively, from where several species were described (e.g., Willem 1901, Wahlgren 1906, Carpenter 1907, Weiner 1980, Greenslade 1995). According to Hogg and Stevens (2002), to date, roughly 15 species of springtails have been recorded from Antarctica. However, this number is obviously underestimated and the true number of species amounts to approximately 25. The exact estimation depends on the current taxonomic understanding of the particular species, consideration of single records of species in the Antarctic, etc. The last annotated list of collembolan species of the South Shetland Islands was compiled by Greenslade (2010).

The Acari of Antarctica were also studied during early Antarctic and Sub-Antarctic expeditions over 100 years ago (Michael 1895, Richters 1904, Trägårdh 1908, Trouessart 1914). The acarological reports of these expeditions represented often little more than a list of the discovered species as well as some descriptions of new species. Acarological research in Antarctica continued sporadically throughout the next decades and was strongly intensified as of the 1950s and 1960s, primarily by researchers from the Bishop Museum as well as the British Antarctic Survey. This later work was usually devoted to the taxonomy of Antarctic mites, with many descriptions of new species as well as taxonomic reviews, which were intensified in the 1980s and continue today (i.e., Wise 1964, Wallwork 1967, Strandtmann et al. 1967, Booth et al. 1985, Usher & Edwards 1986c, Edwards & Usher 1987, Coetzee 1997). Due to these activities, lists of Antarctic Acari could be assembled by Hunter (1967a), Strandtmann (1967) and Wallwork (1967) among others. More comprehensive reviews were compiled by, e.g., Dalenius (1965), Gressitt (1965) and Pugh (1993), which nonetheless often contained little more than species lists with little ecological information per species, while the information concerning species distributions was somewhat more precise than in earlier attempts. Today, over 70 species are reported to occur in Antarctica (Pugh 1993). Regarding specific taxonomical groups, reviews of the Antarctic Oribatida fauna in the Antarctic and Sub-Antarctic were produced by Dalenius & Wilson (1958) and Wallwork (1973), as well as Block & Stary (1996) and Stary & Block (1998). Driven by the International Biology Programme (IBP), as of the late 1960s acarological research in the Antarctic was devoted more to life histories, ecological preferences and adaptations of individual species as well as communities (e.g., Gressitt 1967, Strong 1967, Tilbrock 1967a, b, Block 1984b, Usher & Booth 1986, Block & Convey 1995, Lister et al. 1988, Marshall & Convey 1999, Sinclair et al. 2006). More recent investigations have concerned a completion of the knowledge of mite species occurring in Antarctica as well as delineating their large and small-scale distributional patterns, especially in the maritime Antarctic (e.g., Convey & Quintana 1997, Convey & Smith 1997).

The first Antarctic nematodes were sampled during the Belgica expedition (1897–1899) by the Romanian biologist Emil Racovita in small meltwater accumulations near Beneden Head (Andrássy 1998). These individuals were later described by de Man (1904) as *Plectus antarcticus, Plectus belgicae* and *Mononchus* sp. (later placed in *Coomansus gerlachei*). Today 54 nematode species are known from Antarctica and approximately 85 % of these are endemic (Andrássy 2008). Further new species are constantly being discovered. From the 54 species listed for Antarctica, 32 species have been recorded from the climatically milder maritime Antarctic (which includes the Antarctic Peninsula) and only 22 species from the climatically harsher continental Antarctic (Andrássy 2008). Distributional overlap between Maritime and Continental Antarctica practically does not exist (but see Maslen & Convey 2006). Depending on species, soil-living nematodes feed on bacteria, fungi, algae, dead organic material, plant-root sap, protozoa or other soil animals (Yeates et al. 1993). Due to the usually lacking

vegetation and the low soil-substrate nutrient content, nematode bacterial and algal feeders play a major role in Antarctic soil food webs (Andrássy 1998).

Terrestrial invertebrate communities can only develop in ice-free areas of Antarctica; edaphic species can obviously only find habitat under or between free stones or in soil substrates, which are only found in ice-free areas. Only about 1 % of the entire Antarctic continent is free of ice and 60–80 % (depending on literature source) of this minimal ice-free area is found on and around the Antarctic Peninsula (Fox et al. 1994, Beyer & Bölter 2002). However, the invertebrate fauna of many of these areas have not been studied due to difficult accessibility for research personal. Most of the knowledge of the Antarctic soil fauna originates from studies from areas near research stations or along the routes of research vessels, i.e. from a limited number of areas. Therefore large regions of terrestrial Antarctica still remain to be investigated regarding the occurring soil fauna. On the other hand, ice-free locations –particularly around the Antarctic Peninsula– are being increasingly visited by non-scientific groups, i.e., during cruise-ship voyages in the maritime Antarctic (Lynch et al. 2009, IAATO 2011). Such 'touristic' sites have generally remained unstudied by soil zoologists. They are therefore of particular interest regarding their invertebrate fauna and the increasing cruise-ship traffic opens their availability for the expansion of Antarctic soil-zoological research. A study commissioned by the German Federal Environment Agency provided the opportunity to investigate the terrestrial invertebrate fauna during the austral summers of 2009/2010 and 2010/2011, in particular along the routes of touristic cruise ships, thus increasing the number of potential, previously unstudied sites. Unique was furthermore the possibility of investigating a large number of the occurring taxonomic groups and not only specific major taxa. Major questions asked during the present investigations were whether the invertebrate fauna in these areas is similar to other previously investigated areas or if new species or differing species compositions exist in these areas. The present paper presents the soil-faunistical results of these investigations and reviews the previous knowledge of the distribution and ecology of the native species of the Nematoda, Collembola, Actinedida, Oribatida and Gamasina recorded in the present study. Specific results on Tardigrada from the present study were published separately (McInnes and Pugh 2013). The present paper represents an extract from a report submitted to the German Federal Environmental Agency. Further research questions concerned the introduction of non-native species or the anthropogenic impact on Antarctic soil-faunal communities; these results will be presented in subsequent papers.

2. Materials and methods

2.1. Study sites

Locations along the Antarctic Peninsula that were previously unstudied regarding their invertebrate fauna but accessible by touristic cruise ships during land excursions came into consideration as study sites in the present investigations. Furthermore, additional study sites in the same general geographic area (northern Antarctic Peninsula) were investigated that could be reached by station and research personnel. A total of 13 localities were sampled, nine in the study year 2010, seven in the year 2011 and only three in both study years (Fig. 1).

Detailed information regarding the sampling sites can be found in Russell et al. (2013). The sites are described briefly in the following. Geographic coordinates of the sites are given in Table 1.

The northernmost study sites were located in the South Shetland Islands, with many locations on King George Island. The locality '**Arctowski Station**' was situated on the northeast of the island in the vicinity of the Polish research station Arctowski on a peninsula extending into Admirality Bay. The coast there is generally gravelly, whereas the soil substrate contains more clay further inland. A comparatively rich soil vegetation was present, with an average vegetation cover of 50–100 %. It consisted mainly of mosses, lichens as well as the only naturally occurring Antarctic grass species *Deschampsia antarctica,* so that generally a Deschampsia – moss plant society was present.

Many study sites were located on the southwest of the island, on or around the approximately 7 km long Fildes Peninsula. The locality '**Biologenbucht**' is found on the western side of the peninsula south of the Gemel Peaks, approximately 250 m inland of the coast of the bay of the same name. The sampled areas were located halfway up the southern slope, through which multiple meltwater streams flowed. The soils consisted of a sandy to finely grained substrate interspersed with gravel. Ground vegetation also consisted mainly of mosses and *Deschampsia* with a cover of 25 to close to 100 %.

Two further study sites were located on the eastern side of the Fildes Peninsula, on the northern coast of Maxwell Bay approximately 1 km from the Russian research station Bellinghausen: '**Punta Christian I & II**'. Punta Christian I was located on a cliff above the coast along the foot path leading to Punta Rodriguez. The substrate of this locality was rocky with a very thin sandy soil layer interspersed with gravel. The vegetation consisted of patchily distributed moss cushions (short moss torf and cushion subformation; on average 25 to
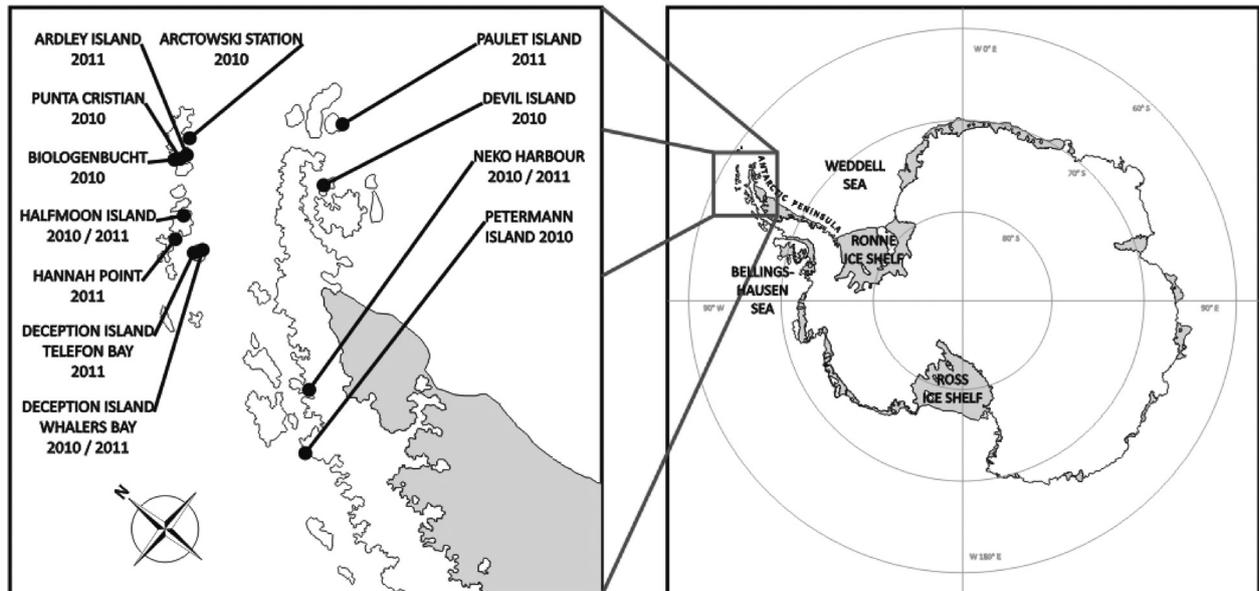
Figure 1. Maritime Antarctic locations investigated in the current study, with the years in which these locations were sampled.

>50% cover) as well as lichens on exposed rock. Punta Christian II was located approximately 250 m from the first site on the lower coastal terrace of the northern Maxwell Bay. The soil substrate was sandy, interspersed with larger stones. The vegetation consisted of an (at times) patchily distributed moss cover (generally a *Sanionia georgico-uncinata* formation; usually <50% cover). The last study area around the Fildes Peninsula was located on '**Ardley Island**', an island on the west side of Maxwell Bay east of the Fildes Peninsula. A major part of the island is environmentally protected (ASPA Nr. 150 'Ardley Island'). The soil substrate consists mostly of crushed rock and gravel. The vegetation was composed of a relatively dense (close to 100% cover) moss carpet (mostly a *Sanionia georgico-uncinata* formation).

The locality '**Halfmoon Island**' is a 2 km long crescent-moon-shaped island northeast of Livingston Island. The study site was located in a gravelly area on a peninsula in the southern part of the island. The soil substrates consisted of stones embedded in a clay matrix; the samples were taken from this matrix. The vegetation if present, then usually <25% cover consisted of sporadically occurring mosses and lichens as well as single patches of *Deschampsia antarctica* (short moss torf and cushion subformation).

The locality '**Hannah Point**' was located on a narrow peninsula in the southwest of the neighbouring Livingston Island. The area is very hilly with steep slopes. The underground consists of larger stones and gravel embedded in a clay matrix. Vegetation was only sporadically present (<25% cover), consisting primarily of a *Prasiola crispa* community. Larger rookeries of Chinstrap and Gentoo Penguins (*Pygoscelis antarctica* and *P. papua*) are found on the peninsula. The actual study sites were located midway up a slope on the rear edge of a Chinstrap Penguin rookery.

Two further sites within the South Shetland Islands were located on Deception Island: 'Whalers Bay' and 'Telefon Bay'. Deception Island is a circular vulcanic island, the center of which represents the volcano's crater and is filled with seawater. The crater is open and connects with the Antarctic Ocean in the southwest. The last eruption occurred in 1996. The island is still geothermally active and especially the coastal soil substrates towards the crater are very warm and can reach temperatures far above 50°C. '**Whalers Bay**' is located on the eastern side of the crater on an extended semicircular coastal terrace consisting of volcanic sand. The area is the site of a whaling station founded at the beginning of the 20th century, the use of which was discontinued at the beginning of the 1930s. The strongly warmed soils of the study area consist of almost purely barren volcanic sands, on which only erratic patches of mosses, lichens and algae were found (initial *Bryum pseudotriquetrum* formation). '**Telefon Bay**' is located in the coastal area in the north of the inner volcanic crater. The soil substrates of the study site also consisted of barren volcanic sands without vegetation and were very warm as well due to the geothermal activity. As in Whalers Bay, many small meltwater streams flow through the area, the exact location of which fluctuate from year to year. In this area, no penguin rookeries or other wildlife colonies are found.

Two study sites were located on islands in the Weddell Sea in the upper northeast of the Antarctic Peninsula

near the exit of the Antarctic Sound into the Weddell Sea. The two localities '**Devil Island**' and '**Paulet Island**' are geologically similar with mountain peaks and flatter valleys as well as coastal terraces. Large rookeries of Adélie Penguins (*Pygoscelis adeliae*) can be found on both islands. The soil substrates of the study area on Devil Island are very sandy with embedded gravel; vegetation was not existent. The substrates of Paulet Island were very rocky with a thin, very muddy clay matrix and vegetation was also not present (except for small patches of *Prasiola crispa*). The study plots were located in an area strongly frequented by penguins along a meltwater stream.

The two southernmost study areas were located on the western side of the Antarctic Peninsula. The locality '**Neko Harbour**' is situated on the eastern edge of the bay of the same name. The study sites were located on an ice-free coastal area, which was otherwise surrounded by glaciers and was the site of a Gentoo Penguin (*Pygoscelis papua*) rookery. The soil substrates in the study areas consisted of larger gravel embedded in clay; the samples were taken from the clay matrix. Vegetation was not present. '**Petermann Island**' is an approximately 1 km long island, lying in the Penola Strait. It generally consists of rock and is largely covered by snow and ice. In coastal areas a few snow- and ice-free spots can be found, on which rookeries of Adélie and Gentoo Penguins (*Pygoscelis adeliae* and *P. papua*) occurred. In the ice-free areas, a few spots of gravelly and non-vegetated sand can be found between larger rocks, from which the samples were taken.

Table 1. The localities actually sampled during the austral summers 2010 und 2011, their exact positions, sampling dates as well as the number of sampling plots (= areas) per locality and the total number of soil cores taken per locality.

Locality	Coordinates	Date	Nr. of plots	Nr. of samples
Devil Island	63°47'54" S, 57°17'24" W	17.I.2010	4	16
Halfmoon Island	62°35'42" S, 59°53'54" W	19.I.2010	3	12
Halfmoon Island	62°35'43" S 59°54'07" W	09.II.2010	6	24
Whalers Bay (Deception Island)	62°58'43" S, 60°33'24" W	19.I.2010	4	16
Whalers Bay (Deception Island)	62°58'43" S, 60°33'24" W	09.II.2010	6	24
Petermann Island	65°10'29" S, 64°08'10" W	20.I.2010	2	8
Neko Harbour	64°51'45" S, 62°26'47" W	21.I.2010	4	16
Arctowski Station (King George Island)	62°09'32" S, 58°27'58" W	25.I.2010	6	24
Biologenbucht (King George Island)	62°11'48" S, 58°59'28" W	21.I.2010	6	24
Punta Cristian (King George Island)	62°11'50" S, 58°56'33" W	22.I.2010	6	24
Punta Cristian II (King George Island)	62°11'53" S, 58°56'47" W	12.II.2010	6	24
Whalers Bay (Deception Island)	62°58'42" S, 60°33'29" W	02.I.2011	6	24
Whalers Bay (Deception Island)	62°58'42" S, 60°33'29" W	07.II.2011	2	8
Telefon Bay (Deception Island)	62°55'43" S, 60°40'48" W	02.I.2011	6	24
Neko Harbour	64°50'41" S, 62°31'53" W	03.I.2011	4	16
Neko Harbour	64°50'41" S, 62°31'53" W	21.I.2011	2	8
Neko Harbour	64°50'41" S, 62°31'53" W	10.II.2011	2	8
Halfmoon Island	62°35'45" S, 59°54'06" W	20.I.2011	6	24
Ardley Island (King George Island)	62°12'38" S, 58°56'40" W	15.I.2011	6	24
Paulet Island	63°34'30" S, 55°46'59" W	06.I.2011	3	12
Hannah Point	62°39'14" S, 60°36'39" W	07.I.2011	4	16

2.2. Sampling

In each of the study sites, preferably six 1-m^{-2} plots representative for the locality (regarding geomorphology, vegetation cover, soil substrates etc.) were identified, from each of which 4 soil cores (including surface vegetation, if present) were taken. Almost all soil cores were obtained with a soil corer (5 cm diameter) and to similar depths (approx. 4–5 cm). Exceptionally, due to substrate conditions, some samples were taken with a small hand shovel, during which care was taken to maintain approximate core sizes. In all sampling sites, the exact diameter and depth of the single samples were recorded, so that all collected data were comparable after data transformation to a standardized sample volume (see below). The substrate samples were packaged in commonplace 2-l plastic freezer bags, labeled and double sealed. During the remaining ship tour, the samples were stored at 5–8°C (e.g., in the ships' flower storeroom) until arrival in Ushuaia, Argentina. The samples were then transported to Görlitz, Germany, usually during the return flight of the samplers, where they arrived in the laboratory generally within 1–2 weeks after sampling, exceptionally after 4 weeks. The data of the individual sampling occasions are given in Table 1.

2.3. Extraction and determination of soil animals

After arrival of the samples in Germany, they were first visually inspected and the original dimensions (diameter, depth) of each sample quantified based on the fieldwork protocols, in order for sample volume to be determined for each sample. In the case that vegetation was present on a soil sample, this vegetation was separated from the soil, whereby half of the vegetation sample was used for species determination of the vegetation and the other half was kept with the soil substrate for animal extraction.

Each sample (soil and the remaining vegetation, if present) was divided into two portions for the two methods used for extracting the invertebrate animals from the samples. For the Nematoda an active wet extraction modified from Baermann (1917) was used, and for the microarthropods (Collembola and Acari) an active dry extraction modified from Macfadyen (1961). For details see Russell et al. (2013). The weight of each extraction sample was precisely documented.

Due to the long transportation route from the Antarctic study sites to Germany, changes in the faunistic conditions of each sample, e.g., due to mortality, reproduction, predation etc., was possibly increased. Since the samples were kept cool during storage on board the ships as well as in the airplanes, larger changes are not likely. Nonetheless, the different transportation times (between sampling and start of extraction) of all samples were documented in order to be able to take these storage times into account during interpretation of the results, if necessary.

The Macfadyen extraction was ended after approximately 13 days at final temperatures of 45°C (sample upper surface) and 30°C (sample bottom surface) and total desiccation of the sample. The collected animals of each sample were transferred to 70 % ethanol and stored for minimally three weeks before microscopic preparation to ensure conservation of the animals. Each Baermann extraction was ended after five days. To prevent predation and therefore a decimation of animals in the collection tube, the extracted animals were collected daily from the tube and the nematodes present immediately killed with 60°C water and subsequently conserved in 0.2 % triethanolamin-formalin solution (TAF) at 4°C.

After extraction and conservation of the animals, they were separated from remaining soil substrate, sorted into the taxonomic major groups (Collembola, Actinedida, Oribatida, Gamasina and Nematoda) under the stereomicroscope at maximally 50x magnification and a preliminary count of the individuals of these major groups present in each sample carried out.

For species determination, microscopic slides of specimens were prepared. The determination of the Collembola and Oribatida took place with the temporary mount technique. The determination of endemic Antarctic Collembola followed the determination keys and taxonomic revisions of Wise (1967), Massoud & Rapoport (1968), Greenslade (1995) and Deharveng (1981). For collembolan species not exclusively occurring in Antarctica, the determination keys of Fjellberg (1998), Pomorski (1998), Potapov (2001), Thibaud et al. (2004) as well as Dunger & Schlitt (2011) were used. Determination of Oribatida followed Hammer (1958) and Wallwork (1962, 1965).

The individuals of the Gamasina was cleared in a glacial acetic acid-glycerin mixture and subsequently mounted in a permanent slide in a gummi-arabicum mixture and determined to species level under a differential interference contrast microscope. Determination of Gamasina followed Hunter (1967b), Lee (1970) and Karg (1976). All individuals of the Actinedida were also mounted in permanent slides in a chloral-hydrate gummi-arabicum mixture. The determination of individuals to species level also took place under a differential interference contrast microscope. The determination followed publications of Strandtmann (1967), Booth (1984), Booth et al. (1985), Usher & Edwards (1986a), Kethley (1990), Kethley & Welbourne (2010) as well as many original species descriptions.

The nematodes of each sample were pipetted in 0.2 % TAF solution onto a large coverslip (mass slide) and counted under a Leica DMI 3000 B inverse microscope at 50x magnification. Subsequently, 100 individuals per sample were determined to species level under an inverse microscope with differential interference contrast. In samples that contained less than 100 nematodes, all individuals were determined. The determination followed publications of Andrassy (1998, 2008), Boström (1995, 1996), Holovachov & Boström (2006), Maslen (1979a), Nedelchev & Peneva (2000, 2007), Peneva et al. (1996), Timm (1971) and further species descriptions. Reference specimens of the Nematoda species per location were embedded in glycerin as permanent slides and sealed with paraffin.

Reference collections of the determined species have been deposited in the collections of the Department of Soil Zoology of the Senckenberg Museum of Natural History in Görlitz, Germany.

2.4. Soil analyses

Soil-substrate parameters were analysed per core to identify possible determinants of the soil-animals' occurrences and distributions. A summary of the results of these analyses are given in the Supplemenatry Material (Tab. S1) available online at www.soil-organisms.org; detailed results of the measurements can be found in Russell et al. (2013). In brief, the following parameters were analysed. Soil temperatures were measured in the field at 5 cm depth during sampling with a digital soil thermometer. The (gravimetric) soil moisture of each sample was determined in the laboratory as the difference between the fresh and dry weight (dried at 105°C) relative to the fresh weight. pH values were measured in 0.1 M KCL-solution according to the specifications of the VDLUFA (1991) as well as DIN (2005). Organic carbon content (C_{org}) of each soil sample [% dry weight] was determined as the difference between dry weight (after drying at 105°C) and incinerated weight (after three hours at 550°C in a muffle furnace). For the determination of the particle-size distribution (soil texture), dried (105°C) soil samples (after removing organic material of more than 2 % by oxidation with concentrated hydrogen peroxide) were passed through a test-sieve cascade of the mesh sizes 20 mm, 6.3 mm, 2 mm, 0.63 mm, 0.2 mm and 0.063 mm. The masses of the soil material remaining in each of these sieves (= particle size fraction) was determined and recorded as the percent of the total weight. For samples containing very little soil substrate (e.g., in the samples from King George Island with much vegetation), mixed samples of the individual samples of one area were

produced and only one measurement per area was made. The analyses of the contents of soil carbon and nitrogen (and C/N ratios) were determined spectrometrically according to DIN (1996) in a Vario Pyro Cube analyzer.

2.5. Data analysis

For each sample, the individual density of each species was extrapolated and standardized to individuals per 100 cm^3 with the formula:

individual densities per 100 cm^3 = $x/n*100$

whereby x represents the number of individuals and n the volume of the actual (Baermann or Macfadyen) extracted sample. The volume of each individual sample was determined from the volume of the total sample (calculated from the diameter and depth of each sample) and the portion of the sample (in percent dry weight) used for the particular extraction method. Extrapolation of the individual densities of each species in each sample was necessary in order to standardize the differently sized samples (particularly concerning sample depth, which was somewhat variable) as well as the different sample portions used in the two extraction methods and thus to guarantee data comparability of all samples as well as all animal groups. Individuals per volume is an unusual unit in modern soil zoology (densities are usually given in individuals per m^2); however, a unit based on volume had to be chosen, since differing sizes of the samples taken in the field (both concerning diameter as well as depth) did not allow a comparable standardization based on surface area. For the specific animal groups, the individual densities of the respective species were summed to obtain the total densities of the respective group. To obtain total values for the microfauna and mesofauna, the densities of the respective animal groups were added together as well.

To determine whether significant differences in densities or species richness existed between localities, the respective data ('total densities' or 'species number per sample') of each animal groups were submitted to a non-parametric variance analysis (ANOVA; modified Friedmann test for multiple observations [= samples] per cell [= area or locality]; Zar 1999) with the main factor 'locality'. This variance analysis is based on ranked data (instead of absolute values) per plot (or locality) as well as on the χ^2- rather than the F-distribution and can easily handle unbalanced sampling designs. A Tukey-like post-hoc test for this non-parametric ANOVA subsequently tested for significant differences between individual localities.

To determine whether significant relationships existed between individual invertebrate animal species and habitat parameters, the zoological data were submitted

per sample to a Spearmann correlation analysis (with the software Statistica V. 10) together with all abiotic soil data as well as the botanical data (species number per sample, vegetation cover in percent). The individual densities of each species per sample represented the zoological data basis, provided sufficient (i.e. >5) individuals of a species for a correlation analysis were present in many samples; the total densities and species numbers (as a measure of species richness) of the taxonomical major groups were also evaluated. From the resulting correlation data matrix, only highly significant correlations (P ≤0.001) were retained.

3. Results and reviews of determined species

3.1. General faunistics

During the two study years, a total of more than 320,000 individuals from all studied animal groups were determined. The majority of individuals (>255,000) were found among the Nematoda, with Tardigrada (over 37,000 ind.) and Collembola (>25,000 ind.) representing the next most frequent animal groups. A total of 98 species could be identified (Tab. A1–A4, Appendix). Again the largest number of species (39) were found within the Nematoda, with Actinedida (25 species) and Tardigrada (see McInnes & Pugh 2013) as well as Collembola (14 and 11 species, respectively) being the next most species-rich groups.

In both years highly significant differences between the total faunas of the studied localities were found both in species richness as well as in densities throughout all animal groups (s. Results of individual animal groups for statistics; Figs 2 & 3; Appendix). Significantly decreasing individual densities from the most northern to the most southern localities was especially apparent among the microfauna, with the exception of very high abundances of Nematoda in Paulet Island in 2011. A north-south density gradient was not as obvious among the mesofauna, although the highest densities were found among the localities of the South Shetland Islands. Decreasing species richness from the northern to the southern localities was found among all groups.

3.2. Collembola

A total of 25,750 collembolan individuals were identified in the present study; 19,299 individuals in 2010 and 6,451 individuals in 2011. This translated into total densities between zero and approx. 600 ind. per 100 cm^3, with an average collembolan density of about 150 ind. per 100 cm^3. Localities in and around King George Island (Arctowski, Biologenbucht, Punta Cristian and Ardley Island) and Whalers Bay of Deception Island showed statiscally higher densities than the other locations (2010: X_r^2 = 112.806; P <0.001; 2011: X_r^2 = 54.932; P <0.001).

According to the correlation analyses, local abundances were related to site location, whereby density correlated negatively with lower latitudes (further south) (correlations are given in the Supplementary Material, Tab. S2, provided online at www.soil-organisms.org), indicating greater abundances the further north the sampling site was. Vegetation cover and collembolan population parameters interacted even more strongly: correlation coefficients were large in both study years (0.554 in 2010 and 0.439 in 2011; Supplementary Material, Tab. S2), indicating that the denser the vegetation cover was, the more individual-rich were the collembolan communities. Among abiotic factors, soil texture (the proportions of gravel, sand and silt/clay) showed the least influence on community parameters; correlations were generally not significant or low. Total densities correlated significantly and negatively only with coarser grained material (Supplementary Material, Tab. S2). Soil moisture apparently relevantly influenced collembolan community abundances, with correlation coefficients as high as 0.499 (in 2011). Parameters such as organic matter, carbon content, nitrogen content and C/N ratio characterize the nutrient status of the soil substrates. Total densities rarely correlated with these factors, only showing larger total abundances related to higher qualities of organic material (= C/N-ratio) in 2010. Collembolan densities were apparently affected negatively by pH only in 2010.

A total of 11 collembolan species were identified in the present investigations (Tab. A1, Appendix), 10 in the year 2010 and eight in the year 2011. To minimize the specifity of local sampling, the locations were grouped together into five areas of increasing latitude, notated here as: King George Island (5 sampled localities), Livingston Island (2 sampled localities), Deception Island (2 sampled localities), Antarctic Peninsula (2 sampled localities) and Weddell Sea (2 sampled localities). In the present study, Petermann Island was devoid of Collembola.

Significant differences among the localities were also observed in species richness (as average number of species per sample) (2010: X_r^2 = 98.725; P <0.001; 2011: X_r^2 = 58.838; P <0.001). The highest species richnesses were observed 2010 in the study sites on King George Island (Fildes Peninsula) and 2011 particularly on Ardley Island, Whalers Bay (Deception Island) and Neko Harbour. As in the total densities, local species
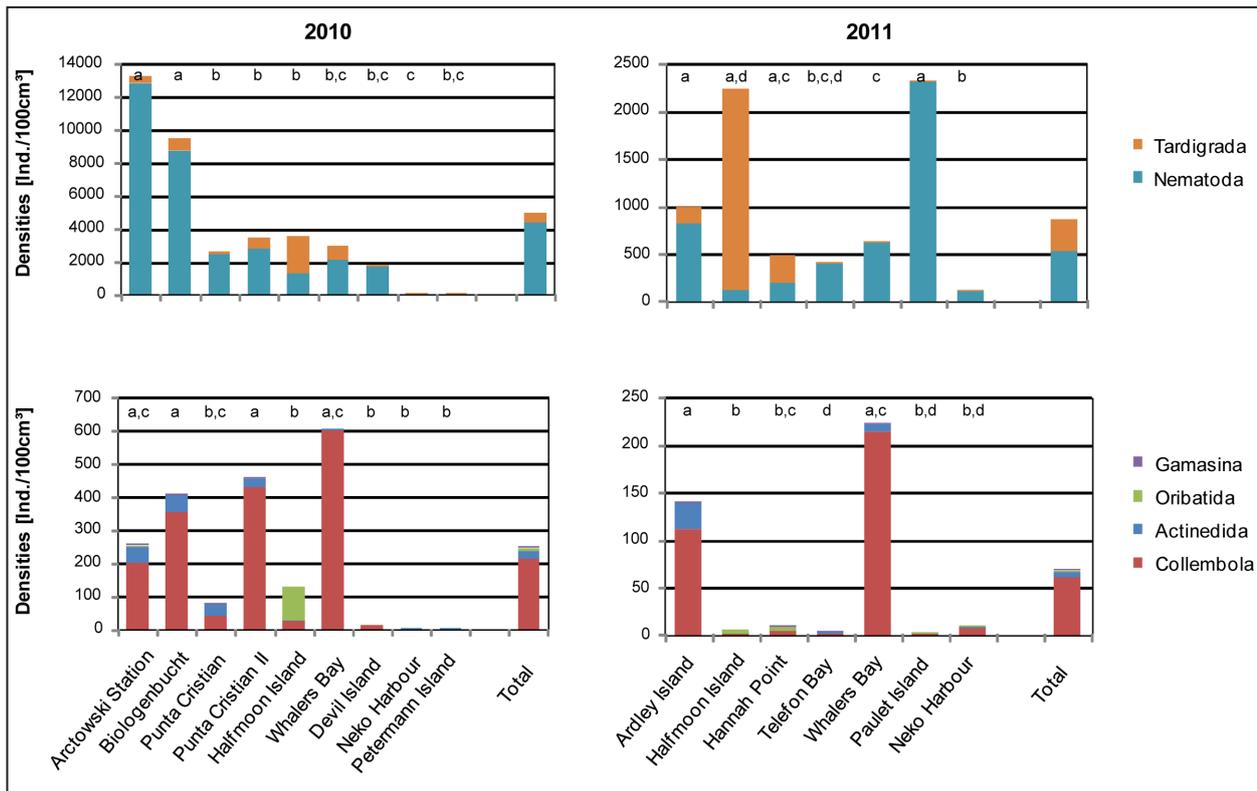
Figure 2. Total densities (in ind. per 100 cm³) of the microfauna (above) and mesofauna (below) in the different localities in 2010 and 2011. Different letters denote significant differences in densities (= the densities of localities with the same letter were statistically *not* different from each other). Please note the different scales of the y-axis of both faunal groups.
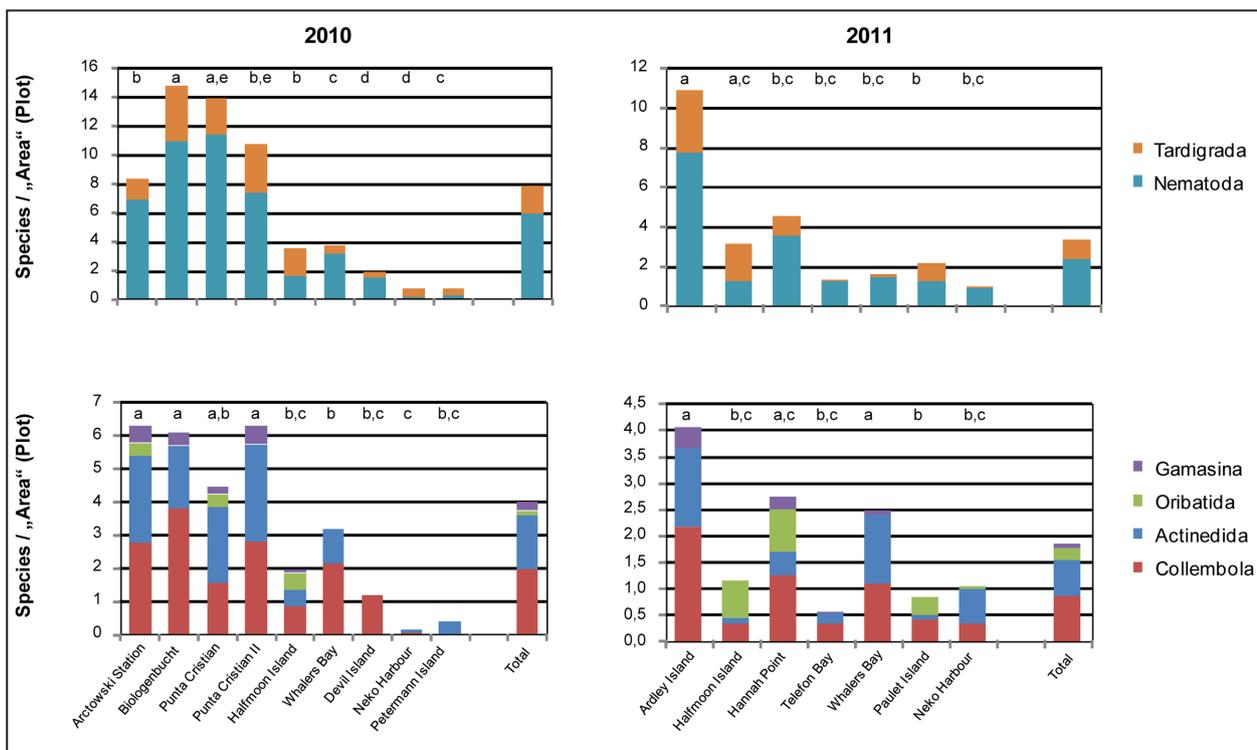

Figure 3. Species richness (as the average number species per area) of the microfauna (above) and mesofauna (below) recorded in the different localities in 2010 and 2011. Different letters denote significant differences in species richness. Please note the different scales of the y-axis of both follow groups.

diversity also showed a strong negative correlation to latitude (Supplementary Material, Tab. S2), indicating greater species richness at lower latitudes. Diversity declined at higher southern latitudes, from 6 species on King George Island to 2 on the Danco and Graham coasts. Vegetation cover correlated as strongly with species richness as it did with total densities (correlation coefficients: 0.521 in 2010 and 0.479 in 2011), indicating that species-richer collembolan communities occurred under denser vegetation cover. Total species richness also correlated negatively with coarser grained soil substrates and positively with finer grain sizes, but only in 2011 (Supplementary Material, Tab. S2). Soil moisture also correlated positively with total collembolan species richness in both years. Species richness related positively to both quantities and qualities of soil organic matter with high and significant correlation coefficients particularly in 2010: the average number of collembolan species was higher in nutrient-richer soils.

The collembolan species recorded in the present study are shown in the Appendix (Tab. A1). In the following, the recorded species are presented and previous knowledge regarding their occurrence in Antarctica reviewed.

Archisotoma brucei (Carpenter, 1907)

A. brucei was recorded in two locations during this study (Deception Island and Devil Island). Its distribution is similar to that of *M. caeca*, as it is widely known from the Subantarctic, but less so from the continental Antarctic; it has also been recorded in New Zealand. It was first described from Laurie Island (South Orkney Islands). It is a littoral species, which probably explains why it was scarce in the present samples. Records of its distribution are shown in Table 2. The species was recorded in Devil Island for the first time in the present study.

The occurrence of *A. brucei* only correlated to habitat parameters in the year 2010 (Supplementary Material, Tab. S2). In this year the species correlated with parameters concerning locality (i.e., sampling date, longitude). In contrast to most other collembolan species, *A. brucei* correlated in this year positively to pH and negatively to finer grained soil textures (i.e., negatively to silt and clay and positively to medium grained sands).

Cryptopygus Willem, 1901

The genus *Cryptopygus* s.s. occurs in the Southern Hemisphere and its species are frequently recorded in Antarctica, the Subantarctic and southern areas of S. America, S. Africa, Australia and New Zealand (Rapoport 1971). Considering their morphology, they are probably analogous to *Folsomia* species in the Northern Hemisphere. Few *Cryptopygus* species are found in the Northern Hemisphere, but their generic position remains obscure and they have little in common with the typical 'southern group' of *Cryptopygus* species. This genus is the species-richest of Antarctic genera – four species have been found so far within the otherwise species-poor Antarctic collembolan fauna. In addition, three monotypic genera, *Neocryptopygus* Salmon, 1965, *Gressitacantha* Wise, 1967 and *Antarctophorus* Potapov, 1991 (known only from Eastern Antarctica) are obviously derived from *Cryptopygus* and their independent generic status is doubtful (Stevens et al. 2005). In the Subantarctic, many more *Cryptopygus* species are known.

Cryptopygus antarcticus Willem, 1901

The species is the best known Antarctic springtail. It has been recorded numerous times throughout the Antarctic Peninsula and associated archipelagos (Tab. 2, Fig. 4A). *C. antarcticus* was recorded in eight localities of the present study. All specimens belong to the nomino-typical subspecies *C. antarcticus antarcticus*. Other subspecies are *C. antarcticus reagens* (Enderlein, 1909), *C. antarcticus maximus* Deharveng, 1981 and *C. antarcticus travei* Deharveng, 1981. *C. antarcticus* was described from a range of localities in the Gerlache Strait, all of which are about 200 km south of the South Shetland Islands (Augustus Island, Harry Island, Danco Territory, Brabant Island, Cap van Beneden, Ile de Cavelier de Cuverville, Wiencke Island and Bob Island). No specific type locality was designated. The species is widely distributed in the maritime Antarctic, commonly occurring in the South Shetland Islands. In a broad understanding, it was also recorded throughout the Subantarctic, but the identity of these populations is doubtful due to molecular and morphological differences found in modern studies (Deharveng 1981, Stevens et al. 2005, Greenslade 2006). In Eastern Antarctica, other species of the genus (*C. cisantarcticus* Wise, 1967, *C. sverdrupi* Lawrence, 1978) or other collembolan taxa replace *C. antarcticus*. Based on modern knowledge, the distribution of this species ranges from Subantarctica to the Antarctic Peninsula. It was recorded in Hannah Point and Neko Harbour – und thus further south – for the first time in the present study.

C. antarcticus was characterized in older studies as a common species living in moss and lichen microhabitats, with higher densities in organically enriched sites (Gressitt et al. 1963, Tilbrook 1967a). On King George Island the species is eurytopic and hydrophilic, occurring in all

Table 2. Known records of occurrence (*x*) of the Collembolan species determined in the present study. The localities are sorted by increasing southern latitude. Localities of the present investigation are shaded grey. *t*: type locality of the given species. Sources: collembolan and soil faunal literature from the Antarctic (as far as available to the authors; shown in the Supplementary Material (Tab. S7) given online at www.soil-organisms.org) and the Biodiversity Database of the Australian Antarctic Data Centre (SCAR Life Sciences programme EBA [Evolution and Biodiversity in the Antarctic]).

	Archisotoma brucei	*Cryptopygus antarcticus antarcticus*	*Cryptopygus badasa*	*Folsomotoma octooculata*	*Friesea grisea*	*Friesea woyciechowskii*	*Hypogastrura viatica*	*Mesaphorura macrochaeta*	*Mucrosomia caeca*	*Proisotoma minuta*	*Tulbergia mixta*
South Sandwich Islands (not specified)		x									
Coronation Island		x									
Larsen Island		x		x							
Lynch Island		x		x		x					
Geddes Island				x							
Signy Island	x	x		x		x					
Signy Island, Gourlay Peninsula		x				x					
Laurie Island	x, t	x		x							
King George Island (not specified)		x			x						x
King George Island, Mackellar Inlet		x		x	x						x
King George Island, Keller Peninsula						x, t					
King George Island, Arctowski Station		x									
King George Island, Arctowski Station		x	x	x	x	x					x
King George Island, Admiralty Bay		x		x	x						x
K. George Isl., Fildes Penin. (not specified)		x	x		x	x					x
King George Island, Biologenbucht		x	x	x	x	x					x
King George Island, Punta Cristian			x	x	x	x					x
King George Island, Potter Cove					x						x
Penguin Island		x		x	x						x
Ardley Isl		x	x	x	x						x
Nelson Island		x		x	x						x, t
Torre Island		x									
Islet near Torre Island		x		x							
Gonzales Island		x		x							
Greenwich Island (not specified)		x		x	x						
Isla de la Fuenta		x		x							
Greenwich Island, Base Arturo Prat											x
Greenwich Island, Yankee Hbr.				x							
Halfmoon Island		x		x	x			x			
Livingston Island, Juan Carlos Station		x									
Livingston Island, Byers Peninsula		x	x, t	x	x	x					x
Livingston Island, False Bay		x		x	x						x

Deception Island (not specified)	x	x		x	x	x	x		x		x
Deception Island, Whalers Bay		x	x				x	x	x	x	
Deception Island, Whalers Bay		x	x	x	x	x	x	x	x	x	x
Esperanza Station		x									
Hope Bay		x		x	x						
Tabarin		x		x	x						
Tower Island		x		x	x		x				
Devil Island	x	x	x				x				
Paulet Island		x									
Auguste Island		x									
Harry Island		x			x						
Alcock Island				x	x						
Brabant Island				x	x						
Brialmont Cove (Danco Coast)		x		x	x						
Cuverville Island	x	x									
Dream Island		x		x	x						
Anvers Island, Norsel Point	x	x		x	x						
Anvers Island, Palmer Station		x		x	x						
Anvers Isandl, Biscoe Point	x										
Anvers Island, Port Lockroy		x		x	x						
Neko Harbour		x					x				
Humble Island		x			x						
Janus & Humble Islands		x		x	x						
Litchfield Island		x		x	x						
Laggard Island		x			x						
Paradise Harbour		x		x	x						
Hovgaard Island		x			x						
Uruguay Island		x		x	x						
Galindez Island		x		x	x						
Green Island		x		x	x						
Darboux Island		x		x	x						
Graham Land (not specified)		x									x
Adelaide Island (not specified)					x						
Adelaide Island, Rothera Point		x	x		x						
Lagoon Island		x	x		x						
Leonie Island		x	x		x		x				
Anchorage Island		x	x		x						
Avian Island		x			x						
Dion Island		x			x						
Faure Island		x			x						
Alexander Island, Ablation Valley			x								
Alexander Island, Mars Oasis			x								
Alexander Island, Two Step Moraine			x								

sites including areas with pioneer and poor vegetation (Bulavintsev 1990). Similar ecological preferences were shown for the colder environments of Alexander Island (Convey & Smith 1997). The species is well transported by both water and wind (Hawes et al. 2007, 2008b), which can partly explain its wide distribution in isolated ice-free habitats of the Antarctic Peninsula. The species shows high if not the highest densities among Antarctic Collembola and sometimes forms swarms (Schulte et al. 2008, Benoit et al. 2009).

The species feeds preferably on algae and lichens more than mosses (Bokhorst et al. 2007). It has been a model object for ecophysiological investigations. Its lacking dehydration resistance was shown by Block et al. (1990). Other commonly studied aspects of its biology have been ice-crystal nucleation (Block & Worland 2001), cold tolerance (Block et al. 1978, Cannon 1986, Burns et al. 2010), feeding (Broady 1979) and diurnal activity (Burn & Lister 1988). Biological characteristics under laboratory conditions were studied by Schaller &
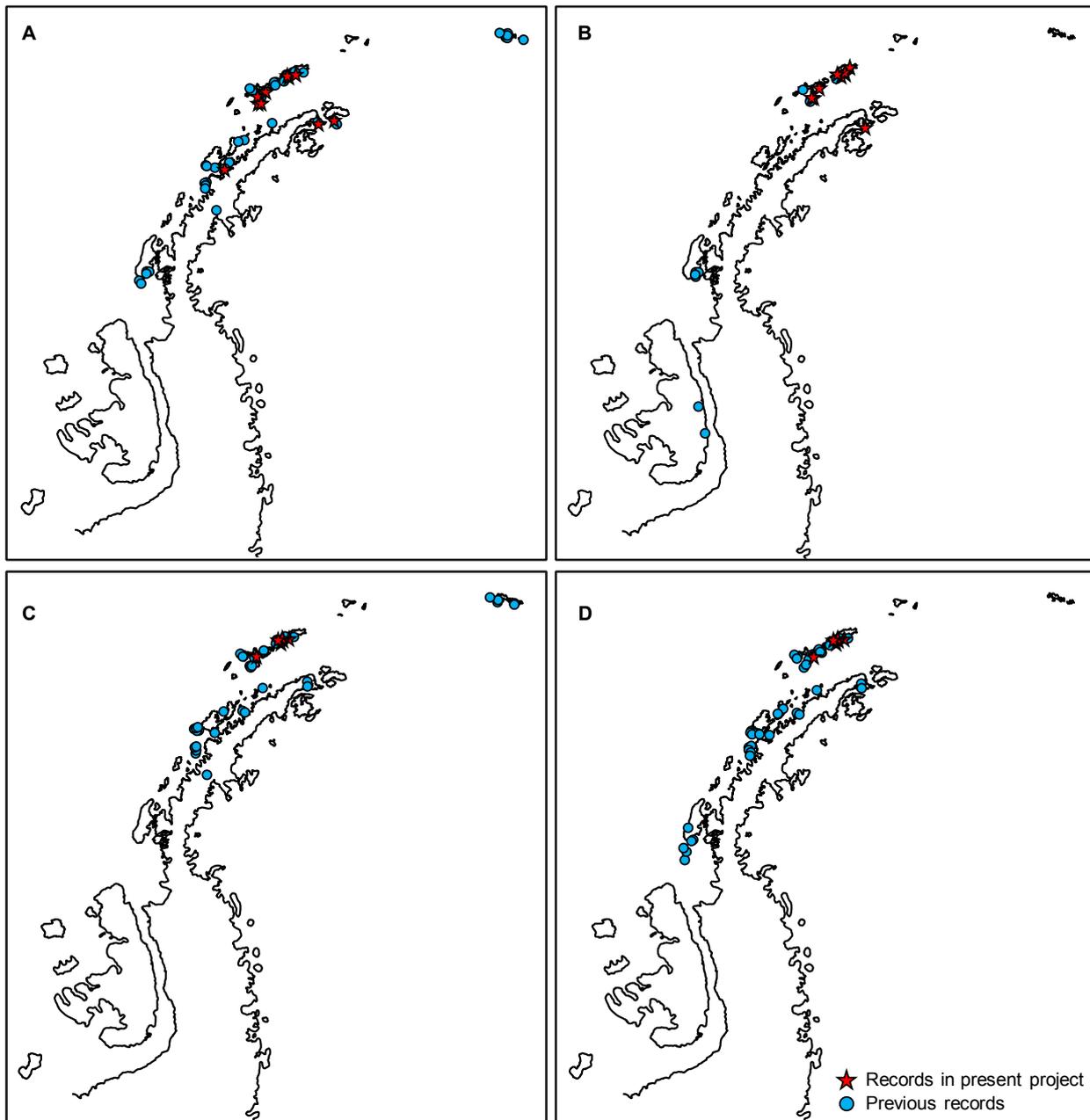
**Figure 4**. Previous (blue points) and present records (red stars) of *Cryptopygus antarcticus* (**A**), *Cryptopygus badasa* (**B**), *Folsomotoma octooculata* (**C**) and *Friesea grisea* (**D**) (Collembola) in the maritime Antarctic. Sources: Collembolan and soil faunal literature from the Antarctic (as far as available to the authors), citations given in the Supplementary Material (Tab. S7) at www.soil-organisms.org.

Kopeszki (1991). This highly cold-tolerant springtail can be indifferent to higher temperatures (Bokhorst et al. 2008). This is partly supported by field experiments made by Day et al. (2009): the abundance of *C. antarcticus* was not significantly greater in warmed cores, provided they did not receive supplemental precipitation (combined warming and precipitation had a great positive effect). *C. antarcticus* has many overlapping generations and a 3–7 year life cycle, which probably reflects the life strategy of a cryophilous microarthropod living in unpredictable environmental conditions – all life stages can survive under low temperatures while overwintering or during catastrophic temperature drops during warmer periods (Burn 1981, 1984). Some correlations were found between soil water content and species density (Booth & Usher 1984). It avoids very dry habitats, reflecting its relatively low desiccation resistance (Hayward et al. 2004).

The occurrence of *C. antarcticus* correlated in the present study positively particularly with amounts of organic matter in soils, soil moisture as well as finer grained soil substrates (sands) in both study years (Supplementary Material, Tab. S2). In the year 2010 the species also correlated with latitude (= locality), while its records from the year 2011 also related positively to vegetation cover and negatively to pH.

Cryptopygus badasa Greenslade, 1995

This species was recorded in eight locations in the present study. The species was first described from Livingston Island (South Shetland Islands). Later it was scarcely recorded throughout the western part of the maritime Antarctic (not recorded in the South Orkney Islands, South Sandwich Islands or Bouvet Island). It is thus a local species for part of the maritime Antarctic. It can be assumed that some older records of *C. antarcticus* in the maritime Antarctic refer to this species. *C. badasa* shares many morphological characters with the latter, but readily differs in smaller size, paler colouration and slender body. Records of its distribution are given in Table 2 and Fig. 4B. The species was recorded in Devil Island and Hannah Point for the first time during the present investigation.

C. badasa correlated in the current study strongly in both years to factors regarding location (i.e., sampling date, latitude) as well as positively to vegetation cover (Supplementary Material, Tab. S2). In the year 2010 it further correlated positively to factors regarding the content and quality of organic material in the sampled soils as well as negatively to temperature. In the year 2011 it also correlated positively to soil moisture.

Folsomotoma octooculata (Willem, 1901)

F. octooculata is one of the common collembolan species in the Antarctic Peninsula (Table 2). It was recorded in six locations in this study. It was described as *Isotoma octooculata* by Willem (1901) from Harry Island, Cape van Benenden in Danco Land and Cavelier de Cuverville Island (all in the Gerlache Strait). It has only been recorded from the maritime Antarctic, including the South Shetland Islands and South Orkney Islands, and can be considered to be a locally endemic species. For all of its records see Table 2 and Fig. 4C. It extends less into higher latitudes than does *C. antarcticus*, as described at the macrogeographical scale of the maritime Antarctic by Usher and Edwards (1986b); this is also generally indicated by its known records (Tab. 2).

F. octooculata was frequently listed (as *Parisotoma octooculata*) in typical Antarctic biotopes, often together with *C. antarcticus* although almost always in lower densities, but often more abundant in ornithogenic and more vegetated habitats (Tilbrook 1967a). Field observations on King George Island showed the species preferring sites with a well developed moss cover and being very abundant in ornithogenic soils enriched with penguin guano (Bulavintsev 1990). *F. octooculata* completes three to four moults during summer, overwintering either in the egg stage or as fourth or fifth instars. The species has a faster growth rate than *C. antarcticus*. It is suspected that *F. octooculata* shows features more characteristic of temperate Collembola, such as pronounced synchronisation of oviposition and hatching with season changes (Burn 1984). A clear circadian pattern is absent in the species (Burn & Lister 1988), unlike in *C. antarcticus* which shows an activity peak during the day. According to Tilbrook (1967a), desiccation-induced mortality occurs sooner in *F. octooculata* than in *C antarcticus*. Schenker (1984) showed less cold-hardiness in this species than in other Antarctic microarthropods.

This species correlated in the present study to latitude as well as positively to vegetation cover in both study years (Supplementary Material, Tab. S2). It showed a positive relation to amounts of organic material and a negative relation to finer grained soil substrates (sands) in 2010 as well as a positive relation to soil moisture in 2011. The correlations to soil temperature were contradictory, with a negative correlation coefficient in 2010 and a positive coefficient in the year 2011.

Friesea grisea (Schäffer, 1891)

A common species of the Antarctic Peninsula, *F. grisea* was recorded in eight locations in the present

investigations. It was first described as a new species from South Georgia, although the description was incomplete. Many records and redescriptions have been made from other locations in Antarctica (for details see Greenslade 2010). Thus far, the species has not been recollected from South Georgia recently, despite several surveys. The true identity of this species in the maritime Antarctic remains doubtful, since the original description is deficient and no subsequent records have been made from South Georgia. A possible alternative name for the records of *Friesea grisea* in Western Antarctica is *Friesea antarctica* (Willem, 1901), the latter having been described from more southern areas as *Achorutoides antarcticus*. *F. grisea* (maintaining the accepted name) is widely distributed in the maritime Antarctic and is common in the South Shetland Islands. Up to now it has been the only 'pan-Antarctic' species of Collembola recorded both from Western and Eastern Antarctic. However, large molecular differences were shown to exist between the western and eastern populations, which strongly restrict the true distribution of *F. grisea* (Torricelli et al. 2010). Based on modern knowledge, the specimens recorded in the present study will possibly receive the status of a Western Antarctic species. Unlike *Cryptopygus antarcticus* (see above), the species was not recorded in the Subantarctic (with the exception of South Georgia). Records of its distribution are shown in Table 2 and Fig. 4D. We do not consider the numerous records of this species in continental (i.e. Eastern) Antarctica, since these all probably refer to another, undescribed species of *Friesea*.

F. grisea often occurs together with *C. antarcticus* and shows a similar ecology (see above; Gressitt et al. 1963, Richard et al. 1994, Convey et al. 1996, Convey & Smith 1997). On King George Island it is an eurytopic species, and like other Antarctic species it shows higher densities in organically enriched soils (Bulavintsev 1990). For the climatic conditions of Marguerite Bay (Maritime Antarctica), it was shown that moisture can be a potential habitat parameter segregating *C. antarcticus* and *F. grisea*: the latter can survive in drier habitats due to its ecological preferences and behavioural strategies (Hayward et al. 2004).

In the present study, this species correlated in both study years to latitude (= locality) as well as positively to vegetation cover and soil moisture and negatively to coarser grained substrates (gravels) (Supplementary Material, Tab. S2). In 2010 the species further correlated positively to various parameters concerning the quantity and quality (C/N-ratio) of organic material in the sampled soils, while in 2011 it also correlated positively to finer grained substrates (sands) as well as negatively to soil pH.

Friesea woyciechowskii Weiner, 1980

The species has only been recorded a few times in Antarctica (three in the present study) and is probably endemic to the warmer parts of the maritime Antarctic (South Shetland and South Orkney Islands). It was first described from King George Island. For all of its known records, see Table 2.

F. woyciechowskii was only recorded in 2010. In this year it only correlated with sampling date (Supplementary Material, Tab. S2), which most likely reflects location.

Mucrosomia caeca (Wahlgren, 1906)

This species was recorded in one location (Whalers Bay on Deception Island) in the current investigation. It is widely known from the Subantarctic and even from southern areas of South Africa, Australia, New Zealand and South America. It was first described from South Georgia (Subantarctic). Deception Island (South Shetland Islands) is the only Antarctic record for this species. It has been found there several times (Tilbrook 1967a, Wise 1971, Greenslade & Wise 1984), but not on other neighbouring islands. The distribution of the species can, however, become wider when considering *Mucrosomia garretti* (Bagnall, 1939) to be its junior synonym. *Mucrosomia garetti* is thus far considered to be a European species, but may also possibly be a population of *M. caeca* introduced to Europe (Potapov 2001). The role of *M. caeca* could be re-estimated even in Subantarctica and the status of this species (native/exotic) is in doubt.

In contrast to almost all other collembolan species, *M. caeca* correlated positively to soil temperature and negatively to quantities and quality of soil organic matter (Supplementary Material, Tab. S2). Since this species was only recorded in Deception Island in this study, these correlations most likely reflect the conditions of this island more than true habitat preferences of the species.

Tullbergia mixta Wahlgren, 1906

The genus *Tullbergia* s.s. is distributed in the Southern Hemisphere (Deharveng 1981, Dunger & Schlitt 2011). Morphologically, it is a large-sized microarthropod untypical for the family Tullbergiidae. Together with a few other 'southern genera', species of the genus *Tullbergia* are the only representatives of blind euedaphic Poduromorpha in high latitudes of the Southern Hemisphere, where they presumably occupy the niche of Onychiuridae, particularly of the similarly large-sized genus *Protaphorura* common in the Arctic. Two species

(*T. mixta* and *T. mediantarctica* Wise, 1967) are known for Antarctica so far (vs. many in the Subantarctic). Their abundances in the maritime Antarctic are not very high. *T. mixta* was recorded in six locations in the present study, five of which are on King George Island. It was first described from Nelson Island (South Shetland Islands). In the opinion of Greenslade (2010), it was probably misidentified as *T. mediantarctica* in material from King George Island. It is most likely endemic to the South Shetland Islands. For its known records, see Table 2.

T. mixta correlated to factors concerning locality as well as positively to vegetation cover in both years (Supplementary Material, Tab. S2). In the year 2010 it further correlated positively to amounts and quality of organic material and soils and 2011 positively to soil moistures. The correlation results regarding soil temperature, however, were contradictory, with a negative correlation in the year 2010 and a positive correlation 2011.

Six species were recorded that are apparently non-native to Antarctica: *Hypogastrura viatica* (Tullberg, 1872), *Protaphorura fimata* (Gisin, 1952), *Folsomia candida* Willem, 1902, *Mesaphorura macrochaeta* Rusek, 1976, *Proisotoma minuta* Tullberg, 1871 and *Deuteraphorura cebennaria* (Gisin, 1956). *P. fimata*, *F. candida* and *D. cebennaria* were sampled by the British Antarctic Survey and identified during the present study. All species were found exclusively on Deception Island (s. Greenslade et al. 2012), with the exception of *H. viatica*, which was also recorded from Neko Harbour and Halfmoon Island. The results of these species will be presented in a subsequent paper.

3.3. Actinedida (Acari)

A total of almost 2100 individuals of actinedid mites were registered in the present study, over 1600 in the year 2010 and more than 450 in 2011. These mites were found in densities between zero (e.g., on Devil island 2010) and almost 50 ind. per 100 cm³ (e.g., in various localities of the Fildes Peninsula in 2010). In both years, highly significant differences between localities were determined (2010: $X_r^2 = 86.317$; P <0.001; 2011: $X_r^2 = 58.461$; P <0.001; Tab. A2, Appendix), whereby particularly the densities found in the localities on or around King George Island were significantly higher in both years than those of the remaining localities.

Within both sampling years, total densities correlated with location, vegetation cover and soil moisture, although positive relationships between location and vegetation cover were stronger in 2010 (Supplementary Material, Tab. S3). Interesting were the contradictory correlations between the two study years regarding soil temperature and the various parameters concerning soil organic material; densities correlated negatively to soil temperature in 2010 but positively in 2011, while a positive relationship to amounts and quality (C/N ratio) of organic matter was discernible in 2010 and a negative relationship to amounts of N and C in 2011.

A total of 23 separate taxa could be proven (Tab. A2, Appendix), 22 in year 2010 and 18 in 2011. As in the densities, differences in species richness (average species number per area) between individual localities were also highly significant (2010: $X_r^2 = 80.604$; P < 0.001; 2011: $X_r^2 = 44.741$; P < 0.001; Tab. A2, Appendix), whereas again species richness was generally found to be higher in the localities on King George Island than in the other localities. However, the highest number of registered species (both years taken together: 17) was found on Whalers Bay, whereas in the other localities between zero (again on Devil Island) and 10–13 taxa (the localities on the Fildes Peninsula) could be determined.

Correlations between species richness and habitat parameters generally paralleled those of densities (Supplementary Material, Tab. S3). Higher species richness correlated with locality as well as increases in vegetation cover and soil moisture. In 2010 species richness correlated negatively with soil pH, meaning more species were found at lower pH values. The contradictory correlations to soil temperature and organic material were also found with species richness.

The species determined in the present study as well as their average densities in the various localities are given in the Appendix (Tab. A2). In the following, the individual species known to occur in the Antarctic are described together with information on their known distribution and ecology. Actinedid mites have been fairly regularly studied in the maritime Antarctic in the past decades, particularly by members of, e.g., the Bishop Museum (Honolulu) or the British Antarctic Survey. The studied sites were widespread throughout the Antarctic Peninsula, as far south as 71° S (Alexander Island), albeit particularly on the west side of the Peninsula and in localities accessible from various research stations (Fig. 5). Although the studied localities in the present study were concentrated in the northern half of the Antarctic Peninsula, with some localities visited that had been studied by other research groups in the past, most of the studied sites represent new additions to the known distribution of the Antarctic actinedid fauna (Fig. 5).

Apotriophtydeus André, 1980

Apotriophtydeus species are very small tydeid mites (= species of the families Meyerellidae, Iolinidae and Tydeidae). Five species of *Apotriophtydeus* are known since the taxonomic revision of Usher & Edwards (1986a). Although these species have been found throughout the maritime Antarctic (Tab. 3, Fig. 6A), there is little information about their habitat preferences. They have been recorded concentrated at 3–6 cm depth within stands of *Deschampsia antarctica* (Usher & Edwards 1984). Usher & Edwards (1986a) described the species as occurring mainly in lichens and mosses, but also described a spatial niche separation of different maritime Antarctic species: *A. penola* in moss-dominated sites, *A. terror* in fellfields and *A. scotia* in a variety of habitats, most frequently drier lichen-dominated habitats and fellfields.

The various species of this genus are often taxonomically difficult to differentiate, species separation at times being only possible via a regression of the sizes of different morphological characters. In the present study, it was thus not possible to differentiate all individuals, usually a representative portion of the species of each sample were thus determined. Possibly two species were recognized: *A. scotia* and *A. wilkesi*. These specimens were primarily found in the present study in the South Shetland Islands,

Figure 5. Previous (blue points) and present records (red stars) of the actinedid species registered in the present study. Sources: acarological and soil faunal literature from the Antarctic (as far as available to the authors, citations given in the Supplementary Material (Tab. S8) at www.soil-organisms.org) as well as the Biodiversity Database of the Australian Antarctic Data Centre.

but also in Neko Harbour (Fig. 6A). They were usually registered with one to few individuals in single samples of the various locations, with the exception of Punta Christian, where the species were more widespread and aggregations of many individuals (>100) were found in single samples. *A. scotia* correlated negatively to soil temperature and this only in 2010 (Supplementary Material 4, Tab. S3).

Bakerdania cf. *antarcticus* (Mahunka, 1967)

Bakerdania antarcticus is a small pygmeoid mite first described in 1967 from the Antarctic Peninsula (Danco Coast near the Chilean Base Gabriel González Vedela; Mahunka 1967). The determination in the present samples is somewhat uncertain, because the original description is incomplete and this genus is very species-rich worldwide. However, this is the only species of this genus having been recorded in the Antarctic, although other species are known from the Subantarctic (i.e., Cross 1964, 1970). Up to now this taxon has only been recorded from the South Sandwich Islands, Livingston Island and Deception Island (Tab. 3). Little is known about its habitat preferences; it has been found associated with birds' nests (Tilbrook 1967b, Goddard 1979b *as Pygmephorus* sp.).

In the present study, *B.* cf. *antarcticus* was only found in three locations of the South Shetland Islands (Tab. 3). Although sometimes only occurring in few individuals in single samples within a locality, the species was actually fairly abundant and widespread near Arctowski Station (King George Island) as well as in Whalers Bay (Deception Island). In 2010, the species correlated positively to soil moisture (Supplementary Material, Tab. S3).

A number of other individuals from families related to this taxon were also registered, particularly Tarsonimidae taxa. Although found in many localities in the present study (Tab A2, Appendix), these were usually only registered as single individuals per sample and were usually juveniles. Their taxonomy is extremely difficult, so that a number of adult individuals are necessary for a secure determination, which was thus not possible here. Although taxa of this family have only been listed as occurring in the Subantarctic by Pugh (1994), based on the present data and level of determination it cannot be evaluated whether they are native to the Antarctic or introduced. Species from this family are often algivorous, fungivorous as well as phytophagous (Krantz & Walter 2009), feeding preferences that coincide with many of the species determined in this study.
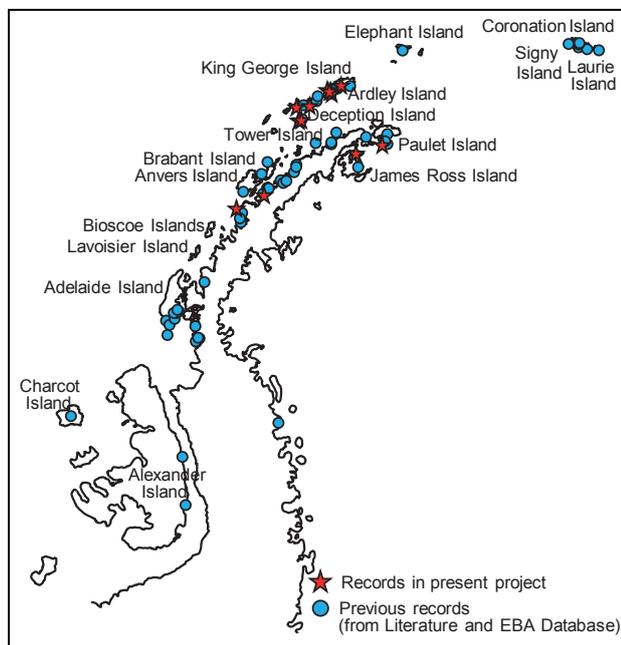
Ereynetes macquariensis Fain, 1962

E. macquariensis also belongs to the typical maritime Antarctic fauna; it has mostly been found in the northern Antarctic Peninsula, South Shetland Islands and the South Sandwich Islands (Tab. 3, Fig. 6B). The species is also known from various Subantarctic islands (Pugh 1993, Marshall et al. 1999). In the maritime Antarctic it has been commonly found in algae-rich soils, *Prasiola* mats, mosses or swards of *Deschampsia antarctica*; it is apparently most frequent and abundant in mosses (Strandtmann & Tilbrook 1968, Goddard 1979b, Usher & Edwards 1984). In moss turf *E. macquariensis* is often evenly distributed throughout the vertical profile, whereby adults can be found deeper in the profile than juveniles (Goddard 1979a, Usher & Booth 1984). As opposed to other species, this species apparently does not often form aggregations (Usher & Booth 1984). It seems to be particularly susceptible to desiccation (Goddard 1979b), which may explain its occurrence in deeper levels of the soil profile. First-stage larvae hatch from eggs apparently in summer (December and
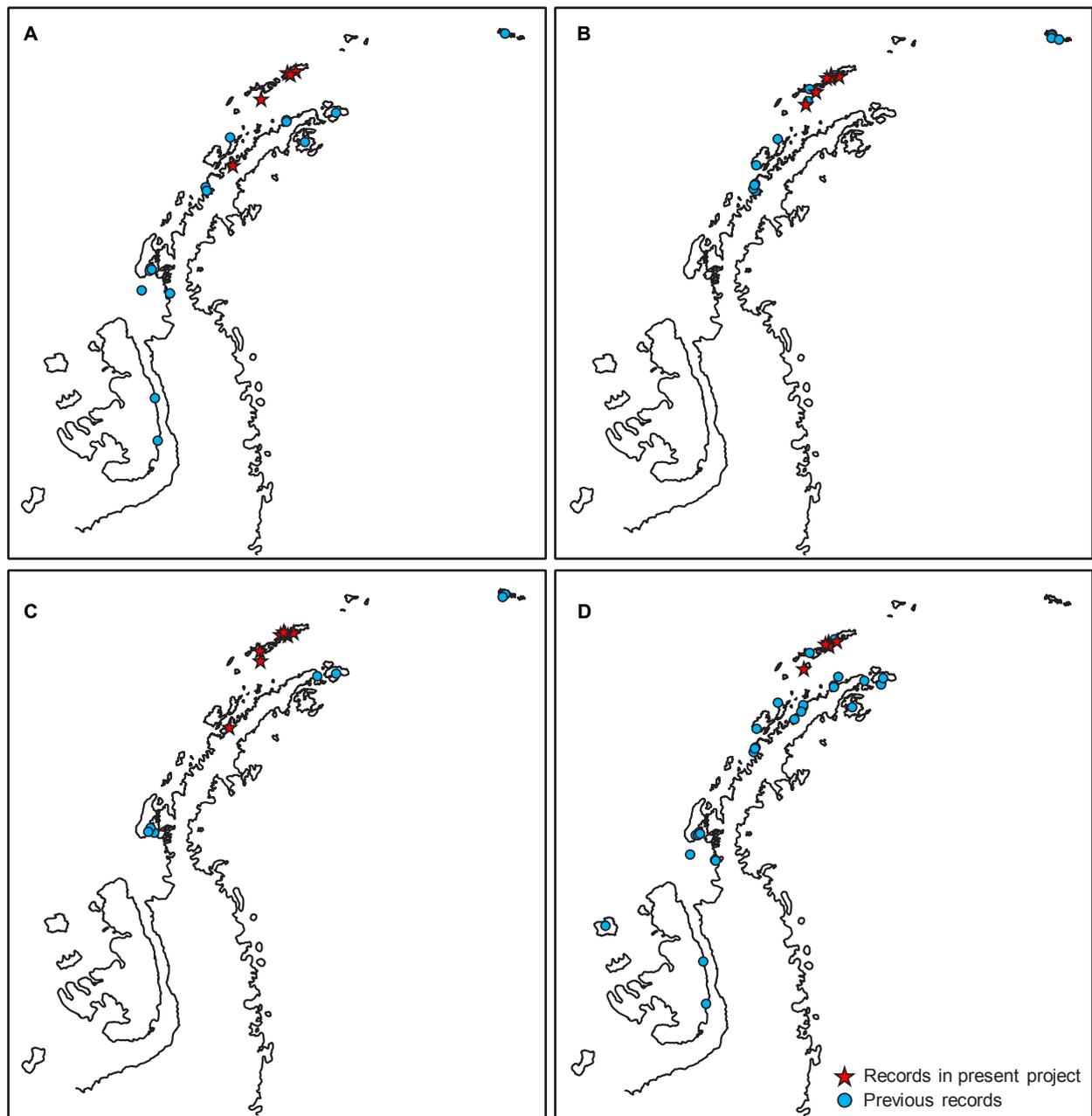
Figure 6. Previous and present records of *Apotriophtydeus*-species (**A**), *Ereynetes macquariensis* (**B**), *Eupodes exiguus* (**C**) and *Nanorchestes nivalis* (**D**) in the maritime Antarctic (blue dots) as well as records from the current study (red stars). Sources: as in Fig. 5.

January), whereas other life-cycle stages can be found throughout the year; the species apparently overwinters as last-stage nymphs (tritonymphs) or adults (Usher & Booth 1986). *E. macquariensis* seems to feed on algae and fungi (Goddard 1982), but may also be predatory (Usher & Booth 1984).

In the present study the species was found primarily in the South Shetland Islands in both study years (Fig. 6B), often in numerous individuals spread throughout many samples in those localities where it occurred. Mostly juveniles were registered. *E. macquariensis* correlated positively to vegetation cover in both study years as well as to amounts and quality of organic material in 2010 and to soil moisture in 2011 (Supplementary Material, Tab. S3). It correlated negatively to (= lower densities in) finer grained soil substrates in 2010.

Eupodes (*Protereuntes*) C. L. Koch, 1835

Eupodes represents another fairly species-rich and widely distributed genus in the Antarctic. This genus is also distributed worldwide in a high variety of habitat types, where it often represents one of the most dominant actinedid taxa in soils. In the Antarctic at least nine species of this genus are known, all of which only occur in the Antarctic or Subantarctic (Pugh 1993, Booth et al. 1985). The most common species of this genus in the maritime Antarctic belong to the subgenus *Protereuntes*, where three species are known (*E. minutus* (Strandtmann, 1967), *E. exiguus* Booth, Edwards & Usher, 1985 and *E. parvus* Booth, Edwards & Usher, 1985, the latter with 2 subspecies).

The genus has generally been found in moss turf or young moss patches as well as in patches of *Deschampsia antarctica*, often highly abundant but more rarely under stones (Gressitt et al. 1963, Gressitt 1967, Usher & Booth 1984). It is generally fairly evenly distributed throughout the vegetation profile, whereby adults can be found highly aggregated in surface layers and juveniles can penetrate deeper into the profile (Usher & Booth 1984). Species of this genus have not been found to have a clear yearly cycle; juveniles often hatch soon after eggs are laid and all life stages can overwinter; their mean generation time has been determined to be 1–2 years (Usher & Booth 1986). They are assumed to feed on fungal hyphae and algae, but may also be scavengers (Strong 1967, Goddard 1982).

Besides the three species listed below, many individuals of this genus found in the present study were juvenile, which could not be determined to species level. It is thus possible that more than the three species listed below were present in the samples.

Eupodes minutus (Strandtmann, 1967)

The most commonly found and most widespread *Eupodes* species in the maritime Antarctic is *E. minutus* (Tab. 3), and earlier studies in Antarctica only recorded this species (Gressitt et al. 1963, Gressitt 1967, Usher & Booth 1984). However, Booth et al (1985) demonstrated that these early records of *E. minutus* also include the other two species listed below. Therefore, much of the information regarding the species, including the distribution given in Table 3, probably concern a combination of different species.

This possibility of species confusion notwithstanding, *E. minutus* has been found widespread in many maritime Antarctic sites as well as in the Subantarctic, e.g., South Georgia (Goddard 1979b), the Macquarie & Prince Edward Islands (Marshall et al. 1999, Barendse 1999 [cit. in Convey et al. 2000b]). The species has been generally found in the upper layers of mosses, *Deschampsia antarctica*, lichens and *Prasiola crispa* mats as well as (rarely) under stones (Goddard 1979a, 1979b, Usher & Edwards 1984, Convey et al. 2000b). It is fairly susceptible to desiccation and avoids dry areas and is photonegative (avoids sunlit areas) (Goddard 1979b). Its main food resources are most likely epiphytic algae as well as fungal hyphae (Strong 1967, Goddard 1982).

E. minutus was found during this study primarily in the locations on and around King George Island, but also on Halfmoon Island as well as Deception Island (Whalers Bay), but only in 2010 (Tab. 3). Within these localities, however, it was only found in single samples in only a few individuals, which is in contrast to previous published reports of the species. No significant correlation to any habitat parameter could be found.

Eupodes parvus Booth, Edwards & Usher, 1985

E. parvus is somewhat larger than the other two species described here. It has been found fairly widely distributed on and around the Antarctic Peninsula (Tab. 3), more so than, e.g., *E. exiguus*, perhaps due to it being more conspicuous. Little explicit information has been given about its habitat preferences other than single observations of records in algal mats, mosses and nests, with highest densities in dead mosses, and absence under stones (Convey & Quintana 1997).

In the present study this species was only found on King George Island and Ardley Island (Tab. 3), which were the most vegetated localities sampled here. It was usually only observed in a few individuals in few samples. *E. parvus* did not correlate significantly to any habitat parameter.

Table 3. Known records of occurrence (*x*) of the acarine species determined in the present study. The localities are sorted by increasing southern latitude. Localities of the present investigation are shaded grey. *t*: type locality of the given species; *Gamas.*: Gamasina. Sources: the Biodiversity Database of the Australian Antarctic Data Centre (SCAR Life Sciences programme EBA [Evolution and Biodiversity in the Antarctic]) and acarological and soil faunal literature from the Antarctic (as far as available to the authors; shown in the Supplementary Material (Tab. S8) provided online at www.soil-organisms.org).

Locality	Actinedida												Oribatida					Gamas.	
	Apotriophydeus spp.	*Bakerdania antarcticus*	*Ereynetes macquariensis* [a]	*Eupodes exiguus*	*Eupodes minutus*	*Eupodes parvus*	*Nanorchestes berryi*	*Nanorchestes „antarcticus"*	*Nanorchestes nivalis* (= *gressitti*)	*Pretriophydeus tilbrooki*	*Rhagidia gerlachei* [b]	*Stereotydeus villosus* [b]	*Alaskozetes antarcticus* [c]	*Halozetes belgicae* [c]	*Globoppia loxolineata* [d]	*Liochthonius mollis* [e]	*Brachychochthonius* sp.	*Hydrogamasellus racovitzai* [b]	*Parasitus tarsispinosus*
South Sandwich Islands		x			x			x					x	x					
Montago Island									x										
Coronation Island		x			x			x		x		x	x	x				x	
Lynch Island	x	x	x	x	x	x						x	x		x			x	
Monroe Island								x		x		x	x	x				x	
Frederiksen Island													x	x					
Signey Island		x	x	x,t	x	x,t	x	x		x	x	x	x	x	x			x	
Laurie Island								x		x		x	x	x				x	
Steepholm (Atriceps Island)		x			x		x					x	x	x	x			x	
Elephant Island								x		x	x		x	x				x	
Gibbs Island (= Narrow Island)													x					x	
K. George Isl., Admirality Bay												x	x	x	x				
Penguin Island								x		x	x	x	x	x	x			x	
K. George Isl., Arctowski Stat.	x	x	x	x	x		x		x	x		x	x	x	x			x	
K. George Isl., Point Thomas													x	x				x	
King George Island, Potter cove												x	x	x				x	
K. George Isl., Punta Cristian	x	x	x	x	x	x		x	x			x	x		x	x		x	
K. George Isl., Biologenbucht		x	x	x	x	x		x			x	x						x	
Ardley Island	x	x	x		x	x												x	
Ardley Island (incl. Rip cove)		x		x	x	x		x			x	x	x	x	x			x	
Nelson Island												x	x	x				x	
Robert Island												x	x					x	
Greenwich Island											x	x							
Halfmoon Island		x			x							x	x					x	
Hannah Point													x					x	
Livingston Island		x	x	x	x	x	x	x	x	x		x	x	x	x, t			x	
Whalers Bay, Deception Island	x	x	x	x	x			x			x	x							x
Deception Island		x	x		x			x		x	x	x	x	x	x,t	x		x	x,t
Astrolabe Island						x		x	x	x			x	x	x			x	x
Joinville Island	x				x			x		x		x		x	x	x		x	
Hope Bay			x					x		x	x		x	x	x			x	

(Tab. 3 continued) Locality	Actinedida												Oribatida					Gamas.	
	Apotriophtydeus spp.	*Bakerdania antarcticus*	*Ereynetes macquariensis* [a]	*Eupodes exiguus*	*Eupodes minutus*	*Eupodes parvus*	*Nanorchestes berryi*	*Nanorchestes „antarcticus"*	*Nanorchestes nivalis* (= *gressitti*)	*Pretriophtydeus tilbrooki*	*Rhagidia gerlachei* [b]	*Stereotydeus villosus* [b]	*Alaskozetes antarcticus* [c]	*Halozetes belgicae* [c]	*Globoppia loxolineata* [d]	*Liochthonius mollis* [e]	*Brachychochthonius* sp.	*Hydrogamasellus racovitzai* [b]	*Parasitus tarsispinosus*
Cape Roquemaurel (Bone Bay, Antarc. Penin.)	x			x	x			x			x		x	x	x			x	
Paulet Island													x						
Paulet Island												x							
Tower Island										x	x	x	x					x	
Dundee Island			x		x	x		x										x	
Young Point (Bone Bay)	x							x	x				x	x	x			x	
Devil Island																			
James Ross Island	x							x, t	x				x	x				x	
Vega Island														x					
Brabant Island	x		x	x	x	x		x	x	x	x	x	x	x	x			x	
Leopardo Island				x	x			x			x	x	x	x	x			x	
Cierva Point (Cierca Cove)				x	x			x		x	x	x	x	x	x			x	
Cockburn Island														x					
Alcock Island																		x	
Spring Point (Brialmont Cove)								x	x				x	x				x	
Melchior Islands											x		x	x	x			x	
Slippery Rock Island														x					
Gaston Island							x				x	x	x		x			x	
Andree Island				x	x			x	x				x	x	x			x	
Meusner Point											x								
Boxing Island (Charlotte Bay)											x		x	x	x			x	
Cuverville Island											x		x	x	x			x	
Brewster Island										x	x		x	x				x	
Danco Island											x,t		x					x	
Cormorant Island													x	x	x			x	
Anvers Island			x	x,t		x,t	x	x[f]		x	x	x	x	x	x			x	
Humble/Torgersen Islands													x		x			x	
Norsel Point (Amsler Island)													x						
G. Videla Base, Paradise Bay	x,t										x	x	x	x					
Port Lockroy (Anvers Island)												x	x	x	x			x	
Neko Harbour	x		x					x									x		
Petermann Island															x				
Petermann Island									x, t										

(Tab. 3 continued)

Locality	Actinedida												Oribatida					Gamas.	
	Apotriophtydeus spp.	*Bakerdania antarcticus*	*Ereynetes macquariensis* [a]	*Eupodes exiguus*	*Eupodes minutus*	*Eupodes parvus*	*Nanorchestes berryi*	*Nanorchestes* 'antarcticus'	*Nanorchestes nivalis* (= *gressitti*)	*Pretriophydeus tilbrooki*	*Rhagidia gerlachei* [b]	*Stereotydeus villosus* [b]	*Alaskozetes antarcticus* [c]	*Halozetes belgicae* [c]	*Globoppia loxolineata* [d]	*Liochthonius mollis* [e]	*Brachychochthonius* sp.	*Hydrogamasellus racovitzai* [b]	*Parasitus tarsispinosus*
Argentine Islands													x	x	x			x	
Galindez/Darboux Island		x		x	x	x	x	x			x	x							
Green Island		x		x	x	x		x			x	x	x	x	x			x	
Darboux Island	x	x			x	x		x				x	x						
Takaki Promontary (Leroux Bay)	x				x	x	x				x		x	x	x	x		x	
Lahille Island													x	x				x	
Vieugue Island																		x	
Oxford Cliff												x	x	x	x			x	
Lagoon/Anchorage Island	x		x				x		x	x	x	x	x	x	x			x	
Adelaide Island, Rothera Point	x,t			x			x		x	x	x	x	x	x	x			x	
northern Marguerite Bay	x		x	x	x	x			x	x	x,t	x							
Leonie Island					x	x	x		x		x	x	x	x	x			x	
Pourquoi-Pas/Pinero Islands													x	x	x			x	
Jenny Island												x	x	x	x			x	
Avian Island										x	x	x	x	x				x	
Horseshoe Island													x						
Dion Island					x					x		x	x	x	x			x	
Lagotellerie Island													x		x			x	
Line Islands										x	x		x	x	x			x	
Camp Point (Square Bay)													x	x				x	
Fauré Island	x						x		x	x		x	x	x	x			x	
Stonnington Island																		x	
Neny Island												x				x			
Roman Four Promontary (Neny Fjord)	x						x						x	x	x			x	
Red Rock Ridge (Neny Fjord)				x	x	x			x			x	x	x	x			x	
Refuge Island					x	x			x		x	x	x	x	x			x	
Terra Firma Island																		x	
Charcot Island					x				x			x	x	x					
Alexander Island	x				x	x			x	x	x	x	x						
Mars Oasis, Alexander Island	x								x	x		x							

[a] Type locality: Macquarie Island (Subantarctic) (Fain 1962), [b] Type locality: Gerlach Strait (undifferentiated) (Trouessart 1903), [c] Type locality: Gerlach Strait (undifferentiated) (Michael 1903), [d] No holotype designated, thus no specific type locality, [e] Type locality in South America, [f] Type locality of *N. gressitti* (Strandtmann 1982), which has since been synonimized (Judson 1995) with *N. nivalis*.

Eupodes exiguus Booth, Edwards & Usher, 1985

E. exiguus is a small eupodid species very similar to *E. minutus*, which apparently has not often been found previously in the maritime Antarctic (Tab. 3, Fig. 6C). Accordingly, almost no ecological information regarding preferred habitat types or nutritional resources could be found.

In contrast to the paucity of published information on *E. exiguus*, it was the most abundant *Eupodes* species found in the present study in both years. It was widespread in the South Shetland Islands, but was also found on the Antarctic Peninsula itself (Fig. 6C). It frequently occurred sympatrically with *E. minutus*, but in densities that were often an order of magnitude larger. Due to the morphologically strong similarity with *E. minutus*, older literature data (before Booth et al. 1985) could possibly result from misdeterminations of *E. exiguus*. However, since the latter species possesses taxonomic characteristics not present in the former species, identification of these characters now allows a certain determination.

E. exiguus correlated positively to vegetation cover as well as amounts and quality of organic material and negatively to soil temperature, but only in 2010 (Supplementary Material, Tab. S3).

Nanorchestes Topsent & Trouessart, 1890

The genus *Nanorchestes* is one of the most common actinedid genera found throughout the world in a plurality of various habitat types. In the Antarctic the genus is widespread and presently 14 species of this genus are known, the majority of which are only known from this continent (Pugh 1993). *Nanorchestes* also occurs widely in the Arctic, but the species found in the two poles are generally different (Strandtmann 1968). The taxonomy of Antarctic *Nanorchestes* underwent a strong revision in the 1980s, with many new species described and the identity of previously determined species of this genus proven highly questionable. Records of *Nanorchestes* from the maritime Antarctic previous to this time usually referred to *N. antarcticus*, of which there are no longer any verified records in this area (Convey & Quintana 1997, Convey et al. 2000a). In the present study five species of this genus were distinguished, only two of which (*N. berryi* and *N. nivalis*) could be determined with absolute certainty.

This genus is found in a wide variety of different habitats in the Antarctic, in moss patches, lichens, soils rich in organic matter, algae (*Prasiola crispa*), the littoral zone and often in large concentrations under stones and rocks (Gressitt 1967, Goddard 1979b, Usher & Booth 1984). In moss turf it is generally found in surface layers, often in large aggregations, whereas juveniles can be found in deeper layers (Goddard 1979a, Usher & Booth 1984). The various species of this genus are all considered to feed on red and green algae as well as partly also on fungal hyphae (Strong 1967, Fitzsimons 1971, Goddard 1979b, 1982, Convey & Quintana 1997).

Members of the genus show a wide tolerance for various environmental conditions, e.g., being active between -20°C and +25°C and showing higher tolerances to lower humidities than other actinedid species and perhaps being the only mite species capable of surviving in barren chalikosystem habitats (Goddard 1979b). It cannot be determined if this wide range of tolerances applies to all species of this genus or is due to the studies being undertaken on individual species, which are now known to be species complexes. This taxon generally has very rapid developmental rates and thus can quickly develop individual-rich populations (Usher & Booth 1986). The average generation time is considered to be two years, whereby all developmental stages can overwinter (Usher & Booth 1986).

Nanorchestes berryi Strandtmann, 1982

N. berryi is also fairly widespread around the Antarctic Peninsula, but has been determined far less often than the following species (Tab. 3). It has generally been found in vegetated habitats, e.g., lichens, mosses or swards of *Deschampsia antarctica*, but rarely under stones (Usher & Edwards 1984, Convey & Quintana 1997, Convey & Smith 1997). The species has sometimes been associated with habitats dryer than those of *N. nivalis* (Convey & Quintana 1997).

In this study, *N. berryi* was generally found in the same locations as the following species (cf. Tab. 3), but in far higher densities and in both study years. The species correlated positively to location and vegetation cover in both years as well as to soil moisture and quantity and quality of organic material in 2011 (Supplementary Material, Tab. S3). The species' occurrence also correlated to soil temperature, however negatively in 2010 and positively in 2011.

Nanorchestes nivalis (Trouessart, 1914) (= *N. gressitti* Strandtmann, 1982)

N. nivalis, previous to Judson (1995) named *N. gressitti*, is the most widespread species of this genus in the maritime Antarctic (Tab. 3, Fig. 6D). For instance, it

occurs on all of the South Sandwich Islands, where it was found in 50% of samples (Convey et al. 2000a), which in the Antarctic may be considered very widespread. It is most likely of maritime Antarctic origin (Convey et al. 2000a), but has also been found in the Subantarctic, e.g., South Georgia (Convey et al. 2000b). It has generally been found in mosses and algal mats, often in high densities (Gressitt 1967, Convey & Quintana 1997, Convey et al. 2000b), as well as in green and red algae on snow (Gressitt 1967), but rarely under stones (but see Convey & Smith 1997).

In the present study the species was only found in 2010 in single to few individuals in individual samples, usually from the vegetated areas in or around King George Island (Fig. 6D). It was also found on Whalers Bay (Deception Island), but only where a light vegetation cover was present. This species showed no overall correlation to any habitat parameter.

Pretriophtydeus tilbrooki (Strandtmann, 1967)

P. tilbrooki represents another tydeid mite that has been very frequently registered throughout the maritime Antarctic in many studies (Tab. 3). As in *Apotriophtydeus* species, this species also represents one of the smallest Antarctic mites (Goddard 1979b). It has been registered in various habitat types, and different studies are often contradictory in this regard; e.g., it has been found both under stones and in vegetation (Strong 1967), was considered scarce in moss turf of Signey Island (Usher & Booth 1984), was found only in mosses and not under stones or in algal mats (Convey & Quintana 1997), but then again in large aggregations in *Prasiola* and lichens with only few specimens found in mosses (Goddard 1979b). Thus, factors other than the vegetation cover seem to determine the species' occurrence. *P. tilbrooki* seems to be less prone to desiccation than other actinedid species and also shows no photonegative behavior (Goddard 1979b). The adult seems to be the main overwintering stage (Goddard 1979a), as opposed to many other mite species, which (also) overwinter as juveniles. This species seems to feed predominantly on algae, fungal hyphae and lichens (Goddard 1982, Strong 1967), but may also be predatory (Convey et al. 2000a).

In the present study *P. tilbrooki* was only found in a few localities (Tab. 3) and even there only as single individuals in sporadic samples. This is in sharp contrast to its wide distribution reported in the literature. Due to so few individuals being registered, it was not possible to statistically analyze its relationship to habitat parameters.

Individuals of the related family Tydeidae were also recorded in the present study. Single specimens were found in sporadic samples spread throughout all the studied localities. Based on the limited possibilities of determination (only adults can be identified, of which there were very few), these specimens have been tentatively labeled '*Lorryia*', although it is likely that more than one genus is included here. Dozens of species of this genus exist worldwide (Kazmierski 1998), the taxonomy of which is extremely difficult. Species of this genus have been listed for maritime Antarctic localities, but these were species parasitic on seals, probably dislodged from the host animals (Pugh 1993), which is also quite possible in the present study.

Rhagidia gerlachei (Trouessart, 1903)

Another species commonly found in studies of the Antarctic mite fauna is *R. gerlachei*, where it is apparently very widely distributed throughout the maritime Antarctic (Tab. 3). One of two *Rhagidia* species occurring in the Antarctic, it is a large and very active predator feeding mainly on Collembola (Gressitt 1967, Strong 1967, Lister 1984 [cited in Convey & Quintana 1997]). It occurs in a wide range of habitats, such as *Prasiola* mats, lichens and mosses (Gressitt 1967, Convey & Quintana 1997), but is most frequently and most abundantly found under or on stones (Dalenius 1965, Strong 1967, Richard et al. 1994, Convey & Quintana 1997, Convey & Smith 1997). It apparently requires very high humidity, which in the maritime Antarctic is generally found under stones and rocks (Strong 1967).

In the present study, *Rhagidia* species were only found in two sites in 2010 (Arctowski Station, Biologenbucht) with only 1–2 individuals per site (Tab. 3). That this taxon was not registered more often in the present study is most likely due to differences in the sampling strategy (soil cores including vegetation and not under or on stones and rocks).

Stereotydeus villosus (Trouessart, 1902)

The genus *Stereotydeus* Berlese 1901 is also one of the most species-rich and widespread actinedid genera in the Antarctic, with eight species occurring on the continent and associated islands (Goddard 1979b, Pugh 1993). Within the family Penthalodidae, there is a strong generic difference between the Arctic and Antarctic faunas, with species of the genus *Penthalodes* Murray, 1877 occurring only in the Arctic (as well as other sites worldwide) while in the Antarctic only species of *Stereotydeus* are present (Strandtmann 1968).

The species *S. villosus* is only known from the maritime Antarctic (Convey et al. 2000b), where it is widespread

(Tab. 3) and occurs in many different habitat types (Strong 1967, Gressitt 1967, Convey & Quintana 1997, Convey & Smith 1997). Nonetheless, it has been found most frequently and in higher densities on or under stones or in rocky habitats than in soil substrates or vegetation (Gressitt 1967, Goddard 1979b, Usher & Booth 1984, Richard et al. 1994, Convey & Quintana 1997, Convey & Smith 1997), but also (more rarely) in mosses, lichens as well as under *Deschampsia antarctica* (Dalenius 1965, Gressitt 1967, Usher & Edwards 1984, Convey & Quintana 1997, Gressitt et al. 1963). The species is somewhat photonegative, with a clear diurnal activity cycle with higher activities at nighttime (Strong 1967, Goddard 1979b). It does not tolerate higher temperatures, becoming torpid above 15°C and dying within minutes at 25°C; on the other hand it remains active down to -16°C (Goddard 1979b). *S. villosus* apparently feeds on fungal hyphae, algae and possibly also on dead plant material (Gressitt 1967, Strong 1967, Goddard 1982).

In contrast to its being one of the most frequently recorded actenidid species in previous studies, in the present investigation it was only found in 2010 and usually only in single or few individuals and in single samples, albeit in a variety of localities (Tab. 3). An exception was the second locality at Punta Christian, where the species was found in many samples and in larger populations. The species did not correlate significantly to any habitat parameter (Supplementary Material, Tab. S3).

As in the Collembola, some species were determined that have not been previously recorded in the Antarctic and, due to their otherwise wide distribution in other parts of the world, potentially represent introduced non-native species: *Alicorhagia* Berlese, 1910 sp., *Coccotydaeolus* cf. *krantzii* Baker, 1965, *Speleorchestes* Trägårdh, 1909 sp. and *Terpnacarus gibbosus* (Womersley, 1944). Most were found – at times particularly abundant – at Whalers Bay (Deception Island) and Neko Harbour, but at times also in other of the studied sites (Appendix, Tab. A2). These species will be discussed in a subsequent publication.

3.4. Oribatida (Acari)

A total of 1107 individuals of the Oribatida were registered in the present study, 938 in the study year 2010 and 169 in 2011. These individuals were registered in total densities between zero in many of the localities and over 100 ind. per 100 cm^3, e.g., in Halfmoon Island in the year 2010. In both study years, significant differences in the total oribatid densities between the various localities could be determined (2010: $X_r^2 = 51.520$; P <0.001; 2011:

$X_r^2 = 94.321$; P <0.001; Tab. A3, Appendix).

Only few consistent and interpretable correlations between total densities of the Oribatida and the background habitat parameters could be discerned (Supplementary Material, Tab. S4). Truly clear was only a positive relationship in both years between total densities and the parameters that characterize the amounts (organic matter content), composition (contents of C and N) as well as quality (C/N ratio) of the organic substance of the soil substrates. In 2010 densities also correlated positively to soil moisture and, in 2011, positively to the vegetation cover as well as negatively to soil pH and soil temperature.

In those localities where Oribatida were recorded, species richness was comparatively low. A total of five species were registered in the two study years (Tab. A3, Appendix), four species in 2010 and only two in 2011. Species richness per locality with Oribatida ranged from a single species to a maximum of three taxa. It must be noted that, in both study years, the vast majority of registered individuals were juveniles (nymphs), which cannot be securely determined to species level.

Strongly significant differences in species richness between the various localities were also discerned (2010: $X_r^2 = 51.621$; P <0.001; 2011: $X_r^2 = 97.664$; P <0.001; Tab. A3, Appendix). Average species richness in the various localities generally followed the differences in total densities of Oribatida, with the exception of some of the study sites and King George Island, which showed very low densities but higher species richness.

The correlations of species richness with habitat background parameters generally followed those of total oribatid densities (Supplementary Material, Tab. S4). In both years, species richness related positively to the amounts of organic material in the soil substrates as well as to vegetation cover. In 2010 the number of registered species related positively to soil moisture and, in 2011, negatively to soil temperature and pH.

In the present study, a total of five species of Oribatida were recorded. Their total densities in the various study locations are given in the Appendix (Tab. A3). Unfortunately, one of the species (*Brachychochthonius sp.*) could not be determined to species level and a further species (*Liochthonius* cf. *mollis*) could not be assuredly determined, due to the fact that both taxa were only present in few specimens. For some of the species, sub-species have been identified in the literature (see, e.g., Pugh 1993); however, since the validity of these sub-species is unclear, their differentiation was not carried out in the present study. The juvenile individuals (nymphs), which constituted a vast majority of all registered specimens of the Oribatida, most likely belong to *Alaskozetes antarcticus*.

Alaskozetes antarcticus (Michael, 1903)

A. antarcticus is most likely of maritime Antarctic origin, where it is widespread (Convey et al. 2000a, Tab. 3, Fig. 7A). The species is distributed circumpolarly with many sub-species (Dalenius 1965), where it occurs not only in the maritime Antarctic, but also in continental Antarctica, the subantarctic as well as the southern tip of New Zealand and possibly also Australia (Pugh 1993, Davies et al. 1997, Starý & Block 1998, Marshall et al. 1999, Australian Data Research Center). In localities where it occurs, *A. antarcticus* is often broadly distributed; for instance, it was found on all of the South Sandwich Islands, occurring in more than half of the samples taken on these islands (Convey et al. 2000a).

The species is commonly found at low altitudes and in the littoral zone of coastal areas (Goddard 1979b, Pugh 1993, Richard et al. 1994, Convey & Quintana 1997, Convey & Smith 1997), at times also in waterlogged sites where it can survive immersion for up to nine months (Richard et al. 1994, Convey & Quintana 1997). It has been found in a wide range of habitats: under and on stones, in algal mats (mostly *Prasiola crispa*), on lichens, mosses as well grass (Gressitt et al. 1963, Dalenius 1965, Gressitt 1967, Tilbrook 1967b, Goddard 1979b, Richard et al. 1994, Convey & Quintana 1997). It is usually found in sites enriched in organic material, i.e., bird nests, guano, Penguin rookeries etc. (Gressitt 1967, Goddard 1979b, 1982, Convey & Quintana 1997, Davies et al. 1997).

The species often occurs in strong aggregations (Gressitt et al. 1963, Strong 1967, Tilbrook 1967a, Goddard 1979b, Convey & Smith 1997). It often overwinters in these dense aggregations; all life stages can overwinter, females often overwinter with eggs, and the overwintering sites can be used for many years (Strong 1967). Although *A. antarcticus* can occur in moist sites, it has often been described as preferring drier habitats (Gressitt et al. 1963, Tilbrook 1967b). The species has been recorded as occurring in lesser densities in warmed soils (i.e. fumuroles) (Convey et al. 2000a). *A. antarcticus* is a detritus feeder and scavenger, feeding on organic detritus, lichens and algae (Strong 1967, Goddard 1982).

In the present study, *A. antarcticus* on its own did not correlate consistently with any of the background habitat parameters (Supplementary Material, Tab. S4). However, when the species was analyzed together with the nymphs (most of which in all likelihood belong to this species), it showed in both years a positive relationship to amount and quality of the organic material of the soil substrates. As with total densities, the species correlated 2010 positively to soil moisture and in 2011 positively to vegetation cover and negatively to soil temperature and soil pH-value.

Globoppia loxolineata (Wallwork, 1965)

G. loxolineata has hitherto been recorded mostly from the Antarctic Peninsula and the neighbouring islands (Starý & Block 1998; Tab. 3, Fig. 7B), where according to the frequency of its records it appears to not be seldom. Further records are also from the South Shetland and South Orkney Islands, the continental Antarctic as well as the Subantarctic, i.e., Heard Island in the Indian Ocean (Pugh & Dartnall 1994, Block & Starý 1996, Starý et al. 1997, Convey et al. 2000a, Australian Data Research Center).

The species has been found in a wide range of habitats, from under and on stones, in algal mats, lichens, mats of mosses and grass, to nests of birds etc. (Gressitt 1967, Goddard 1979b, Pugh 1993, Convey & Quintana 1997). It apparently occurs less than the previous species in wet sediments, but seems also to avoid dry barren areas (Goddard 1979b, Convey & Quintana 1997). It has usually been found more as scattered individuals and seems not to form large aggregations as does the previous species (Strong 1967, Goddard 1979b). The maximum densities of the species can be found in early spring and late summer (Goddard 1979b).

The main overwintering stages appear to be middle juvenile stages (deutonymphs), but otherwise no clear yearly cycle is apparent; the species does not overwinter in aggregations as does the previous one (Strong 1967, Goddard 1979b). *G. loxolineata* is most likely a scavenger, feeding also on dead plant material and fungal hyphae (Gressitt 1967, Strong 1967).

This species was only recorded in the present study from two locations on the Fildes Peninsula of King George Island and only in 2010 (Tab. A3, Appendix). Therefore no significant correlations between its densities and background habitat factors could be discerned.

Halozetes belgicae (Michael, 1903)

This species is with many subspecies distributed circumpolarly and widely in the Antarctic and Subantarctic (Pugh 1993, Pugh & Dartnall 1994, Starý & Block 1998, Convey et al. 2000a, Sanyal 2004). It is also one of the most widespread oribatid mite species in the maritime Antarctic (Tab. 3). Despite its being so widespread, little has been recorded about the habitat preferences and feeding habits of *H. belgicae*. It is been found in the littoral and supralittoral zones, on algae, lichens as well as in mosses (Gressitt 1967, Tilbrook 1967b, Pugh 1993, Pugh & Dartnall 1994).

As *H. belgicae* was only recorded in few specimens in only one location in this study (Tab. A3, Appendix),

no statistical analysis of its relationship with habitat background parameters could be undertaken.

Liochthonius cf. *mollis* (Hammer, 1958)

L. mollis is hitherto known from the Subantarctic islands in the Indian and Atlantic oceans, southern South America as well as the Antarctic South Shetland Islands (Starý & Block 1998). The species' distribution apparently just barely reaches the margin of the Antarctic zone; the study sites in the present study most likely represent the southern border of its distributional area. It has thus only rarely been recorded in the Antarctic (Tab. 3, Fig. 7C), where it has been found among vegetation (Pugh 1993). Little else is known about its habitat preferences, ecological tolerances or biology.

In the present study, it was only recorded once as single individuals from Punta Christian (Fildes Peninsula, King George Island). Therefore, no statistical analysis could be undertaken for the species.
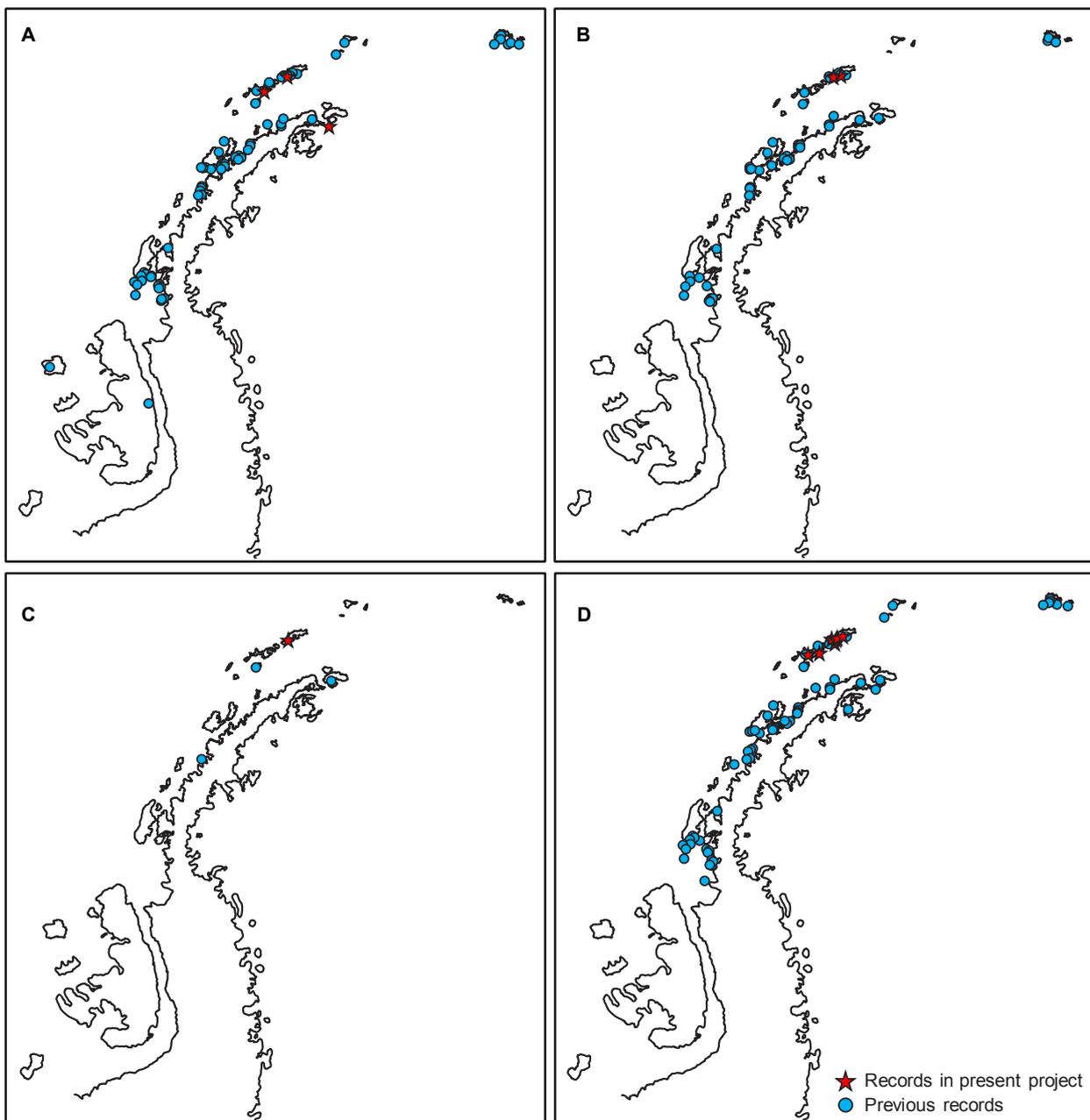

Figure 7. Records of *Alaskozetes antarcticus* (**A**), *Globoppia loxolineata* (**B**), *Liochthonius mollis* (**C**) (Oribatida) and *Hydrogamasellus racovitzai* (**D**) (Gamasina) in the maritime Antarctic. Sources as in Fig. 5.

No non-indigenous species of the Oribatida were recognized.

3.5. Gamasina (Acari)

A total of 131 individuals of the Gamasina were recorded in the present study, 88 in the year 2010 and 43 in 2011. In many localities no gamasine mites at all were registered. In those localities where Gamasina were found, maximum densities were more than 70 ind. per cm^3 in 2010 and 30 ind. per cm^3 in the year 2011. As in the other microarthropod groups, significant differences in the total densities of Gamasina could also be discerned between the various locations (2010: $X_r^2 = 43.433$; P <0.001; 2011: $X_r^2 = 33.739$; P <0.001; Tab. A3, Appendix). In the year 2010, the significant differences were mostly between localities with Gamasina and those without, while in 2011 significant differences also existed between localities in which gamasine mites were found.

Significant positive correlations between gamasine total densities and vegetation cover could be discerned in both years (Supplementary Material, Tab. S5). In 2010, the densities of Gamasina correlated positively to amounts and quality of organic material, while in 2011 the densities correlated positively to soil moisture.

Species richness of the Gamasina was the lowest for all microarthropod groups. Four species were registered in total (Tab. A3, Appendix), two in the year 2010 and three in 2011. Although total species richness was low, a significant difference in the average number of species per sample could be discerned between the various locations in both years (2010: $X_r^2 = 4.312$; P <0.001; 2011: $X_r^2 = 34.280$; P <0.001; Tab. A3, Appendix).

Species richness of the Gamasina correlated significantly with parameters representing locality as well as (positively) to vegetation cover and soil moisture in both years (Supplementary Material, Tab. S5). Only in the year 2010 did species richness correlate positively with amounts and quality of organic material in the soil substrates.

Altogether four species of the Gamasina were determined in the present study. Unfortunately, due to few specimens being available for deeper taxonomical study, two of the species could not be determined to species level because in one species only two larvae (Gen. sp. 1) were recorded, and in the other species only one protonymph (Gen. sp. 2). For a secure determination, in most cases adults are necessary. The determined species and their average total densities in the various localities are given in the Appendix (Tab. A3).

Hydrogamasellus racovitzai (Trouessart, 1903)

H. racovitzai is a large, conspicuous mite, which has been found to be widely distributed throughout the maritime Antarctic (Tab. 3, Fig. 7D). However, the species has also often been recorded in the Subantarctic (Pugh & Dartnall 1994, Convey & Quintana 1997). This species has been recorded from a wide range of habitats, e.g., on or under stones, in algal mats, on lichens, mosses, grass as well as in bird nests (Dalenius 1965, Tilbrook 1967b, Richard et al. 1994, Convey & Quintana 1997, Convey & Smith 1997). In mosses it apparently occurs in the upper layers (0–3 cm) (Goddard 1979a). In which habitat type the maximum densities are found seems to be more dependent on location than habitat type; the most common factor apparently being availability of abundant prey (Strong 1967).

H. racovitzai is a very active predator, feeding mostly on Collembola and mites (Gressitt 1967, Strong 1967, Goddard 1982). It shows a clear circadian activity pattern, being more active around midnight; it has been shown that the species has a weak negative relationship to temperature (Burn & Lister 1988). These factors may assist its ability to catch Collembola, which may be slowed by lower temperatures.

This species was the most abundant taxon of the Gamasina found in the present study, where it was recorded exclusively from the South Shetland Islands (Tab. 3, Fig. 7D). Its correlations with habitat parameters generally followed those of total gamasine densities (Supplementary Material, Tab. S5). In both years this species correlated consistently with latitude (as an indicator of locality) as well as positively with vegetation cover. In 2010 this species' densities correlated positively with quantities of organic matter in the sampled substrates, and in 2011 positively with soil moisture.

Parasitus tarsispinosus Hunter, 1967

The species *P. tarsispinosus* has only been recorded once the maritime Antarctic, where it was found 'under wood on an ash plain' on Deception Island (Hunter 1967a, Downie 2002). In the present study, it was also only found once in multiple individuals of two samples on Deception Island. Its record in the present study confirms its occurrence in viable populations on Deception Island. It was recorded nowhere else in the present study. This species occurred in far too few samples or localities to be able to carry out a statistical analysis of its relationship to habitat parameters, or of its distribution within the study localities.

No non-indigenous species of the Gamasina were recognized.

3.6. Nematoda

In the present study, more than 255,000 nematode individuals were extracted and quantified. From these, a total of 18,322 (maximally 100 individuals per sample) were determined taxonomically. Average densities of between 0.8 (Neko Harbour) and 11,344 (Arctowski Station) ind. per 100 cm^3 were detected. Mean species richness ranged between 0.2 (Neko Harbour) and 11.3 (Punta Christian I) species per sample. In both study years, the individual and species richness of the nematodes differed significantly among the various localities (densities: 2010: X_r^2 = 110.208; P <0.001; 2011: X_r^2 = 70.866; P <0.001; species richness: 2010: X_r^2 = 140.621; P <0.001; 2011: X_r^2 = 84.804; P <0.001; Tab. A4, Appendix), whereby in 2010 the northernmost study sites on King George Island showed the highest densities (Arctowski Station) and species richness (Biologenbucht and Punta Christian). In contrast, in 2011 the highest densities were found in the soils from Paulet Island, one of the more southern islands in the present study. However, these high total densities were caused by an extremely high population growth of a single species, *Pelodera teres*-group. In 2011, the largest species richness (on average 7.5 species per sample) was found on Ardley Island.

Vegetation cover had a significant positive influence on total individual densities, especially in 2010 (Supplementary Material, Tab. S6). This effect was also present in 2011, but quantitatively less so. Nematodes in soil samples with a vegetation cover were individual-richer than in samples without vegetation. The degree of vegetation cover also had a significant influence on the number of species per sample (Supplementary Material, Tab. S6). Soil samples without vegetation were species-poorer than samples with vegetation.

A strong correlation existed between locality (longitude and latitude) and nematode individual densities as well as species richness (Supplementary Material, Tab. S6). The nematode communities became poorer from northeast to southwest, in respect to both densities

as well as species richness. The densities and species numbers of the Antarctic nematode fauna correlated furthermore in both study years clearly with soil moisture (Supplementary Material, Tab. S6): the moister the study site, the richer was the nematode fauna. Not as consistent in both study years, but nonetheless at times positively correlated were nematode numbers (individuals and in 2010 also species) and soil organic matter (measured as mass loss on ignition), nitrogen content, carbon content and C/N ratio. The correlation analyses furthermore showed a slight, if not always consistent, relationship between soil particle size and densities as well as species numbers, with richer nematode communities in soils with higher contents of fine sand, clay or silt.

Very little is known about the actual feeding strategies of Antarctic nematode species. But based upon the morphology of the mouth cavities and mouthparts such as 'stylets', teeth and 'spears', the food resources can be estimated, especially when explicit nutrient-resource studies exist for related species of the same genus (Yeates et al. 1993). In the present study the nematode communities were accordingly dominated by bacterial feeders (Fig. 8). In the study sites on King George Island and Ardley Island, relatively large, omnivorous species also occurred. These species fed predominantly on green algae, as could be determined by the typical intestinal
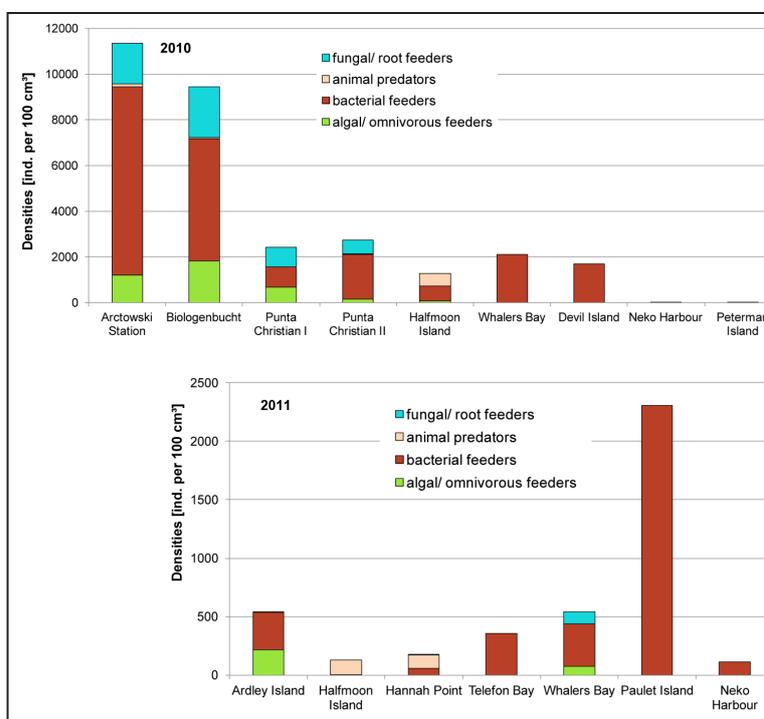

Figure 8. Average densities (individuals per 100 cm^3) of the various feeding types recorded in 2010 (above) and 2011 (below) in the different localities. The assignment of the recorded species to specific feeding types is given in the Appendix, Table A4. The localities are sorted from left to right by increasing southern latitude. Please note the different scales of the y-axes.

colour. Particularly diverse feeding types were present in the nematode communities from King George Island, most likely due to the rich vegetation in these sites. Besides bacterial and algal feeders, also fungal/ root feeders were found here, which pierce and suck roots and/ or fungal hyphae. Predatory nematodes showed a very site-specific distribution: a single predatory species, whose prey most probably consists of protists and smaller soil animals (Nematoda, Rotatoria, as well as juvenile Tardigrada and Collembola), was recorded in the present study from Halfmoon Island (in both study years) and Hannah Point, where they accounted for a considerable part (43 %–96 %) of the total nematode numbers. Furthermore, predatory nematodes occurred in smaller numbers in the sites near Arctowski Station and in the Biologenbucht on King George Island.

A total of 39 nematode species were recorded in the 13 study sites in the study years 2010 und 2011. The determined species and their average densities in the different localities are given in the Appendix (Tab. A4). From these 39 species, 20 were previously known from the Antarctic (Andrássy 1998, Nedelchev & Peneva 2000, Holovachov & Boström 2006). Three of these 20 Antarctic species exhibit a broad (global) distribution (Andrássy 1998): *Ceratoplectus armatus*, *Eumonhystera vulgaris* and *Geomonhystera villosa*. The remaining 17 species are, however, only known from the Antarctic and therefore can be considered to be endemic: *Acrobeloides arctowskii*, *Aphelenchoides haguei*, *A. helicosoma*, *Coomansus gerlachei*, *Ditylenchus parcevivens*, *Enchodelus signyensis*, *Eudorylaimus coniceps*, *E. paradoxus*, *E. pseudocarteri*, *Mesodorylaimus anarcticus*, *M. chipevi*, *Plectus antarcticus*, *P. belgicae*, *P. insolens*, *P. tolerans*, *Teratocephalus rugosus*, *T. tilbrooki* (describing authors and years of description see below).

Cervidellus cf. *vexilliger* as well as the Rhabditidae *Pelodera strongyloides*-group., *P. teres*-group, *P. parateres*-group *and Rhabditis marina*-group are recorded from the Antarctic for the first time in the present study, although Andrássy (1998) states that the genera *Cervidellus* and *Pelodera* have been previously mentioned for the maritime Antarctic nematofauna, albeit without specification of the species. A further 14 species could be putatively but clearly discerned when mounted in the microscopic slides (Tab. A4, Appendix), but could not yet be determined to species level with the available literature and may represent undescribed species.

With the relatively detailed investigation of the 13 different Antarctic study sites (localities), the present investigations contribute vastly to the assessment of the nematode fauna of Maritime Antarctica (Fig. 9). With the exception of Deception Island, Livingston Island (with Hannah Point in the present investigation) and Arctowski

Station on King George Island, the localities studied here were, to the best of our knowledge, for the first time the subject of extensive nematological investigations. In the following, those species that were previously known from the Antarctic – whether showing a global or endemic distribution – are presented in more detail. Furthermore, some information is provided for those species of the present study which belong to genera that had previously been reported from Maritime Antarctica, i.e. *Cervidellus*, *Panagrolaimus* and *Pelodera*. Since especially among the Nematoda the morphological characteristics of the specimens recorded in the present study repeatedly deviated from known species' descriptions, some relevant morphological details are given in the following presentation and review of the recorded species. In contrast to the microarthropods, little is known about differential ecological preferences of the individual species, because in most previous studies on Nematoda in the maritime Antarctic only mosses and other vegetation was sampled and not soil substrates. Therefore, in the following, such preferences are mostly indicated in the correlations (if significant) determined in the present study.

Acrobeloides arctowskii Holovachov & Boström, 2006

The morphologically very distinctive nematode species *A. arctowskii* had previously been recorded
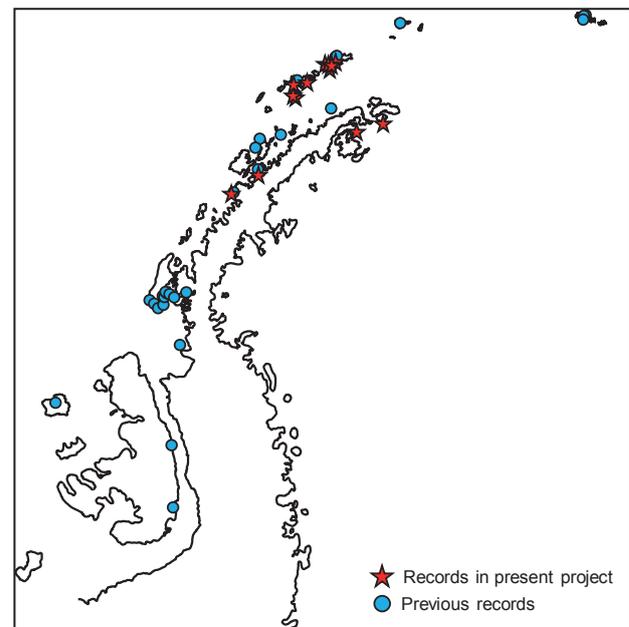

Figure 9. Previous (blue points) and present records (red stars) of the nematode species determined in the present study. Sources given in the Supplementary Material (Tab. S9) at www.soil-organisms.org.

exclusively from King George Island, and here only from the type locality, the Polish station 'Henryk Arctowski'. In the present study, this site of occurrence could be confirmed. As in the original description, *A. arctowskii* was determined from samples near Arctowski Station, in which the higher plant species *Deschampsia antarctica* rooted. The present study could furthermore increase the distributional area of the species by the addition of Deception Island, where it was recorded from Whalers Bay in both study years (Tab. 4). Since the corresponding samples from this site were devoid of vegetation (with the exception of the sporadically occurring algae *Prasiola crispa*), the records of this species suggest that an association with *Deschampsia antarctica* or other higher plants is not a prerequisite for a colonization success of *A. arctowskii*. Based upon the structure of its oral cavity, *A. arctowskii* is likely a bacterial feeder and possibly also facultatively fungivorous, as are other species of the genus *Acrobeloides*. A slight tendency towards soils with higher contents of rough gravel and medium sand was observed.

Aphelenchoides Fischer, 1894

Aphelenchoides species possess a stylet in their oral cavity, with which they pierce plant-root and fungal cells and suck out their contents. The majority of *Aphelenchoides* species, for which the nutrient-resource spectrum has been studied, feed primarily on fungi. Some species can also survive and reproduce after feeding on algae, lichens, root epidermis cells or hair-root cells (Yeates et. al 1993). Besides the two species listed below, a third *Aphelenchoides* species was recorded from Deception Island soil samples, which cannot be assigned to a known species and is possibly new to science.

Aphelenchoides haguei Maslen, 1979

A. haguei was described for the first time by Maslen (1979a) from moss patches on Signy Island. Since then the species has also been recorded from soil samples and exhibits a broad distribution throughout the maritime Antarctic (Tab. 4). Due to the almost complete lack of vegetation in the study sites of Whalers Bay on Deception Island (vegetation cover 0 % or sporadically <25 %), it can be assumed that representatives of *A. haguei* here feed exclusively on fungal cells and also possibly from algae. On King George Island, plant root cells could also be an additional food resource. The species' occurrence was positively correlated to vegetation cover and organic matter in 2010 (Supplementary Material, Tab. S6).

Aphelenchoides helicosoma Maslen, 1979

A. helicosoma was first recorded and described by Maslen (1979a) from the same moss patches on Signy Island as were the type specimens of *A. haguei*. This concurs with the present investigation, where both species were frequently present in the same soil sample (King George Island, Biologenbucht and Punta Christian). It further suggests that the two species have similar habitat demands. From the architecture of their mouth cavity and armature (stylet), only a very general feeding type (s. above) can be derived. It is unknown whether the two species are competitors for the same food resources. From present knowledge, *A. helicosoma* seems less widely distributed within Maritime Antarctica than *A. haguei* (4 vs. 11 islands, Tab. 4).

Ceratoplectus armatus (Bütschli, 1873)

According to Andrássy (2005), *C. armatus* shows a world-wide distribution with reports from Europe, Asia, Africa, North- and South America and New Zealand. Within Maritime Antarctica, Maslen (1979b) lists Coronation Island, Signy Island, Elephant Island and Galindez Island as sites of occurrence for *C. armatus*. Future analyses, at best combined with molecular methods, will have to prove if *C. armatus* is indeed a single species with a world-wide distribution or if it rather comprises many, more locally distributed cryptic species. Until then and on the basis of mere morphological characters, the present investigation adds Biologenbucht at King George Island and Ardley Island to the distributional map of *C. armatus* (Fig. 10A). At Biologenbucht, the species' densities were significantly correlated to vegetation cover, soil moisture, C/N-ratio and soil particle size, with higher densities of *C. armatus* in moister soils with denser vegetation, higher C/N-ratio, lower contents of coarse gravel and higher contents of fine sand (Supplementary Material, Tab. S6).

Cervidellus cf. *vexilliger* (de Man, 1880)

The specimens reported here from Arctowski Station, King George Island, morphologically resemble *C. vexilliger* redescribed by Boström & de Ley (1996) in all distinctive and most of its morphometric characters. Nonetheless, small deviations exist, e.g. the pharynx being slightly longer and the tail being less stout (tail length/ tail width: 2.7–2.8 vs. 1.9–2.6). According to Andrássy (2005), *C. vexilliger* shows a world-wide distribution (with its southern-most occurrence in Chile),

but again it is not certain whether these findings and also the present findings from Antarctica belong to the species *C. vexilliger* or to a species group (s. above). From the maritime Antarctic, Spaull (1973) reported *Cervidellus* from Signy Island, Elephant Island, Intercurrence Island and Galindez Island, albeit without specification of the species (Fig. 10B). As for the present investigation, there were no significant correlations identified to any of the habitat parameters measured.

Coomansus gerlachei (de Man, 1904)

C. gerlachei is widely distributed throughout the Antarctic islands, from Coronation Island down to Charcot Island (e.g. Spaull 1973, Peneva et al. 1996, Convey et al. 2000b, Tab. 4). In the present study, individuals of the species were found in high frequencies (e.g., on Halfmoon Island in 100 % [2010] and 92 % [2011] of the samples) and surprisingly high densities (on average 113–555 ind. per 100 cm³; Tab. A4, Appendix) on Halfmoon Island (in both years), King George Island (Arctowski Station) and Hannah Point on Livingston Island. *C. gerlachei* is a relatively large, predatory nematode species. In the present study, it was one of only two nematode species exhibiting a significant positive correlation to soil nitrogen content (Supplementary Material, Tab. S6). Its high dominance within the nematode communities of the locations mentioned above – in 22 of 36 studied samples from Halfmoon Island, *C. gerlachei* was the only recorded nematode species – indicates that it does not primarily feed on other nematode species, but probably on juvenile individuals of its own species as well as rotifers, protists and smaller tardigrades, and also juvenile collembolans, as collembolan mouthparts were visible in the intestine of several mounted specimens from Biologenbucht.

Ditylenchus parcevivens Andrassy, 1998

The presence of representatives of the tylenchid genus *Ditylenchus* in Maritime Antarctica was reported by a variety of authors (the first being Spaull 1973) and from a number of different sites, e.g. Signy Island and Livingston Island (Tab. 4). Andrássy, who first described *D. parcevivens* in 1998 from a not further determined sample of 'fine silt' on Signy Island, assumed it likely that all those *Ditylenchus* spp. referred to the same species, namely *D. parcevivens*. According to Yeates et al. (1993) representatives of *Ditylenchus* feed either on fungi or are migratory endoparasites on plants. In view of the scarce vegetation cover in Antarctica, even at Arctowski Station, Biologenbucht and Punta Christian

on King George Island, where we found *D. parcevivens*, a fungivorous feeding mode seems far more likely than a dependence on available (possibly even specific) plant roots. The species' occurrence was correlated to the quantity of organic material (Supplementary Material, Tab. S6), which further indicates fungi as the main food resource.

Enchodelus signyensis Loof, 1975

Loof (1975) first described the species from moss samples (*Tortula excelsa*) taken from Signy Island (Tab. 4). He further recorded *E. signyensis* at Coronation Island, Elephant Island and Galindez Island from the vicinity of *Deschampsia antarctica*, and at Alamode Island from moss cushions (*Depanocladus uncinatus*) (Loof 1975). In the present investigation, *E. signyensis* was only found in two soil samples at Arctowski Station, in the vicinity of *Deschampsia antarctica* and *Colobanthus quietensis*, as well as of the mosses *Sanionia* sp., *Syntrichia filaris* and *Syntrichia magellanica*. Densities of *E. signyensis*, however, were too small to reveal correlations between vegetation cover and the occurrence of *E. signyensis*. According to Yeates et al. (1993), representatives of *Enchodelus* are omnivorous feeders (feeding on a variety of different food sources) or unicellular eucaryote feeders and are thus not predominantly dependent on the availability of plant roots. Still, living in the vicinity of plant roots and moss cushions in Antarctica at least guarantees hot spots of nutrient turnover and diverse niches and by this a broad diversity of food sources.

Eudorylaimus Andrássy, 1959

In the present study, three species of *Eudorylaimus* were determined, all of which were present on King George Island. Nematodes of the genus *Eudorylaimus* are relatively large with a body length usually exceeding 1 mm. According to Yeates et al. (1993), representatives of *Eudorylaimus* are omnivorous feeders, i.e. feeding on a variety of food sources. All three *Eudorylaimus* species of the present investigation were repeatedly observed to contain a green-colored intestine, suggesting that green algae are a main part of their diet.

Eudorylaimus coniceps Loof, 1975

E. coniceps is widely distributed throughout the maritime Antarctic. Previous records extend from

Coronation Island and Signy Island in the north to Alexander Island in the south of the Antarctic Peninsula (Andrássy 1998 and EBA-Datenbank; Tab. 4). The present investigation could expand records of this species to King George Island (Biologenbucht, Punta Christian, Ardley Island) and Halfmoon Island. In 2010, the species' occurrence was correlated with vegetation cover, organic matter content and soil particle size, with higher densities of *E. coniceps* in soils with denser vegetation and higher contents of organic matter and coarse sand (Supplementary Material, Tab. S6).

Eudorylaimus paradoxus Loof, 1975

E. paradoxus was first described from Signy Island. Paratypes were isolated from a *Deschampsia antarctica* cushion at Elephant Island. At Intercurrence Island, *E. isokaryon* was also found in association with the moss *Brachythecium* sp. Apart from Signy Island, Elephant Island and Intercurrence Island, *E. paradoxus* has also been reported from Coronation Island, Galindez Island (here again associated with *Deschampsia antarctica*) and Limpet Island. The present study adds King George Island
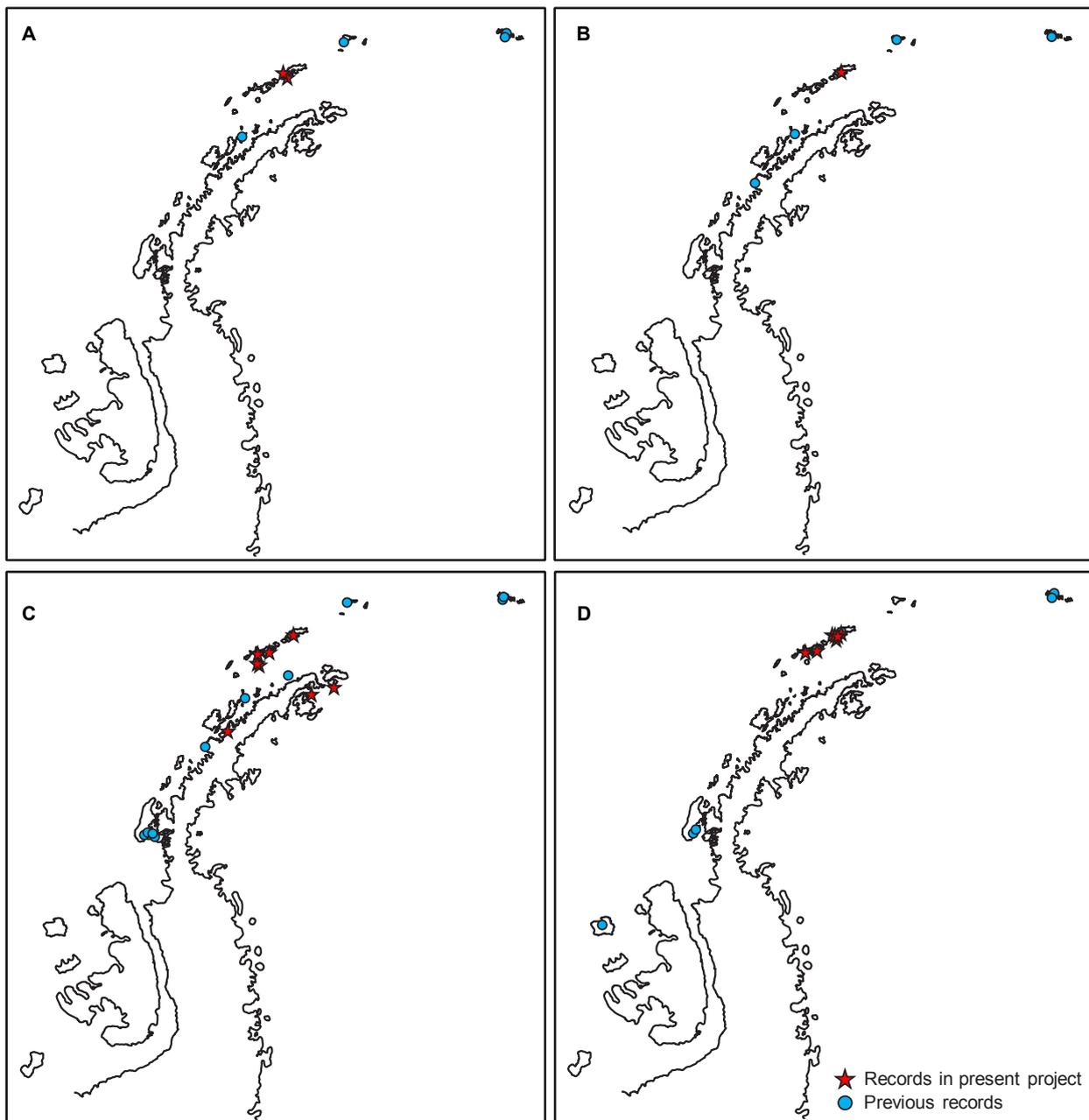
Figure 10. Previous and present records of *Ceratoplectus armatus* (**A**), *Cervidellus* sp. (**B**), *Panagrolaimus* sp. (**C**) and *Teratocephalus tilbrooki* (**D**) in the maritime Antarctic (blue dots) as well as records from the current study (red stars). Sources: as in Fig. 9.

(Arctowski Station, Biologenbucht and Punta Christian) to the distribution of this species (Tab. 4). Little is known about its habitat preferences and ecological tolerances; the present study, however, revealed a positive correlation between its densities and vegetation cover, organic matter, C/N-ratio and contents of fine sands, silt and clay (Supplementary Material, Tab. S6).

Eudorylaimus pseudocarteri Loof, 1975

E. pseudocarteri shows a distribution throughout Maritime Antarctica as similarly wide as *E. coniceps* (Tab. 4). The present findings add all four study sites on King George Island as well as Hannah Point on Livingston Island to the list of records. Here, densities of *E. pseudocarteri* were slightly (in 2010) and significantly (2011) correlated to vegetation cover; the denser the vegetation, the more individuals of this species were found in the soil beneath (Supplementary Material, Tab. S6).

Mesodorylaimus Andrássy, 1959

Six *Mesodorylaimus* species have been reported from Antarctica, two of which were first described by Loof (1975): *M. (Calcaridorylaimus) signatus* from Signy Island and *M. imperator* from Emperor Island. Nedelchev & Peneva (2000) gave descriptions of another three species (*M. antarcticus*, *M. chipevi* and *M. masleni*) from Livingston Island (South Shetland Islands). Nedelchev & Peneva (2000) presented a key for the Antarctic *Mesodorylaimus* species, including *M. bastiani* (Bütschli, 1873), unfortunately without information on localities of occurrence and authors. According to Andrássy (2005), *M. bastiani* is a terricolous and semi-aquatic species with a world-wide distribution (from Europe to Australia); the other five species recorded in Antarctica are presently thought to be endemic. In the present investigation, *M. antarcticus* and *M. chipevi* were identified as well as the morphospecies *Mesodorylaimus* sp., which can be assigned to none of the aforementioned species presently known from Antarctica.

Mesodorylaimus antarcticus Nedelchev & Peneva, 2000

To our knowledge, *M. antarcticus* has thus far only been reported from the type location on Livingston Island, where they had been recorded from moss cushions (*Sanionia* sp.). We add King George Island and Neko Harbour. No significant correlations to any of the measured habitat parameters could be identified.

Mesodorylaimus chipevi Nedelchev & Peneva, 2000

M. chipevi has also only been reported from Livingston Island, from various moss and soil samples covered by *Deschampsia antarctica* (Nedelchev & Peneva 2000). In the present study, *M. chipevi* was isolated from soil samples near Arctowski Station (King George Island). The species showed a slight tendency towards moister soils with higher contents of organic carbon and rough gravel (Supplementary Material, Tab. S6).

Panagrolaimus sp.

To our knowledge, no *Panagrolaimus* species has been described from Maritime Antarctica to date, even though representatives of the genus *Panagrolaimus*, but without specific identification, have been reported from a variety of Antarctic islands: e.g. by Spaull (1973) from Coronation Island, Signy Island, Elephant Island, Astrolabe Island, Intercurrence Island, Galindez Island and Pourqoui Pas Island (Fig. 10C). Our records of *Panagrolaimus* sp. from Arctowski Station, Halfmoon Island, Hannah Point, Telefon Bay, Whalers Bay, Paulet Island, Devil Island and Neko Harbour (Tab. A4, Appendix) all appear to belong to a single, yet undescribed species. Whether these concern the same species mentioned by Spaull (1973) must still be clarified. Our first conjecture (Russell et al. 2013) was that the *Panagrolaimus* species of the present investigation might be *P. magnivulvatus* Boström, 1995, which was first described from nunataks in Dronning Maud Land, eastern Antarctica and has to date only been reported from Continental Antarctica. Against this taxonomic assignment speaks – in spite of certain similarities – above all the shape of the vulval lips, which are not quite as protruding as described by Boström (1995) for *P. magnivulvatus*. No significant correlation to any habitat parameter could be found, with the exception of a tendency towards soils with a high content of fine sands.

Pelodera A. Schneider, 1866

Representatives of *Pelodera* are often reported from decaying substances, where they feed on bacteria and reproduce explosively as the fresh carbon- and nitrogen-rich sources ensure a strong bacterial growth. According

Table 4. Previous and present records (*x*) of the 17 nematode species determined in the present study, which were previously known to be endemic in maritime Antarctica. The localities are sorted by increasing southern latitude. Localities of the present investigation are shaded grey. *t*: type locality of the given species. Sources given in the Supplementary Material (Tab. S9) available online at www.soil-organisms.org).

	Acrobeloides arctowskii	*Aphelenchoides haguei*	*Aphelenchoides helicosoma*	*Coomansus gerlachei*	*Ditylenchus parcevivens*	*Enchodelus signyensis*	*Eudorylaimus coniceps*	*Eudorylaimus paradoxus*	*Eudorylaimus pseudocarteri*	*Mesodorylaimus antarcticus*	*Mesodorylaimus chipevi*	*Plectus antarcticus*	*Plectus belgicae*	*Plectus insolens*	*Plectus tolerans*	*Teratocephalus tilbrooki*	*Teratocephalus rugosus*
Coronation Island				x		x	x	x	x			x					
Signy Island		x, t	x, t	x	x, t	x, t	x, t	x, t	x, t			x	x	x, t		x, t	x, t
Elephant Island		x		x		x	x	x	x			x	x				
King George Island	x, t	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Halfmoon Island		x					x									x	x
Livingston Island		x		x					x	x, t	x, t		x		x		x
Deception Island	x	x		x								x	x				x
Astrolabe Island																	
Paulet Island																	
Devil Island												x					x
Intercurrence Island				x				x				x					
Danco Coast + Brabant Island				x, t								x, t	x, t				
Neko Harbour - Antarctic Peninsula										x							
Petermann Island													x				
Galindez/Darboux Island				x		x		x				x					
Bunger Hills												x					
Adelaide Island		x	x					x	x			x	x			x	
Lagoon/Anchorage Island		x		x				x				x	x		x		
Blaikrock Island						x						x					
Killingbeck Island												x					
Leonie Island		x		x				x				x				x	x
Limpet Island				x				x				x					
Pourqoui pas Island												x					
Cone Island												x					
Avian Island				x								x					
Guebriant Islands				x			x					x					
Emperor Island							x					x		x, t			
Alamode Island		x				x						x					
Charcot Island				x		x	x	x				x				x	x
Alexander Island		x				x	x	x				x	x		x		

to Andrássy (1998), representatives of the genus *Pelodera* have been previously mentioned for Maritime Antarctica, albeit without specification of the species.

Pelodera teres-group

The ornithogenic soils on Paulet Island represented the habitat for a *Pelodera* species, which – with an average of 2309 ind. per 100 cm^3 predominated in all of the 12 soil samples taken from this island (Tab. A4, Appendix). This species, which morphologically belongs to the species complex *P. teres*-group, is reported here for the first time from Antarctica. According to Sudhaus (2011), the *P. teres*-group consists of three valid species, but many more synonyms have been given in the past and many cryptic (local) species may still be hidden in the complex. Representatives of the *P. teres*-group are typically isolated from compost, manure and dung, where they feed on bacteria. On Paulet Island, nutrient resources originate almost exclusively from penguin guano. In the samples of 2011, a corresponding strong positive relationship between individual numbers of *P. teres*-group and soil nutrient content (measured as soil organic material content [mass loss at ignition], soil nitrogen and carbon content) was determined (Supplementary Material, Tab. S6).

Pelodera strongyloides-group

In similarly high densities (on average 1378 ind. per 100 cm³), a second species of *Pelodera* was found in the present investigation on Devil Island. Morphologically it belongs to the species complex *P. strongyloides*-group, which according to Sudhaus (2011) comprises 10 valid species. One of these, *P. arnboumi* was described by Boström (1996) from the Subantarctic island South Georgia. The present specimens differ from *P. arnboumi* by being larger (1250–1940 µm vs. 560–880 µm) and the tail being more or less cupola-shaped (vs. conical) and stouter (tail length/ tail width: 1.2–1.7 vs. 2.8). As also none of the descriptions of the other nine species of the *P. strongyloides*-group fit the species recorded here, the present findings might belong to a yet undescribed species.

Plectus Bastian, 1865

Andrássy (1998) listed five *Plectus* species occurring in Maritime Antarctica: *P. antarcticus, P. belgicae, P. insolens, P. meridianus* and *P. tolerans*. From the Subantarctic island South Georgia, Boström (1996) further reported *P. rhizophilus*. Two (maybe even four, see below) of the species previously known from Maritime Antarctica were also registered in the present investigation. Besides these four species listed below, a fifth *Plectus* species was recorded from King Georg Island samples, which we could not yet assign to a known species and which is possibly new to science.

Plectus antarcticus de Man, 1904

Of all the endemic species within the genus, *P. antarcticus* shows the most wide-spread distribution. The present investigation adds King George Island (Arctowski Station and Biologenbucht), Whalers Bay (Deception Island) and Devil Island to the list of records (Tab. 4). When *P. antarcticus* was first described from Dancoland, Brabant Island, Palmer Peninsula, it was the second nematode species ever reported from Antarctica. Andrássy (1998) redescribed the species from a neotype, which had been collected from the vicinity of the type locality in 1985. According to Andrássy 1998, *P. antarcticus* prefers mossy habitats. The nematodes recorded in the present investigation were, however, extracted from soil samples. At three of the four locations with *P. antarcticus*, mosses (*Bryum pseudotriquetrum, Sanionia* sp*., Cephaloziella* sp. and *Ceratodon pururens*) were present. The soils of Devil Island, on the other hand, were bare of any vegetation. No significant correlations were identified to any of the habitat parameters measured, but a tendency towards fine-textured soils existed (Supplementary Material, Tab. S6).

Plectus cf. *belgicae* de Man, 1904

P. belgicae was first described from Cap Beneden (Danco Land Coast, Antarctic Peninsula). Andrássy (1998) gave a detailed description together with drawings of specimens sampled from various mosses at Signy and Elephant Island (Tab. 4). The specimens of the present investigation resemble *P. belgicae*, but differ from Andrássy's description by a longer body and tail (body: 760–930 µm vs. 680–780 µm, tail: 100–120 µm vs. 79–85 µm) and the number of tubular supplementary organs in males (2 vs. 1). According to Andrássy (1998), none of the *Plectus* species occurring in Maritime Antarctica is supposed to have two tubular supplementary organs: males of *P. antarcticus* and *P. tolerans* both have 3, *P. belgicae* and *P. murrayi* 1, and *P. meridianus* none at all (only a 'papilla like swelling'). If we assume that the number of tubular supplementary organs in *Plectus* is

stable and therefore a decisive character (which, however, Zell [1993: p. 68] negates, e.g. *Plectus communis* having one or two tubular supplementary organs), this discrepancy indicates that an affiliation with *P. belgicae* and all other *Plectus* species so far registered for Maritime Antarctica is questionable and suggests that *Plectus* cf. *belgicae* might concern a yet undescribed species. As for the present findings, the presence and development of vegetation cover in both years as well as the associated higher soil moisture (only in 2011) correlated positively with the densities of *P.* cf. *belgicae* (Supplementary Material, Tab. S6).

Plectus insolens Andássy, 1998

The type locality of *P. insolens* is Signy Island, where specimens were collected from a thin layer of soil on rock covered by moss and from roots of the perennial grass *Deschampsia antarctica* (Andrássy 1998). With King George Island (Ardley Island), the present investigation adds, to our knowledge, a second site to its distribution. At Ardley Island, *P. insolens* was recorded from soils that showed patches of moss (*Sanionia* sp., *Warnstorfia sarmentosa* and *Andreaea regularis*). Densities of *P. insolens* were positively correlated to the presence of a moss cover and the associated higher soil moisture (Supplementary Material, Tab. S6).

Plectus cf. *tolerans* Andássy, 1998

Andrássy described *Plectus tolerans* from Emperor Island, where the type specimens had been isolated from moss samples (*Drepanocladus unicatus*). *P. tolerans* is morphologically very similar to *P. antarcticus*. An unambiguous separation of the two species, in our opinion, requires the analysis of male specimens. All specimens collected from Hannah Point and King George Island (all sites) in the present study were female and resemble *P. tolerans* due to a plumper and more strongly bent tail. Morphometric measures of body length, buccal tube and lip region, however, are intermediate between those given for *P. tolerans and P. antarcticus*, and 'the wide nuclei in younger oocytes', a character which according to Andrassy (1998) clearly distinguishes *P. tolerans* from *P. antarcticus*, was often found to be wide in one oocyte and small in the other oocyte of one and the same female. As in the two previously mentioned *Plectus* species, the occurrence of *P.* cf. *tolerans* was also positively correlated to soil moisture (only in 2011) and the presence of a vegetation cover (Supplementary Material, Tab. S6).

Rhabditis marina-group Bastian, 1865

According to Andrassy (2005), *R.* (*Pellioditis*) *marina* is found with a world-wide distribution in a wide variety of different habitats in limnic sands and inland salines in Europe, as well as in marine sands of coastal regions in Europe, Africa, North and South America and Australia. In contrast and like others before him, Sudhaus (2011) identified *R. marina* as a superspecies comprising many, probably more locally distributed ('mostly allo- or parapatric') cryptic species and distinguished four valid species within the species complex, which he transferred to the new genus *Litoditis*. All four species have been reported from intertidal zones, where they dwell in rotting plant or algal material (Sudhaus 2011). For reasons of assignability, we retain the original name, but refer to the species complex sensu Sudhaus (2011), to which with the findings in Telefon Bay, Deception Island, we possibly add a new species but at least a new record from Maritime Antarctica (Supplementary Material, Tab. S6). In Telefon Bay, *R. marina*-group was present in 13 of the 24 soil samples, with highest densities (74 to 1992 individuals per 100 cm^3) in four samples collected closest (less than 20 m) to the shoreline. It is unknown whether the beach held accumulations of rotting seaweed. The species showed no correlation to any other habitat parameter.

Teratocephalus de Man, 1876

Three species of the bacterivorous genus *Teratocephalus* have been described from Antarctica. All three species have their type locality on Signy Island (South Orkney Islands), and all three were described by Maslen (1979a): *T. rugosus* and *T. tilbrooki* were both extracted from 'dry' moss turfs at the Signy Island Reference Site 1 (SIRS 1) and from 'swamp' moss carpets at the Signy Island Reference Site 2 (SIRS 2), with *T. rugosus* having its core area in the humid SIRS 2 and *T. tilbrooki* in the dry SIRS 1. *T. pseudolirellus*, on the other hand, was found in neither of the two reference sites, but was recorded from moss cushions (*Tortula excelsa*) at Marble Knolls. In the present investigation as well, *T. rugosus* and *T. tilbrooki* were occasionally sampled at the same site, in rare cases even from the same samples, e.g. at Punta Christian. In contrast to previous findings, however, the *Teratocephalus* specimens of the present investigation were not isolated from moss cushions, but from soil samples. From previous knowledge, *T. rugosus* seems to be less widely distributed within Maritime Antarctica than *T. tilbrooki* (2 vs. 5 islands). With the additions of the present investigation, their distribution is now more balanced (7 vs. 7 islands), but the records of *T. tilbrooki* still reach much further south to Charcot Island (Tab. 4).

Teratocephalus rugosus Maslen, 1979

The present investigation added King George Island (Arctowski Station, Biologenbucht, Punta Christian and Ardley Island), Halfmoon Island, Deception Island and Devil Island to the distributional area of *T. rugosus*. The species' abundance here was not correlated with any of the habitat parameters measured, but a slight tendency towards soils with higher contents of rough gravel was observed.

Teratocephalus tilbrooki Maslen, 1979

With Arctowski Station, Biologenbucht, Punta Christian and Ardley Island (all assigned to King George Island in Tab. 4) and Halfmoon Island, we add further findings to the list of *T. tilbrooki* records (Fig. 10D). Its densities were positively correlated to the presence of a moss cover and the associated higher soil moisture as well as to quantity and quality of organic material in 2010 (Supplementary Material, Tab. S6).

4. Discussion

4.1. Microarthopods (= Collembola & Acari)

Of the various Antarctic soil invertebrate groups, microarthropods (Collembola, Acari) have been previously most intensively studied. This background allows an in-depth comparison between earlier studies and the present results. Based on this comparison, the microarthropod fauna (= mesofauna) found in the present investigations can be considered typical for the maritime Antarctic. Almost all of the recorded species have been previously found in Maritime Antarctica. A number of the registered taxa are also endemic to Antarctica, e.g., the collembolans *Cryptopygus antarcticus*, *Friesea grisea*, *Folsomotoma octooculata* and the acarines *Globoppia loxolineata*, *Nanorchestes berryi*, *N. gressitti*, the *Eupodes parvus* subspecies or the *Apotriophytydeus* species. Close to 90 % of the known continental Antarctic species and almost 50 % of the maritime Antarctic mesofauna are endemic (Marshall & Pugh 1996, Hogg & Stevens 2002). The level of endemism, however, is lower at the generic level. Whereas a major proportion of the genera occurring in the continental Antarctic are endemic, most of the genera found in the maritime Antarctic are cosmopolitan and even resemble the Arctic fauna (Marshal & Pugh 1996, Strandtmann 1967). Examples of more widely dispersed

species can be found among the Oribatida (Acari). All of the oribatids recorded in this study exhibit a broad distribution in the Antarctic and Subantarctic, which can reach to New Zealand (*Alaskozetes antarcticus*) or South America (*Liochthonius mollis*). Nonetheless, as far as can be ascertained from literature reviews (Pugh 1993, Block & Starý 1996, Starý & Block 1998) and other sources (e.g., Convey & Smith 1997), especially the oribatid species *Alaskozetes antarcticus*, *Globoppia loxolineata* and *Halozetes belgicae* belong to the typical species inventory of the region studied here.

The endemic species and even the entire species composition of soil-animal communities occurring in Continental and Maritime Antarctica are generally different (Hogg & Stevens 2002). The faunas of the two areas are highly separated by a biogeographical boundary between Continental Antarctica and the Antarctic Peninsula, the so-called Gressitt Line (Convey et al. 2000b, Chown & Convey 2007, Convey 2011). It must be remarked that, of the presently recorded collembolan species, only two were previously known to be distributed throughout the continental Antarctic: *Cryptopygus antarcticus* and *Friesea grisea*. The records of the latter in Eastern Antarctic have been practically refuted based on their morphology (Deharveng 1981 and subsequent publications), so that this species most likely does not occur in the Eastern Antarctic. The same has been fairly well proven by Torricelli et. al. (2010) for *Friesea grisea,* the 'only species which has been described for both major regions of the continent'. Thus, up to now, probably no species of Collembola occurs in both the western (maritime) and eastern parts of Antarctica.

In terrestrial habitats of the Antarctic, large site-to-site differences in species composition are common (e.g., Wise et al. 1964, Tilbrook 1967b, Richard et al. 1994, Sohlenius et al. 1995), which was also found in the present study. However, only few species are restricted to specific sites (= local endemics). Also the present study found no local endemics. Furthermore, no expansions to the previously known zoogeographical distribution boundries of the recorded species could be found. Previous studies show that the distributional areas of almost all species extend further north (e.g., to the South Orkney Islands) as well as much further south within the maritime Antarctic (e.g., Palmer Land, Graham Coast or even Alexander Island). Nonetheless, the soil fauna of many of the investigated localities had never been surveyed before. Therefore, the number of proven sites of distribution for most of the recorded species has been increased by the present study, especially within the South Shetland Islands.

Although a number of different locations were examined during these investigations, the study areas

were somewhat limited in range within the maritime Antarctic. Nonetheless all collembolan species endemic to Maritime Antarctica were recorded in the present study. According to Greenslade (1995, 2010), the following species have been reliably recorded from the South Shetland Islands: *Hypogastrura viatica, Tullbergia mixta*, *Protaphorura fimata*, *Friesea grisea*, *Friesea woyciechowskii*, *Cryptopygus antarcticus antarcticus*, *Cryptopygus badasa*, *Mucrosomia caeca*, *Folsomia candida*, *Archisotoma brucei* and *Folsomotoma octooculata*. According to literature data, other parts of the maritime Antarctic (Antarctic Peninsula, South Orkney Islands and others) have not shown records of any other species. The species *Hypogastrura antarctica* Salmon, 1962 (= *H. viatica*), *Tillieria penai* Weiner & Najt, 1994 (= *T. mixta*), *Achorutoides antarcticus* Willem, 1901 (= *F. grisea*), *Cryptopygus crassus* Carpenter, 1907 (= *C. antarcticus*), *Cryptopygus nanjiensis* Yue & Tamura, 2001 (= *C. antarcticus*) are considered to be junior synonyms of species of the main list. The 'basic species set' of the maritime Antarctic (as defined here: *Cryptopygus antarcticus, Friesea grisea, Folsomotoma octooculata*, *Cryptopygus badasa, Tullbergia mixta, Friesea woyciechowskii*) was registered on almost all locations on and around King George Island (this set is formally incomplete only in Punta Cristian, where *C. antarcticus* is lacking). In contrast, not all mite species known to occur on and around the Antarctic Peninsula were registered in the present study, e.g., the oribatid *Magellozetes antarcticus* or the actinedid *Rhagida leechi*, most likely due to the restricted study area. Moreover, some widely distributed taxa often found abundant in previous studies were only found sporadically in the present investigation, e.g., the oribatids *Globoppia loxolineata* and *Liochthonius mollis* or the actinedids *Pretriophtydeus tilbrooki*, *Rhagidia gerlachei* or *Stereotydeus villosus*. Furthermore, although the collembolan species were registered in relative proportions similar to other studies, the abundances and dominances of closely related mite taxa were recorded in opposite proportions to those found in previous investigations, e.g. the actinedids *Eupodes parvus* and *Eupodes exiguous* or *Nanorchestes berryi* and *N. nivalis*. This is partly due to the fact that densities of individual species vary strongly from sample to sample and their distribution is very patchy even at short distances (Richard et al. 1994, Ohyama & Shimada 1998). The most plausible explanation for these different dominances is, however, that the substrates sampled in the present studies were different from those often sampled during general species inventories. Many basic surveys of Antarctic microarthropods simultaneously investigate different microhabitats (e.g., algal mats, vegetation and stones) or even largely concentrate on the underside of stones (e.g., Janetschek 1967, Goddard 1979a, Convey et al. 1996, Thor 1996, Convey & Quintana 1997, Stevens & Hogg 2002). Many authors consider the underside of medium-sized stones to be an important habitat for terrestrial microarthropods in Antarctica. This microhabitat is characterized by, e.g., a greater availability of soil moisture or organic carbon and tend to heat strongly in summer and retain temperatures often more than 10°C above air temperatures, allowing the animals to be more active while at the same time avoiding exposed microhabitats (Wise et al. 1964, Tilbrook 1967b, Caruso & Bargagli 2007, Hawes et al. 2008a). Many species aggregate and are therefore found in higher densities under stones, whereas other, mostly smaller species are more commonly found in soil substrates (Wise et al. 1964, Bowra et al. 1966, Goddard 1979a, Booth & Usher 1986, Caruso & Bargagli 2007). However, sampling stones can only be achieved by experienced researchers and is time consuming. Most of the sampling in the present study took place during land excursions from cruise ships, which are highly limited in time. The sampling design employed here also required equivalent samples from the various locations (s. Russell et al. 2013), not allowing specific microhabitats to be directly addressed in single samples. Furthermore, sampling often took place by inexperienced personnel, requiring a straightforward and standardized sampling method. Thus, the investigation of soil substrates (including surface vegetation) excluding the specific sampling of stone undersides was necessitated by the study limitations.

Antarctic soil faunal communities are generally known to be species-poor and lacking major taxonomical groups common in more temperate climates (e.g., Carabidae, Lumbricidae, Diplopoda etc.; Block 1984b, Marshall & Pugh 1996, Hogg & Stevens 2002). Over the last decades, the number of microarthropod species known from the maritime Antarctic has increased steadily (Tab. 5). Recent publications list up to 47 microarthropod species occurring naturally in the maritime Antarctic (e.g., Hogg & Stevens 2002, Convey 2005). In an intensive literature review, Pugh (1993) even lists approximately 70 different terrestrial species of the Acari having been found in the maritime Antarctic, although these also include synanthropic taxa occurring around research stations etc. With over 40 registered species (plus 4–8 potentially non-native species), the present study thus recorded a large proportion of the maritime Antarctic microarthropod fauna.

The mesofaunal species richnesses found in the individual localities generally correspond to the species numbers recorded in previous studies in other sites (cf. Tab. 5). The number of species found in maritime

Table 5. Microarthropod species numbers recorded in previous studies in maritime Antarctic localities.

	Study	Region/Locality	Microarthropods	Collembola	Acari	Actinedida	Oribatida	Gamasida	Astigmata/Other
Maritime Antarctica	Russell et al. 2013 (present study)	N. Maritime Antarctica	**45**	11	34	25	5	4	
	Tilbrook 1967a	Maritime Antarctica	**22**	7	15	7	5	2	1
	Gressitt 1967	N. Maritime Antarctica	**37**	5	32	5	4	2	0
	Wallwork 1973	Maritime Antarctica	**33**	8	25	10	15	0	0
	Block 1984b	Maritime Antarctica	**40**	8	32	10	14	4	4
	Pugh 1993	Maritime Antarctica			70	27	20	9	14
	Marshall & Pugh 1996	Maritime Antarctica			17				
	Convey 2005	Maritime Antarctica	**46**	10	36				
	Hogg & Stevens 2002	Maritime Antarctica	**47**	15	32	13	15	4	0
Region	Convey et al. 2000a	South Sandwich Islands	**19**	8	11	2	6	3	0
	Gryziak 2009	South Shetland Islands			28	13	12	2	1
	Usher & Edwards 1986 cit. in Convey & Quintana 1997	South Shetland Islands	**17**						
Individual sites	Strong 1967	Palmer Station	**14**	4	10	4	5	1	0
	Goddard 1979a	Signy Island			10	6	2	1	1
	Goddard 1979b	Signy Island			18	8	2	4	4
	Block 1982 cit. in Richard et al. 1994	Signy Island	**13**	3	10				
	Usher & Booth 1984	Signy Island	**10**	4	6	5	0	1	0
	Usher & Edwards 1984	Lynch Island	**13**	3	10	7	2	1	0
	Usher & Edwards 1986 cit. in Convey & Quintana 1997	Marquerite Bay	**11**						
	Richard et al. 1994 & Convey et al. 1996	Byers Peninsula, Livingston Island	**21**	6	15	9	5	1	0
	Convey & Quintana 1997	Cierva Point, Danco Coast	**15**	3	12	6	4	1	1
	Convey & Smith 1997	Marguerite Bay	**20**	4	16	9	6	1	0
	Convey & Smith 1997	Alexander Island	**9**	2	7	6	1	0	0
	Convey et al. 2000b	Charlot Island	**7**	0	7	3	4	0	0

Antarctic habitats is generally much lower than those of temperate zones (cf. Pertersen & Luxton 1982) and are often even only half of that found in Subantarctic sites (Pugh 1993, Hogg & Stevens 2002). The reasons for such low species numbers are considered to be – besides the geographic isolation of Antarctica – the necessity of occurring species to be adapted for survival under the adverse climatic Antarctic conditions (Gressitt et al. 1961, Block 1984b, Marshall & Pugh 1996). Various adaptations are found in Antarctic species, the most obvious of which being an ability to withstand very cold temperatures. Most species actually show a high range of temperature tolerances (Sanyal 2004), but are nonetheless cold tolerant, being able to withstand temperatures down to -20°C and even lower (e.g., Janetschek 1967, Tilbrook 1967b, Block 1984b, Day et al. 2009). This is usually achieved by super-cooling abilities, such as avoidance of ice nucleators (including emptying the gut) and/or antifreeze proteins in the body (Block 1984b, Lister et al. 1988, Hogg & Stevens 2002, etc.). Some species are actually incapable of tolerating warmer temperatures, e.g., above 20°C (Janetschek 1967).

A further adaptation is an extended life cycle relative to species from temperate climates (Goddard 1979a, Block 1984b, Booth & Usher 1986, Lister et al. 1988, Marshall & Pugh 1996). Generation times can be as long as 2 to

3 years (as opposed to ca. 1 year in temperate zones), whereby species can overwinter in various stages and hatching from eggs can occur either immediately or in following years (Janetschek 1967, Strong 1967, Goddard 1979a, Booth & Usher 1986). This has been considered to be an adaptation to unpredictable yearly weather conditions (Booth & Usher 1986) and can lead to highly variable densities from year-to-year. The necessity for such adaptations limits the numbers and identities of the species occurring in Antarctic terrestrial habitats.

Some of the localities sampled in the present study were in comparison to other studied localities or to previous studies in the maritime Antarctic found to be extremely species-poor (e.g., Paulet Island, Devil Island or Petermann Island). Since the sampling design used on these islands was identical to that of all other localities, this species poverty can be considered to be a general characteristic of these islands. The islands were extremely rocky with very thin and/or poorly developed soil substrates. Vegetation was also hardly or not developed on these islands; however, other localities also bore no vegetation and nonetheless showed a higher species richness. Thus, the lack of soil substrate (with the corresponding organic material and microorganisms) was the most likely cause of the low species richness registered in these localities.

Among the microarthropod groups, Actinedida were the most species-rich, followed by Collembola. This also appears to be typical for terrestrial maritime Antarctic arthropod faunas. Most previous surveys of soil fauna in the maritime Antarctic report Actinedida (usually called Prostigmata in the literature) with the highest species numbers, followed by Collembola and then the other mite groups (see citations in Tab. 5). This is in contrast to temperate regions, where microarthropod communities are often dominated by Collembola and Oribatida.

Only few previous studies report total average densities of Acari, Collembola or total microarthropods (Tab. 6). A comparison of these studies shows a large range of registered densities, generally averaging between 2,000 and 50,000 individuals m^{-2} with maximum densities at times reaching more than 400,000 individuals m^{-2}. A comparison of these literature values with the present study is difficult, due to the necessary standardization of all samples to individuals per 100 cm³ in the present analyses. Nonetheless, considering an individual sample size of 5 cm Ø and 5 cm depth (which was the most common sample size, with approximately half of each sample used for extraction of microarthropods), the density values calculated here can be very roughly translated into individuals m^{-2} (Tab. 6). Although these values can only be considered rough approximations, they show that the densities found in the present studies

generally compare to those found in previous studies in the maritime Antarctic. As opposed to species richness, the recorded densities were comparable and often higher than those generally found in temperate climates (cf. Petersen & Luxton 1982). In many localities, the densities found here can actually be considered to be very high, often due to aggregations of individual species. The extremely high densities found in, e.g., the second locality at Punta Christian (King George Island), Halfmoon Island or Whalers Bay on Deception Island (all in 2010) were indeed due to high densities of single species. On the other hand, the islands mentioned above proving to be very species-poor (or also Telephone Bay on Deception Island) also generally showed low densities. However, this was true in all samples of these localities, so this tends to be a general characteristic of these islands where high densities of single species do not occur, most likely for the same reasons mentioned above. As opposed to species richness, the highest densities were mostly found among the Collembola, which also appears to be common in Antarctic microarthropod communities (Tab. 6).

The results acquired in the present study clearly showed a decline in diversity (densities and species richness) at higher latitudes. The fauna of Deception Island is obviously the species richest, which appears to be an anomaly, but can be explained by the special climatic conditions (warmed fumerol soils offering better habitat conditions than most Antarctic habitats) as well as its anthropogenic history (as a whaling station as well as a popular touristic visitation site, possibly imparting increased species dispersal). Declines in diversity at higher latitudes also appears to be typical for the maritime Antarctic soil fauna, as a number of authors have also remarked on this tendency (e.g., Usher & Edwards 1986b, Convey & Quintana 1997, Caruso & Bargagli 2007, Gryziak 2009). A clearer decline of collembolan diversity was shown at a larger scale by Usher and Edwards (1986b), where the number of species decreased from five to three on islands of the maritime Antarctic from the north-east to south-west (South Shetland Islands – Graham coast – northern Adelaide Island). This cannot be regarded as a general rule, however, since surveys in more southern regions of the maritime Antarctic have revealed relatively species-rich microarthropod communities (much species-richer than continental sites at the same latitude; Convey & Smith 1997). Thus, this tendency may be only true for the northern maritime Antarctic, in which the present investigations took place.

At the larger scale of the maritime Antarctic, the total densities of mesofaunal groups as well as densities of particular species are determined mainly by locality. This is confirmed in the present study, where the most

Table 6. Microarthropod densities recorded in previous studies in maritime Antarctic localities (as far as available). Numbers in individuals per m^2. The densities given for the present study are generalized transformations from individuals per 100 cm^3 and are thus only rough approximations. True densities are given in the Appendix.

Study	Locality	Microarthropods	Collembola	Acari
Tilbrook 1967a	maritime Antarctic	2,000-45,000 (max: 78,000)		
Goddard 1979a	Signy Island			1,300-28,000
Block 1982 cit. in Richard et al. 1994	Signy Island	20,000-99,000		
Usher & Edwards 1984	Lynch Island	11,000-29,000 (max: 68,000)		
Usher & Booth 1984	Signy Island		8,000-50,000 (max: 107,000)	4,000-30,000 (max: 96,000)
Richard et al. 1994 & Convey et al. 1996	Byers Peninsula (Livingston Isl.)	<1,000-21,000 (max: 46,000)	(dominant)	
Convey & Smith 1997	Alexander Island	240-3,000 (max: 20,500)		
Convey & Smith 1997	Marguerite Bay	43,000-121,000 (max: 433,000)	(dominant)	
Convey & Quintana 1997	Cierva Point, Danco Coast	5,000-50,000 (max: 83,000)		
Convey et al. 2000b	Charlot Island			12,000-44,000
Russell et al. 2013 (Present study)	Arctowski Station	236,000	116,000	120,000
	Biologenbucht	255,000	206,000	50,000
	Punta Cristian	69,000	25,000	44,000
	Punta Cristian II	288,000	247,000	41,000
	Ardley Island	101,000	64,000	36,500
	Halfmoon Island (2010)	730,000	15,000	717,000
	Halfmoon Island (2011)	49,000	670	48,000
	Hannah Point	20,000	1,900	18,000
	Telefon Bay	1,900	1,100	900
	Whalers Bay (2010)	347,000	346,000	1,600
	Whalers Bay (2011)	145,000	124,000	21,000
	Paulet Island	9,900	300	9,600
	Devil Island	6,600	6,600	0
	Neko Harbour (2010)	140	50	90
	Neko Harbour (2011)	5,700	3,600	2,100
	Petermann Island	275	0	275

significant differences in densities and species richness of all taxonomic groups was between localities. Such a dependence is similar to the large-scale distribution pattern described in eastern Antarctica, where the presence of a species is strongly affected by colonization/recolonization of refugia periodically covered with ice (Caruso et al. 2009b, Stevens & Hogg 2003, 2006). If true, local species richness varies considerably depending on the geographical position of the locality. The large-scale distribution pattern in the maritime Antarctic is probably more influenced by climatic determinants than their history, since almost all endemic species are distributed widely throughout the Antarctic Peninsula. In the present study, the highest densities of Collembola and Acari were found on King George Island and Deception Island. However, this is not confirmed by other publications, where high densities were also found in more southern latitudes (e.g., Tilbrook 1967a, Usher & Edwards 1986b). We suggest that such strong differences between locations are caused by local differences at medium scales (characteristics of the particular coast, exposition of slope, soil parameters, development of vegetation, etc.).

In total, all of the parameters mentioned above characterizing the registered microarthropod communities show very typical relationships for Antarctic soil faunas. Therefore, the data obtained in

the present sampling can be considered representative for the studied habitats. Due to the wide distribution of most species occurring in the maritime Antarctic, some authors consider Antarctic species to have a low habitat specificity and correspondingly broad tolerance for a wide range of habitat conditions, indicating a more generalist nature (Tilbrook 1967b, Richard et al. 1994, Convey & Quintana 1997). The correlation analyses performed here cannot substantiate this opinion. Most major taxonomic groups (total densities and species richness) and many individual species showed significant relationships to specific habitat parameters.

The strongest correlations among microarthropods were to vegetation cover. In Antarctic habitats, a strong dependence of total and individual species' densities on vegetation cover has been shown by, e.g., Tilbrook (1967b), Goddard (1979a), Usher & Booth (1984), Booth & Usher (1986), Richard et al. (1994), Convey et al. (1996), Frati et al. (1997) and Gryziak (2009). This could likely be an indirect effect, since few of the recorded species are directly herbivorous. Hogg & Stevens (2002) consider vegetation to be more a source of habitat than of food for Antarctic Collembola and Acari. On the other hand, vegetated areas are most probably richer in microorganisms (bacteria, fungi, algae) due to plant-root exudates. Since almost all of the recorded species are microbivorous (cf. Strandtmann et al. 1967, Goddard 1979a, 1979b, Block 1984b), vegetation could likely be a habitat with richer nutritional resources (cf. Sinclair 2001). Independent of the mechanisms involved, however, the present study results show the degree of vegetation cover to be a very important habitat factor determining densities and species richness.

At the local scale of patchy environments within the Antarctic, habitat factors (e.g., soil properties and nutrient status) appear to be more important than biotic interactions in influencing microarthropod assemblages (Adams et al. 2006, Hogg et al. 2006). The dependencies found in the present study mostly confirmed the known regularities of the microhabitat distribution of Antarctic microarthopods. In general, soil moisture is often a limiting factor affecting the distribution and abundance of species (Wise et al. 1964, Dalenius 1965, Strandtmann et al. 1967, Strong 1967, Ohyama 1978, Block 1984b, Booth & Usher 1984, Frati et al. 1997, Hogg & Stevens 2002, Sinclair et al. 2006, Day et al. 2009). More than directly affecting species distributions, temperature can more often determine the amount of biologically available water. The present results confirm a potential limitation by soil moisture, since all major taxonomic groups and many individual species showed significantly higher densities (and species richness with the major groups) at higher soil moistures.

For most microarthropod groups and species, soil organic matter (total amounts, concentrations of C and N and or C/N-relationship) was an important determinant factor in the present study. The dependency of soil Collembola and Acari on soil organic matter has been confirmed in a number of studies (e.g., Wise et al. 1964, Booth & Usher 1984, Sanyal 2004, Adams et al. 2006). Although this is true for most of the groups studied here, the correlations with parameters indicating increased organic material were strongest among the Oribatida in the present study. This is not surprising, since many Oribatida are considered to be – as opposed to almost all other soil microarthropods– particulate detritus feeders (Krantz & Walter 2009), which is probably also true of the oribatid species occurring in Antarctica. Gryziak (2009) found Oribatida to be limited to older, more developed soils, which are generally more enriched in organic matter. Therefore, on the one hand, vegetated soil substrates with a higher content of dead organic matter most likely offer a spatially and climatically more hospitable habitat than predominantly mineral sand, gravel or rock substrates. On the other hand, soil organic matter represents a primary nutrient resource for Antarctic Oribatida. Again, organic matter may be an indirect, but nonetheless important influencing factor, providing a more substantial basis for microorganisms, which in turn provide nutrient resources for the soil fauna.

The weakest correlations to habitat parameters were found with the wholly predacious Gamasina. Except for vegetation cover, abiotic soil parameters were apparently not as important in determining the occurrence of this mite taxon as in the other faunal groups. Prey availability is most likely the more important determining factor (Lister et al. 1988), although this was not specifically studied. Other soil factors, such as pH or soil texture (= grain size distribution), showed few or no correlations to densities or species richness of Gamasina. This may be due to the fact that such correlations truly do not exist. However, it is more probable that the limited number of study sites and the usually very low densities of this animal group (as partly also true among the Oribatida) render the statistical determination of actually occurring relationships to habitat parameters difficult. On the other hand, a low influence of these factors on soil microarthropods has also been found in other studies (e.g., Wise et al. 1964, Adams et al. 2006). Therefore, the most important habitat factors determining species richness and population sizes of the mesofauna – with the possible exception of Gamasina in the present study were vegetation cover, soil organic material and soil moisture. Correlations of some microarthopod species or major groups to individual habitat parameters (in particular soil temperature) were contradictory between study

years. This is probably due to year-to-year differences in this factor and that the temperature measurements represented only momentary conditions and not averages over longer time periods, which would more likely influence population sizes.

4.2. Nematoda

Despite fewer previous studies than for microathropods, compared to other, even European areas, the Antarctic nematode fauna has been fairly well studied during the last 40 years (e.g., Spaull 1973, Maslen 1979a, 1979b, Andrassy 1998, Holovachov & Boström 2006). However, some previous Antarctic studies did not investigate soil-borne nematode communities, but concerned the microfauna from moss cushions and lichens. The 13 studied localities and over 300 soil samples in the present study thus represent a relatively extensive investigation and provide a considerable data source. Of the 39 morpho-species found, 20 have previously been recorded from the maritime Antarctic. Of those, 17 are considered to be endemic and three are considered to have a worldwide distribution. The existence of such cosmopolitan species has repeatedly been doubted (e.g. Maslen & Convey 2006), and it was speculated that populations from different parts of the world may in fact belong to many different, rather locally distributed species that share a very similar morphology (Sudhaus 2011); a question that was not the topic of the present study and that can only be answered by thorough comparisons, combining morphological and molecular characters (Sudhaus 2011). In a biogeographical context, Antarctica is unique also in regard to its nematode fauna for two reasons. Firstly, as stated above, most of the nematode species recorded from Antarctica are endemic or at least unknown elsewhere. Secondly, as in the microarthropods, hardly any overlap in nematode species inventory exists between Maritime and Continental Antarctica; these two regions also represent separate biogeographical zones for Nematoda (Maslen & Convey 2006). An intersection of the two zones could be Alexander Island, which is species-richer than neighbouring islands to the north and even harbours 10 % more species than the rest of Maritime Antarctica altogether (Maslen & Convey 2006). First evidence of the occurrence of supposedly continental Antarctic nematode species in the maritime Antarctic was given by Maslen & Convey (2006) from Adelaide Island, Alamode Island und Charcot Island, where nematode specimens were found that morphologically strongly resembled the continental species *Plectus murrayi* and *P. frigophilus*. The number of total species that have been previously reported in Antarctica (= gamma diversity) is very small in comparison to other climatic zones (Wharton 2003). Andrássy (2008) only lists 32 known species in the maritime Antarctic. The present study already recorded 22 to 23 nematodes species alone in the individual-richest sites (Biologenbucht, Arctowski Station and Punta Christian I on King George Island). In the species-poorest locality (Peterman Island), on the other hand, only one species was found. The species composition of the nematode fauna is thus very different from island to island. This high regional ß-diversity suggests barriers to species' distributions, which could result from deficient nutrient resources or ecological conditions or simply be due to physical barriers that cannot be crossed (Spaull 1973).

Spaull (1973) and Maslen (1979a, 1979b) studied the nematode fauna in soil and vegetation samples from 15 and 16 maritime Antarctic islands, respectively, among which only Deception Island was also studied in the current study. These authors determined that nematode diversity measured either as the number of genera or species per site decreased with increasing southern latitude. The authors supposed a relationship between diversity and decreasing temperatures from north to south, with the corresponding increase in abiotic stress as well as the decreasing ice- and snow-free periods, in which colonization and population establishment of nematode species can take place. The present study could confirm the decrease in species diversity from north(east) to south(west), albeit in a much smaller region of the maritime Antarctic. Nematode diversity was furthermore associated with the degree of vegetation cover, which also at least in trend decreased from northeast to southwest. On the other hand, nematode diversity was also associated with soil water and nutrient contents, which differed strongly among the various localities, but did not show a gradient from north to south. While the present study could thus confirm the tendency of decreasing species richness with increasing southern latitude, the causal relationship behind this tendency is more likely due to site-specific environmental conditions, which differentially affected the occurrence of the nematode species.

As aquatic life forms, nematodes are dependent upon the availability of water for their various activities, e.g., mobility, feeding, growth, respiration and reproduction. Since terrestrial habitats periodically or regularly dry out, many soil-borne nematode species are capable of anhydrobiosis, an ametabolic state of dormancy, in which an individual can survive adverse conditions for many years (Wharton 2002). In the McMurdo Dry Valleys, 30 to 80 % of all nematodes are present in a state of anhydrobiosis (Treonis et al. 2000). When sufficient water returns, the individual becomes active within minutes or

hours (Wharton 2002). Although large amounts of water exist in Antarctica, this water is mostly biologically not available, since it is bound in ice, snow, clay or soil-bound organic material. The availability of water therefore plays a major role in the distribution of terrestrial microfaunal species in Antarctica (Wharton 2003). The present results confirm this, where the highest correlations to soil moisture were found among the Nematoda, concerning total densities and species richness as well as partly the populations of individual species.

Desiccation-induced anhydrobiosis also protects these species from other environmental stressors, e.g., extremely low temperatures. However, even without a foregoing anhydrobiosis, many Antarctic nematode species are capable of surviving temperatures as low as -30°C and intracellular ice crystals without damage (Smith et al. 2008, Wharton et al. 2005). In light of these survival strategies, it is not surprising that nematodes also represent the individual- and species-richest animal group in the terrestrial Antarctic as in temperate zones. The contradictory correlation results between 2010 and 2011 regarding temperature are apparently more a factor of the localities in which the individual species were found (as well as yearly weather differences) and the fact that among the species-poorest communities (albeit individual-rich) were found in the warmed soils of Whaler's Bay.

Terrestrial Antarctic nematodes feed primarily on bacteria, cyanobacteria and algae. The nematode species recorded in the present study were clearly dominated by bacterial feeders, which in trend increased in the climatically harsher western study sites in the Weddle See. Bacterivores also represented the most numerous feeding type among the nematodes of the climatically milder localities on King George Island and Ardley Island. However, in these sites, this feeding type was also accompanied by algal and fungal or root-feeding species. Microbial biomass (e.g., as a nutrient resource for nematodes) is generally low in Antarctica due to low soil nutrient contents (Andrássy 1998). An exception is represented by the ornithogenic soils on Paulet Island, from which an outstandingly strong population of one bacterivorous nematode species (*Pelodera teres*-group) was detected in the present study. These very high densities of one species are most likely due to the (relative to most Antarctic soils) high nitrogen content and presumed correspondingly rich source of bacteria. Sohlenius et al. (2004) also observed that representatives of the bacterivorous genera *Plectus* and *Panagrolaimus* developed their highest population densities in organic soils and mosses as well as in the organic material under the algae *Prasiola*. In turn, such microhabitats were particularly found in the vicinity of colonies of the snow petrel (*Pagodroma nivalis*), whose droppings provided a rich nutrient input into the soils. The high positive correlations to parameters of organic matter as well as to vegetation presumably indicate indirect effects to these feeding-type relationships, where these factors simply reflect higher microbial communites in sites with higher levels of vegetation cover or soil organic matter.

Interesting are the correlation results to soil texture, where significant corelations were predominately found with the Nematoda as opposed to the microarthropod groups. The negative correlations to coarser grains and positive correlations to finer grained material indicate that the species and communities recorded here preferred finer grained material, possibly reflecting finer (moisture-filled) pore spaces.

Due to the usually sporadic or lacking vegetation cover and the correspondingly weak soil food webs, only few plant-parasitic and predatory nematode species are found in Antarctic soils (Andrássy 1998). Exceptions are represented by as yet mostly undescribed species from the genera *Tylenchus* (from Signy Island), *Filenchus* (from Livingston Island, King George Island and Ardley Island) as well as *Aphelenchoides vaughani, A. helicosoma* and *A. haguei* (all occurring from Signy Island to Alexander Island), all of which feed on plant-root and/or fungal cells (Spaull 1973, Maslen 1979a, Chipev et al. 1996 and the present study). Also the predatory nematode species *Coomansus gerlachei* is broadly distributed in Maritime Antarctica (Peneva et al. 1996), with at times astonishingly high densities despite the minimal supply of prey, as could be shown in the present study on Halfmoon Island and Hannah Point. The high dominance of representatives of this species in the nematode communities of these two localities indicates that they do not feed primarily from other nematodes species, but rather (or also) from Rotatoria, Protozoa and juvenile Collembola and Tardigrada.

4.3. Conclusions

The soil fauna recorded in the present study is obviously typical for the maritime Antarctic. With Nematoda representing the most individual- and species-rich taxonomic groups and Collembola being the next-most individual-rich group and actinedid mites the next-most species-rich, the numerical relationships between the different faunal groups is also typical for the region. The species composition observed in the various study sties were also highly similar to that recorded in other maritime Antarctic localites, even if not all known maritime Antarctic species were determined in the current study (with the exception of Collembola, where

all known species were observed). Nonetheless, the sites of occurrence in the martime Antarctic could be expanded for most of the recorded species in the present study. Differences were indeed noted concerning the dominances of individual species within the major faunal taxa. However, these are most likely due to specific locality conditions and sampling differences to previous studies. While no new endemic species were identified among the microarthopods (Collembola and Acari), several nematode taxa were found that are probably new to science and will be described elsewhere. Thus the results of the present study generally confirm previous soil-zoological knowledge of Maritime Antarctica. The study furthermore greatly increases the knowledge of the specific environmental preferences of the recorded species.

5. Acknowledgements

6. References

Adams, B. J., R. D. Bardgett, E. Ayres, D. H. Wall, J. Aislabie, S. Bamforth, R. Bargagli, C. Cary, P. Cavacini, L. Connell, P. Convey, J. W. Fell, F. Frati, I. D. Hogg, K. K. Newsham, A. O'Donnell, N. Russell, R. D. Seppelt, M. I. Stevens (2006): Diversity and distribution of Victoria Land biota. – Soil Biology & Biochemistry **38**: 3003–3018.

Andrássy, I. (1998): Nematodes in the sixth continent. – Journal of Nematode Morphology and Systematics **1**: 107–186.

Andrássy, I. (2005): Free-living nematodes of Hungary. Volume I. – Pedozoologica Hungarica 3, Hungarian Natural History Museum, Budapest: 518 pp.

Andrássy, I. (2008): *Eudorylaimus* species (Nematoda: *Dorylaimida*) of continental Antarctica. – Journal of Nematode Morphology and Systematics **11**: 49–66.

Baermann, G. (1917): Eine einfache Methode zur Auffindung von Ankylstommum (Nematoda) Larven in Erdproben. – Geneeskundig Tijdschrift voor Nederland-Indië **57**: 131–137.

Benoit, J. B., M. A. Elnitsky, G. G. Schulte, Jr. R. E. Lee, D. L. Denlinger (2009): Antarctic collembolans use chemical signals to promote aggregation and egg laying. – Journal of Insect Behavior **22**: 121–133.

Beyer, L., M. Bölter (2002): Geoecology of Antarctic Ice-Free Coastal Landscapes. – Springer, Berlin Heidelberg New York: 427 pp.

Block, W. (1982): The Signy Island terrestrial reference sites XIV. Population studies on Collembola. – British Antarctic Survey Bulletin **55**: 33–49.

Block, W. (1984a): An insect introduction to the maritime Antarctic. – Biological Journal of the Linnaean Society **23**: 33–39.

Block, W. (1984b): Terrestrial microbiology, invertebrates and ecosystems. – In: Laws, R. M. (ed.): Antarctic Ecology. – Academic Press, London: 163–236.

Block, W. & P. Convey (1995): The biology, life cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus*. – Journal of Zoology, London **236**: 431–449.

Block, W. & J. Starý (1996): Oribatid mites (Acari: Oribatida) of the maritime Antarctic and Antarctic peninsula. – Journal of Natural History **30**: 1059–1067.

Block, W. & M. R. Worland (2001): Experimental Studies of Ice Nucleation in an Antarctic Springtail (Collembola, Isotomidae). – Cryobiology **42**: 170–181 (2001).

Block, W., S. R. Young, E. M. Conradi-Larsen & L. Sømme (1978): Cold tolerance of two Antarctic terrestrial arthropods. – Experientia **34**: 1166–1167.

Block, W., P. M. Harrisson & G. Vannier (1990): A comparative study of patterns of water loss from two Antarctic springtails (Insecta, Collembola). – Journal of Insect Physiology 36: 181–187.

Bokhorst, S., A. Huiskes, P. Convey, P. M. van Bodegom & R. Aerts (2008): Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. – Soil Biology & Biochemistry **40**: 1547–1556.

Bokhorst, S., C. Ronfort, A. Huiskes, P. Convey & R. Aerts (2007): Food choice of Antarctic soil arthropods clarified by stable isotope signatures. – Polar Biology **30**: 983–990.

Booth, R. G. (1984): A new species of mite in the genus *Nanorchestes* (Acari, Prostigmata) from Signy Island, South Orkney Islands. – British Antarctic Survey Bulletin **63**: 111–116.

Booth, R. G. & M. B. Usher (1984): Arthropod communities in a maritime Antarctic moss-turf habitat: effects of the physical and chemical environment. – Journal of Animal Ecology **53**: 879–893.

Booth, R. G. & M. B. Usher (1986): Arthropod community in a maritime antarctic Moss-turf habitat: Life history strategies of the prostigmatid mites. – Pedobiologia **29**: 209–218.

Booth, R. G., M. Edwards & M. B. Usher (1985): Mites of the genus *Eupodes* (Acari, Prostigmata) from maritime Antarctica: a biometrical and taxonomic study. – Journal of Zoology, London **207**: 381–406.

Boström, S. (1995): Populations of *Plectus acuminatus* Bastian, 1865 and *Panagrolaimus magnivulvatus* n. sp. (Nematoda) from nunataks in Dronning Maud Land, East Antarctica. – Fundamental and Applied Nematology **18**: 25–34.

Boström, S. (1996): One new and two known nematode species from the Subantarctic Islands South Georgia and East Falkland Island. – Fundamental and Applied Nematology **19**: 151–158.

Boström, S. & P. de Ley (1996): Redescription of *Cervidellus vexilliger* (de Man, 1880) Thorne, 1937 (Nematoda: Cephalobidae) and taxonomical consequences. – Fundamental and Applied Nematology **19**: 329–340.

Bowra, G. T., M. W. Holdgate & P. J. Tilbrook (1966): Biological Investigations in Tottanfjella and Central Heimefrontfjella. – British Antarctic Survey Bulletin **9**: 63–70.

Broady, P. A. (1979): Feeding studies on the collembolan Cryptopygus antarcticus Willem at Signy Island, South Orkney Islands. – British Antarctic Survey Bulletin **48**: 37–46.

Bulavintsev, V. I. (1990): Complexes of microarthropods of the Fildes Peninsula, Ardley and Nelson Island found during ecological monitoring in Antarctica. – Sovetskaia Antarktischeskaia Ekspeditsiia: Informatsionny Biulleten', **113**: 101–108 [In Russian].

Burn, A. J. (1981): Feeding and growth in the Antarctic collembolan Cryptopygus antarcticus. – Oikos **36**: 59–64.

Burn, A. J. (1984): Life cycle strategies in two Antarctic Collembola. – Oecologia (Berlin) **64**: 223–229.

Burn, A. J. & A. Lister (1988): Activity patterns in an Antarctic arthropod community. – British Antarctic Survey Bulletin **78**: 43–48.

Burns, G., M. A. S. Thorne, G. Hillyard, M. S. Clark, P. Convey, M. R. Worland (2010): Gene expression associated with changes in cold tolerance levels of the Antarctic springtail, Cryptopygus antarcticus. – Insect Molecular Biology **19**: 113–120.

Cannon, R. J. (1986): Diet and acclimation effects on the cold tolerance and survival of an Antarctic springtail. – British Antarctic Survey Bulletin **71**: 19–30.

Carpenter, G. H. (1907): Collembola from the South Orkney Islands. – Proceedings of the Royal Society of Edinburgh **1905/6**: 473–483.

Caruso, T. & R. Bargagli (2007): Assessing abundance and diversity patterns of soil microarthropod assemblages in northern Victoria Land (Antarctica). – Polar Biology **30**: 895–902.

Caruso, T., I. D. Hogg, A. Carapelli, F. Frati & R. Bargagli (2009b): Large-scale spatial patterns in the distribution of Collembola (Hexapoda) species in Antarctic terrestrial ecosystems. – Journal of Biogeography **36**: 879–886.

Chipev, N., V. Peneva & S. Nedelchev (1996): Abundance and distribution of nematode feeding groups in relation to habitat on Livingston Island, South Shetland Islands, Antarctica. – Bulgarian Antarctic Research Life Sciences: 82–92.

Chown, S. L. & P. Convey (2007): Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. – Philosophical Transactions of the Royal Society of London B **362**: 2307–2331.

Convey, P. (2005): Antarctic Terrestrial Ecosystems: Responses to Environmental Change. – Polarforschung **75**: 101–111.

Convey, P. (2011): Antarctic terrestrial biodiversity in a changing world. – Polar Biology **34**: 1629–1641.

Convey, P. & R. D. Quintana (1997): The terrestrial arthropod fauna of Cierva Point SSSI, Danco Coast, northern Antarctic Peninsula. – European Journal of Soil Biology **33**: 12–29.

Convey, P. & R. I. L. Smith (1997): The terrestrial arthropod fauna and its habitats in northern Marguerite Bay and Alexander Island, maritime Antarctic. – Antarctic Science **9**: 12–26.

Convey, P., P. Greenslade, K. J. Richard & W. Block (1996): The terrestrial arthropod fauna of the Byers Peninsula, Livingston Island, South Shetland Islands - Collembola. – Polar Biology **16**: 257–259.

Convey, P., P. Greenslade & P. J. A. Pugh (2000a): The terrestrial micro-arthropod fauna of the South Sandwich Islands. – Journal of Natural History **34**: 597–609.

Convey, P., R. I. L. Smith, H. J. Peat & P. J. A. Pugh (2000b): The terrestrial biota of Charcot Island, eastern Bellingshausen Sea, Antarctica: an example of extreme isolation. – Antarctic Science **12**: 406–413.

Coetzee, L. (1997): The antarctic mite genus *Maudheimia* (Acari, Oribatida. – Navorsinge van die Nasionale Museum (Bloemfontein) **13**: 101–134.

Cross, E. A. (1964): Pyemotidae (Acarina: Tarsonemoidea) from Macquarie Island. – Pacific Insects Monograph **7** (Supplement): 642–646.

Cross, E. A. (1970): Acarina: Prostigmata: Tarsonemoidea: Pyemotidae of South Georgia. – Pacific Insects Monograph **23**: 115–120.

Dalenius, P. (1965): The Acarology of the Antarctic Regions. – Monographiae Biologicae; Biogeography and Ecology in Antarctica **15**: 414–430.

Dalenius, P. & O. Wilson (1958): On the soil fauna of the Antarctic and of the Sub-Antarctic Islands. The Oribatidae (Acari). – Arkiv för Zoologi, N.S. **11**: 393–425.

Dastych, H. (1989): An annotated list of Tardigrada from the Antarctic. – Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg **9**: 136–137.

Davies, K. F., P. Greenslade & B. A. Melbourne (1997): The invertebrates of sub-Antarctic Bishop Island. – Polar Biology **17**: 455–458.

Day, T., C. T. Ruhland, S. L. Strauss, J.-H. Park, M. L. Krieg, M. A. Krna & D. M. Bryant (2009): Response of plants and

the dominant microarthropod, *Cryptopygus antarcticus*, to warming and contrasting precipitation regimes in Antarctic tundra. – Global Change Biology **15**: 1640–1651.

de Man, J. G. (1904): Nématodes libres. – In: Résultats du voyage du S. Y. Belgica en 1897-1898-1899 sous le commendemant de A. de Gerlache de Gomery. – Zoologie: 1–55.

Deharveng, L. (1981): Collemboles des Iles subantarctiques de l'Océan Indien. – Comité National Français des Recherches Antarctiques **48**: 33–109.

DIN (1996): Soil quality - Determination of organic and total carbon after dry combustion (elementary analysis) (DIN/ISO 10694:1995). – Deutsches Institut für Normung e. V., Berlin.

DIN (2005): Soil quality - Determination of pH (DIN/ISO 10390:2005). – Deutsches Institut für Normung e. V., Berlin.

Downie, R. H. (2002): An Overview of the Flora and Fauna of Deception Island. – In: Valencia, J. & R. Downie (eds): Workshop on a Management Plan for Deception Island. – Instituto Antártico Chileno: 1–109.

Dunger, W. & B. Schlitt (2011): Synopses on Palaearctic Collembola. Vol. 6/1: Tullbergiidae. – Soil Organisms **83**: 1–168.

Edwards, M. & M. B. Usher (1987): The adult and juvenile stages of two predatory mites, *Rhagidia gerlachei* and *Tuberostoma Leechi*, in the maritime Antarctic. – Antarctic Survey Bulletin **74**: 37–48.

Fain, A. (1962): Insects of Macquarie Island. Acarina: Trombidiformes: Ereynetidae. – Pacific Insects **4**: 921–928.

Fitzsimons, J. M. (1971): On the food habits of certain Antarctic Arthropods from coastal Victoria Land and Adjacent Islands. – Pacific Insects Monograph **25**: 121–125

Fjellberg, A. (1998): The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha. – Fauna Entomologica Scandinavica **35**: 184 pp.

Fox, A. J., A. Paul & R. Cooper (1994): Measured properties of the Antarctic ice sheet derived from the SCAR Antarctic digital database. – Polar Record **30**: 201–206.

Frati, F., P. P. Fanciulli, A. Carapelli & R. Dallai (1997): The Collembola of northern Victoria Land (Antarctica): distribution and ecological remarks. – Pedobiologia **41**: 50–55.

Freckman, D.W. & R. A. Virginia (1997): Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. – Ecology **78**: 363–369.

Goddard, D. G. (1979a): The Signy Island terrestrial reference sites: XI. Population studies on the Acari. – British Antarctic Survey Bulletin **48**: 71–92.

Goddard, D. G. (1979b): Biological observations on the free-living mites of signy island. – British Antarctic Survey Bulletin **49**: 181–205.

Goddard, D. G. (1982): Feeding biology of free-living Acari at Signy Island, South Orkney Islands. – British Antarctic Survey Bulletin **51**: 290–293.

Greenslade, P. (1995): Collembola from the Scotia Arc and Antarctic Peninsula including descriptions of two new species and notes on biogeography. – Polskie Pismo Entomologiczne, **64**: 305–319.

Greenslade, P. (2006): Invertebrates of Macquarie Island. Kingston, TAS. – Australian Antarctic Division: 326 pp.

Greenslade, P. (2010): South Shetlands Collembola fauna revisited. – Antarctic Science **22**: 233–242.

Greenslade, P. & K. A. J. Wise (1984): Additions to the collembolan fauna of the Antarctic. – Transactions of the Royal Society of South Australia **108**: 203–205.

Greenslade, P., M. Potapov, D. Russell & P. Convey (2012): Lessons from history – Global Collembola (Springtails) on Deception Island. – Journal of Insect Science **12**: 1–16.

Gressitt, J. L. (1965): Biogeography and ecology of land arthropods of Antarctica. – Monographiae Biologicae - Biography and Ecology in Antarctica **15**: 431–490.

Gressitt, J. L. (1967): Notes on arthropod populations in the Antarctic Peninsula-South Shetland Islands-South Orkney Islands area. – Entomology of Antarctica (Antarctic research series) **10**: 373–391.

Gressitt, J. L., R. E. Leech & K. A. J. Wise (1963): Entomological investigations in Antarctica. – Pacific Insects **5**: 287–304.

Gressitt, J.L., T. C. Maa, I. M. Mackerras, S. Nakata & L. W. Quate (1961): Problems in the Zoogeography of Pacific and Antarctic insects. – Pacific Insects Monograph **2**: 1–94.

Gryziak, G. (2009): Colonization by mites glacier-free areas in King George Island, Antarctica. – Pesquisa Agropecuária Brasileira **44**: 891–895.

Hammer, M. (1958): Investigations on the oribatid fauna of the Andes mountains. I. The Argentine and Bolivia. – Biologiske Skrifter udgivet af Det Kongelige Danske Videnskabernes Selskab **10**: 1–129.

Hawes, T. C., M. R. Worland, P. Convey & J. S. Bale (2007): Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography. – Antarctic Science **19**: 3–10.

Hawes, T. C., J. S. Bale, M. R. Worland & P. Convey (2008a): Trade-offs between microhabitat selection and physiological plasticity in the Antarctic springtail, *Cryptopygus antarcticus* (Willem). – Polar Biology **31**: 681–689.

Hawes, T. C., M. R. Worland, J. S. Bale & P. Convey (2008b): Rafting in Antarctic Collembola. – Journal of Zoology **274**: 44–50.

Hayward, S. A. L., M. R. Worland, P. Convey & J. S. Bale (2004): Habitat moisture availability and the local distribution of the Antarctic Collembola Cryptopygus antarcticus and Friesea grisea. – Soil Biology & Biochemistry **36**: 927–934.

Higashi, S. & H. Sugawara (1992): Springtails in the Antarctica. – Insectarium **29**: 52–58.

Hogg, I. D. & M. I. Stevens (2002): Soil Fauna of Antarctic Coastal Landscapes. – In: Beyer, L. & M. Bölter (eds): Geoecology of Antarctic Ice-Free Coastal Landscapes. – Springer, Berlin Heidelberg New York: 265–280.

Hogg, I. D., S. C. Cary, P. Convey, K. K. Newsham, A. G. O'Donnell, B. J. Adams, J. Aislabie, F. Frati, M. I. Stevens & D. H. Wall (2006): Biotic interactions in Antarctic terrestrial ecosystems: Are they a factor? – Soil Biology & Biochemistry **38**: 3035–3040.

Holovachov, O. & S. Boström (2006): Description of *Acrobeloides arctowskii* sp. N. (Rhabditida: Cephalobidae) from King Georg Island, Antarctica. – Russian Journal of Nematology **14**: 51–56.

Hunter, P. E. (1967a): Rhodacaridae and Parasitidae mites (Acarina: Mesostigmata) collected by the British Antarctic Survey, 1961-1964. – British Antarctic Survey Bulletin **13**: 31–39.

Hunter, P. E. (1967b): Mesostigmata: Rhodacaridae, Laelapidae (mesostigmatic mites). – Antarctic Research Series **10**: 35–39.

IAATO (2011): IAATO Overview of Antarctic Tourism: 2010-11 Season and Preliminary Estimates for the 2011-12 Season. – Antarctic Treaty Consultative Meeting XXXIV, IP **106**: 19 pp.

Janetschek, H. (1967): Arthropod ecology of South Victoria Land Antarctica. – Entomology of Antarctica. Antarctic research series **10**: 205–293.

Judson, M. (1995): Identity of the Antarctic mite *Gainia nivalis* Trouessart (Acari, Nanorchestidae). – Bulletin du Muséum National d'Histoire Naturelle **17**: 83–86.

Karg, W. (1976): Revision der Milbengattung Hydrogamasellus Hirschmann, 1966 (Acarina, Parasitiformes). – Deutsche Entomologische Zeitschrift, Neue Fassung **233**: 37–55.

Kazmierski, A. (1998): Tydeinae of the world: generic relationships, new and redescribed taxa and keys to all species. A revision of the subfamilies Pretydeinae and Tydeinae (Acari: Actinedida: Tydaidae) – part IV. – Acta Zoologica Cracoviensia **41**: 283–455.

Kethley, J. (1990): Acarina: Prostigmata (Actinedida). – In: Dindal, D. L. (ed.): Soil Biology Guide. – Wiley, New York: 667–756.

Kethley, J. & W. C. Welbourne (2010): Artificial key to the families of soil Prostigmata. Unveröff. Manuscript, OSU Acarological Sommer Program. – Soil Acarology: 368 pp.

Krantz, G.W. & D. E. Walter (2009): A Manual of Acarology. 3rd Edn. – Texas Tech University Press; 3 edition: 807 pp.

Lee, D. C. (1970): The Rhodacaridae (Acari, Mesostigmata); classification, external morphology and distribution of genera. – Records of the South Australian Museum **163**: 1–219.

Lister, A., W. Block & M. B. Usher (1988): Arthropod predation in an Antarctic terrestrial community. – Journal of Animal Ecology **57**: 957–971.

Loof, P. A. A. (1975): Dorylaimoidea from some subantarctic islands. – Nematologica **21**: 219–255.

Lynch, H. J., K. Crosbie, W. F. Fagan & R. Naveen (2009): Spatial patterns of tour ship traffic in the Antarctic Peninsula region. – Antarctic Science **22**:123–130.

Macfadyen, A. (1961): Improved funnel-type extractors for soil arthropods. – Journal of Animal Ecology **30**: 171–184.

Mahunka, S. (1967): *Pygmephorus antarcticus* n.sp., eine neue Milbenart von der Antarktis (Acari: Tarsonemini). – Opuscula Zoologica Budapest **7**: 227–228.

Marshall, D. J & P. Convey (1999): Compact aggregation and life-history strategy in a continental Antarctic mite. – In: Bruin, J., L. P. S. van der Geest & M. W. Sabelis (eds): Ecology and Evolution of the Acari. – Kluwer Academic Publishers, Dordrecht Boston London 557–567.

Marshall, D. J. & P. J. A. Pugh (1996): Origin of the inland Acari of Continental Antarctica, with particular reference to Dronning Maud Land. – Zoological Journal of the Linnean Society **118**: 101–118.

Marshall, D. J, N. J. M. Gremmen, L. Coetzee, B. M. OConnor, P. J. A. Pugh, P. D. Theron & E. A. Ueckermann (1999): New records of Acari from the sub-Antarctic Prince Edward Island. – Polar Biologay **21**: 84–89.

Maslen, N. R. (1979a): Six new nematode species from the maritime Antarctic. – Nematologica **25**: 288–308.

Maslen, N. R. (1979b): Additions to the nematode fauna of the Antarctic Region with keys to taxa. – British Antarctic Survey Bulletin **49**: 207–229.

Maslen, N. R. & P. Convey (2006): Nematode diversity and distribution in the southern maritime Antarctic – clues to history? – Soil Biology and Biochemistry **38**: 3141–3151.

Massoud, Z. & E. H. Rapoport (1968): Collemboles Isotomides d'Amerique du sud et de l'Antarctique. – Biologie de l'Amerique Australe **4**: 307–337.

McInnes, S. J. & P. J. A. Pugh (1998): Biogeography of limno-terrestrial Tardigrada, with particular reference to the Antarctic fauna. – Journal of Biogeography **25**: 31–36.

McInnes, S. J. & P. J. A. Pugh (2013): The impact of tourists on Antarctic tardigrades: an ordination-based model. – Journal of Limnology **72**: 128–135.

Michael, A. D. (1895): Ueber die auf Süd-Georgien von der deutschen Station 1882-1883 gesammelten Oribatiden. – Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten **12**: 69–72.

Michael, A. D. (1903): Résultats du voyage du S. Y. Belgica en 1987, 1988, 1989. Rapport Scientifiques. – Zoologie Nr. 4. Acarida (Oribatidae) **17**: 1–6 + 2 plates.

Nedelchev, S. & V. Peneva (2000): Description of three new species of the genus *Mesodorylaimus* Andrássy, 1959 (Nematoda: Dorylaimidae) from Livington Island, Antarctica, with notes on *M. imperator* Loof, 1975. – Russian Journal of Nematology **8**: 161–172.

Nedelchev, S. & V. Peneva (2007): Description of the male of *Mesodorylaimus chipevi* Nedelchev & Peneva, 2000 (Nematoda: Dorylaimidae) from Livingston Island, Antarctica. – Russian Journal of Nematology **15**: 75–78.

Ohyama, Y. (1978): Population density of free-living mites in the ice-free areas around Syowa Station, East Antarctica. – National Institute of Polar Research **60**: 47–56.

Ohyama, Y. & S. Hiruta (1995): The terrestrial arthropods of Sør

Rondane in eastern Dronning Maud Land, Antarctica, with biogeographical notes. – Polar Biology **15**: 341–347.

Ohyama, Y. & K. Shimada (1998): Ecological survey of Collembolans in King George Island, maritime Antarctic. – Edaphologia **60**: 23–35.

Peneva, V., N. Chipev & S. Nedelchev (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.

Petersen, H. & Luxton, M. (1982): A comparative analysis of soil fauna populations and their role in decomposition processes. – Oikos **39**: 284–422.

Pomorski, R. J. (1998): Onychiurinae of Poland. – Genus (Suppl.): 201 pp.

Potapov, M. (1991): *Antarctophorus* - a new genus of Isotomidae (Collembola) from Antarctica. – Revue Ecologie et Biologie du Sol **28**: 491–495.

Potapov, M. (2001): Synopses on Palaearctic Collembola. vol. 3: Isotomidae. – Abhandlungen und Berichte des Naturkundemuseums Görlitz **73**: 1–603.

Pugh P. J. A. (1993): A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. – Journal of Natural History **27**: 323–421.

Pugh P. J. A. (1994): Non-indigenous Acari of Antarctica and the sub-Antarctic islands. – Zoological Journal of the Linnean Society **110**: 207–217.

Pugh, P. J. A. & H. J. G. Dartnall (1994): The Acari of fresh and brackish-water habitats in the Antarctic and sub-Antarctic regions. – Polar Biology **14**: 401–404.

Rapoport, E. H., (1971): The geographical distribution of Neotropical and Antarctic Collembola. – Pacific Insects Monograph **25**: 99–118.

Richard, K. J., P. Convey & W. Block (1994): The terrestrial arthropod fauna of the Byers Peninsula, Livingston Island, South Shetland Islands. – Polar Biology **14**: 371–379.

Richters, F. (1904): Vorläufiger Bericht über die antarktische Moosfauna. – Verhandlungen der Deutschen Zoologischen Gesellschaft **24**: 236–239.

Russell, D. J., K. Hohberg, V. Otte, A. Christian, M. Potapov, A. Brückner & S. J. McInnes (2013): The Impact of Human Activities on Soil Organisms of the Maritime Antarctic and the Introduction of Non-Native Species in Antarctica. – UBA Texte Nr. 22/2013, Federal Environment Agency, Dessau, 232 pp. + XXXVIII.

Ryan P. G., B. P. Watkins, R. I. L. Smith, H. Dastych, A. Eicker, W. Foissner, H. Heatwole, W. R. Miller & G. Thompson (1989): Biological survey of Robertskollen western Dronning Maud Land Antarctica area description and preliminary species lists. – South African Journal of Antarctic Research **19**: 10–20.

Salmon, J. (1949): The Collembola of the United States Antarctic Service Expedition 1939-41. – Royal Entomological Society of London **18**: 161–162.

Salmon, J. T. (1962): A new species and redescriptions of Collembola from Antarctica. – Pacific Insects **4**: 87–889.

Sanyal, A. K. (2004): Diversity of Invertebrate Fauna of Schirmacher Oasis, East Antarctica. – Zoological Survey of India **17**: 173–187.

Sanyal, A. K. & S. K. Gupta (2005): Acari from Antarctic continent: one new species of *Proctolaelaps* (Mesostigmata: Ascidae) and some new reports (Prostigmata, Astigmata, Mesostigmata, Cryptostimata). – Proceedings of the Zoological Society (Calcutta) **58**: 79–84.

Sanyal, A. K. & A. K. Hazra (2008): A review on studies on Collembola (Insecta) and mite (Acari) in Schirmacher Oasis, East Antarctica. – Bionotes **10**: 118–120.

Schaller, Von F. & H. Kopeszki (1991): Zur Biologie von Cryptopygus antarcticus (Willem 1902). – Österreichische Akademie der Wissenschaften, Abt. I, **198**: 217–228.

Schenker, R. (1984): Effects of temperature acclimation on cold-hardiness of Antarctic micro-arthropods. – Revue de Écologie et de Biologie du Sol **21**: 205–220.

Schulte, G. G., M. A. Elnitsky, J. B. Benoit, D. L. Denlinger & R. E. Lee (2008): Extremely large aggregations of collembolan eggs on Humble Island, Antarctica: a response to early seasonal warming? – Polar Biology **31**: 889–892.

Sinclair, B. J. (2001): On the distribution of terrestrial invertebrates at Cape Bird, Ross Island, Antarctica. – Polar Biology **24**: 394–400.

Sinclair, B. J., M. B. Scott, C. J. Klok, J. S. Terblanche, D. J. Marshall, B. Reyers & S. L. Chown (2006): Determinants of terrestrial arthropod community composition at Cape Hallett, Antarctica. – Antarctic Science **18**: 303–312.

Smith, T., D. A. Wharton & C. J. Marshall (2008): Cold tolerance of an Antarctic nematode that survives intracellular freezing: comparisons with other nematode species. – Journal of Comparative Physiology **178**: 93–100.

Sohlenius, B. & S. Bostrom (2008): Species diversity and random distribution of microfauna in extremely isolated habitable patches on Antarctic nunataks. – Polar Biology 31: 817–825.

Sohlenius, B., S. Boström & K. I. Jönsson (2004): Occurrence of nematodes, tardigrades and rotifers on ice-free areas in East Antarctica. – Pedobiologia **48**: 395–408.

Sohlenius, B., S. Bostrom & A. Hirschfelder (1995): Nematodes, Rotifers and Tardigrades from nunataks in Dronning-Maud-Land, East Antarctica. – Polar Biology **15**: 51–56.

Somme, L. (1986a): New records of terrestrial arthropods from Dronning Maud Land Antarctica. – Polar Research **4**: 225–230.

Somme, L. (1986b): Terrestrial Arthropods of Bouvetoya. – Polar Research **4**: 231–233.

Spaull, V. W. (1973): Distribution of soil nematodes in the maritime Antarctic. – British Antarctic Survey Bulletin **37**: 1–6.

Starý, J., W. Block & P. Greenslade (1997): Oribatid mites (Acari: Oribatida) of sub-Antatctic Heard Island. – Journal of Natural History **31**: 545–553.

Starý, J. & W. Block (1998): Distribution and biogeography of oribatid mites (Acari: Oribatida) in Antarctica, the sub-Antarctic islands and nearby land areas. – Journal of Natural History **32**: 861–894.

Stevens, M. I. & I. D. Hogg (2002): Expanded distributional records of Collembola and Acari in southern Victoria Land, Antarctica. – Pedobiologia **46**: 485–495.

Stevens, M.I. & I. D. Hogg (2003): Long-term isolation and recent range expansion from glacial refugia revealed for the endemic springtail *Gomphiocephalus hodgsoni* from Victoria Land, Antarctica. – Molecular Ecology **12**: 2357–2369.

Stevens M. I. & I. D. Hogg (2006): Contrasting levels of mitochondrial DNA variability between mites (Penthalodidae) and springtails (Hypogastruridae) from the Trans-Antarctic Mountains suggest long-term effects of glaciation and life history on substitution rates and speciation processes. – Soil Biology & Biochemistry **38**: 3171–3180.

Stevens, M., P. Greenslade, I. D. Hogg & P. Sunnucks (2005): Southern Hemisphere springtails: could they have survived glaciation of Antarctica? – Molecular Biology and Evolution **23**: 874–882.

Strandtmann, R. W. (1967): Terrestrial Prostigmata (Trombidiform mites). – Antarctic Research Series **10**: 51–80.

Strandtmann, R. W. (1968): A comparison of the prostigmatic eupodiforme mites of the north and south polar regions. – Proceedings 13th International Congress of Entomology, Moscow **3**: 354–354.

Strandtmann, R. W. (1982): Notes on Nanorchestes. V. Two new species of Nanorchestes (Acari: Nanorchestidae) from the Antarctic Peninsula and South Atlantic Islands. – Pacific Insects **24**: 252–258.

Strandtmann, R. W. & P. J. Tilbrook (1968): Some Prostigmata (Acari) from Signy Island, South Orkney Islands, and Deception Island, South Shetland Islands. – British Antarctic Survey Bulletin **17**: 51–57.

Strandtmann, R. W., D. Pittard & P. Schaefer (1967): Prostigmatic mites and other terrestrial arthropods of Antarctica. – Antarctic Journal: 106–107.

Strong, J. (1967): Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. – Entomology of Antarctica **10**: 357–371.

Sudhaus, W. (2011) Phylogenetic systematisation and catalogue of paraphyletic "Rhabditidae" (Secernentea, Nematoda). – Journal of Nematode Morphology and Systematics **14**: 113–178.

Thibaud, J.-M., H.-J. Schulz & M. M. da Gama (2004): Synopses on Palaearctic Collembola. vol. 4: Hypogastruridae. – Abhandlungen und Berichte des Naturkundemuseums Görlitz **75**: 1–287.

Thor, G. (1996): Mites collected in Heimefrontjella and Vestfjella (Dronning Maud Land, Antarctica). – Fauna Norvegica Serie B **43**: 69–73.

Tilbrook, P. J. (1967a): Arthropod ecology in the maritime Antarctic. – Antarctic Research Series **10**: 331–356.

Tilbrook, P. J. (1967b): Terrestrial invertebrate fauna of maritime Antarctic. – Philosophical transactions of the Royal Society of London Series B-Biological Sciences **252**: 261–278.

Timm, R. W. (1971): Antarctic soil and freshwater nematodes from McMurdo Sound Region. – Proceedings of the Helminthological Society of Washington **38**: 42–52.

Tin, T., Z. L. Fleming, K.A. Hughes, D. G. Ainley, P. Convey, C. A. Moreno, S. Pfeiffer, J. Scott & I. Snape (2009): Impacts of local human activities on the Antarctic environment. – Antarctic Science **21**: 3–33.

Torricelli, G., A. Carapelli, P. Convey, F. Nardi, J. L. Boore & F. Frati (2010): High divergence across the whole mitochondrial genome in the "pan-Antarctic" springtail *Friesea grisea*: evidence for cryptic species? – Gene **449**: 30–40.

Trägårdh, I. (1908): The Acari of the Swedish South Polar Expedition. – Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901-1903 **5**: 1–34.

Treonis, A. M., D. H. Wall & R. A. Virginia (2000): The use of anhydrobiosis by soil nematodes in the Antarctic Dry Valleys. – Functional Ecology **14**: 460–467.

Trouessart, E. L. (1903): Résultats du voyage du S. Y. Belgica en 1987, 1988, 1989. Rapport Scientifiques. – Zoologie Nr. 4. Acariens (Trombidiidae, Eupodidae, Gamasidae) R **16**: 1–10 + 1 Plate.

Trouessart, E. L. (1914): Deuxième Expédition Antarctique Française (1908-1910); Acariens. – Ouvrage Publié, Ministère de l'Instuction Publique, Paris: 1–16.

Usher, M. B. & R. G. Booth (1984): Arthropod communities in a maritime Antarctic moss-turf habitat: three-dimensional distribution of mites and Collembola. – Journal of Animal Ecology **53**: 427–441.

Usher, M. B. & R. G. Booth (1986): Arthropod communities in a maritime Antarctic moss-turf habitat - multiple scales of pattern in the mites and Collembola. – Journal of Animal Ecology **55**: 155–170.

Usher, M. B. & M. Edwards (1984): The terrestrial arthropods of the grass sward of Lynch Island, a specially protected area in Antarctica. – Oecologia (Berlin) **63**: 183–184.

Usher, M. B. & M. Edwards (1986a): A biometrical study of the family Tydeidae (Acari, rostigmata) in the maritime Antarctic, with descriptions of three new taxa. – Journal of Zoology, London **209**: 355–383.

Usher, M. B. & M. Edwards (1986b): The selection of conservation areas in Antarctica: an example using the athropod fauna of Antarctic islands. – Environmental conservation **13**: 115–122.

Usher, M. B. & M. Edwards (1986c): Two new species of tydeid mite (Acarina, Prostigmata) from the maritime Antarctic. – British Antarctic Survey Bulletin **73**: 1–7.

VDLUFA (1991): Methodenbuch Band 1: Die Untersuchung von Böden. 4. Aufl. – VDLUFA-Verlag, Speyer.

Wahlgren, E. (1906): Antarktische und subantarktische Collembolen gesammelt von der schwedischen Südpolarexpedition. Wissenschaftliche Ergebnisse der Schwedischen Südpolar–Expedition, 1901–1903 (Stockholm, 1908). – Zoologie **1**: 1–22.

Wallwork, J. A. (1962): A redescription of *Notaspis antarctica* Michael, 1903 (Acari: Oribatei). – Pacific Insects **4**: 869–880.

Wallwork, J. A. (1965): The Cryptostigmata (Acari) of Antarctica with special reference to the Antarctic Peninsula and South Shetland Islands. – Pacific Insects 7: 453–468.

Wallwork, J. A. (1967): Cryptostigmata (Oribatid mites). In: J. L. Gressitt (ed.): Entomology of Antarctica. – American Geophysical Union Antarctic Research Series **10**: 105–122.

Wallwork, J. A. (1973): Zoogeography of some terrestrial micro-arthropoda in Antarctica. – Biological Reviews of the Cambridge Philosophical Society **48**: 233–259.

Weiner, W. M. (1980): *Friesea woyciechowskii* sp. n. Collembola, Neanuridae from King George Island, South Shetland Islands, Antarctica. – Polskie Pismo Entomologiczne **50**: 491–495.

Wharton, D. A. (2002): Nematode survival strategies. – In: Lee, L. The biology of nematodes. – Taylor & Francis, London, New York: 389–411.

Wharton, D. A. (2003): The environmental physiology of Antarctic terrestrial nematodes: a review. – Journal of Comparative Physiology, B. Biochemical, Systematic and Environmental Physiology **173**: 621–628.

Wharton, D. A., J. Barrett, G. Goodall, C. J. Marshall & H. Ramlov (2005): Ice-active proteins from the Antarctic nematode Panagrolaimus davidi. – Cryobiology **51**: 198–207.

Willem, V. (1901): Les Collemboles recueillis par l'Expedition Antarctique Belge. – Annales de la Société Entomologique de Belgique **45**: 260–262.

Wise, K. A. J. (1964): New records of Collembola and Acarina in Antarctica. – Pacific Insects **6**: 522–523.

Wise, K. A. J. (1967): Collembola (Springtails). – Antarctic Research Series **10**: 123–148.

Wise, K. A. J. (1971): The Collembola of Antarctica. – Pacific Insects Monograph **25**: 57–74.

Wise, K. A. J., C. E. Fearon & O. R. Wilkes (1964): Entomological Investigations in Antarctica, 1962-63 season. – Pacific Insects **6**: 541–570.

Womersley, H. & R. W. Strandtmann (1963): On some free living prostigmatic mites of Antarctica. – Pacific Insects **5**: 451–472.

Yeates, G. W., T. Bongers, R. G. M. De Goede, D. W. Freckman & S. S. Georgieva (1993): Feeding habits in soil nematode families and genera – an outline for soil ecologists. – Journal of Nematology **25**: 315–331.

Zar J. H. (1999): Biostatiscal Analysis. 4th Edn. – Prentice Hall, London Sydney Toronto: 663 pp.

Zell, H. (1993): Die Gattung *Plectus* Bastian, 1865 sensu lato (Nematoda, Plectidae). Ein Beitrag zur Ökologie, Biogeographie, Phylogenie und Taxonomie der Plectidae. – Andrias **11**: 3–90.

Appendix. Lists of all taxa of the various soil animal groups recorded in the different study sites (= 'localities') in the study years 2010 and 2011, including information on their species-specific average densities (in individuals per 100 cm³ substrate) as well as total densities (in individuals per 100 cm³ substrate) and total number of recorded taxa ('species') of the respective animal group. Localities are sorted from top to bottom by increasing southern latitude; darker shading reflects higher latitudes of a locality.

Table A1. Collembola.

Locality	Region	*Archisotoma brucei*	*Cryptopygus antarcticus*	*Cryptopygus badasa*	*Cryptopygus caeacus*	*Folsomotoma octooculata*	*Friesea grisea*	*Friesea woyciechowskii*	*Hypogastrura viatica*	*Mesaphorura macrochaeta* *	*Proisotoma minuta* *	*Tullbergia mixta*	**Total densities**	**Total number of species**
Arctowski Station (2010)	King George Isl.		102	85		5.2	5.1	0.7				3.8	**202**	**6**
Biologenbucht (2010)	King George Isl.		53	197		9.1	9.1	0.2				89.7	**358**	**6**
Punta Cristian (2010)	King George Isl.			37		1.7	0.3	0				4.1	**43**	**3**
Punta Cristian 2 (2010)	King George Isl.			397		7.0	0.9	1.3				24.8	**431**	**5**
Ardley Island (2011)	King George Isl.		37	35		9.7	2.9					26.1	**111**	**5**
Halfmoon Island (2010)	Livingston Isl.					10.4	15.6		0.2				**26**	**3**
Halfmoon Island (2011)	Livingston Isl.		0.1						1.1				**1.2**	**2**
Hannah Point (2011)	Livingston Isl.		1.9	0.1			1.4						**3.4**	**3**
Whalers Bay (2010)	Deception Isl.			48	0.1	1.3			551	1.3	0.1		**602**	**6**
Whalers Bay (2011)	Deception Isl.			0.1					1.8				**1.8**	**2**
Telefon Bay (2011)	Deception Isl.	0.04	8.5	0.04	0.2				206			0.2	**215**	**6**
Neko Harbour (2010)	Antarctic Peninsula								0.1				**0.1**	**1**
Neko Harbour (2011)	Antarctic Peninsula		4.0						2.4				**6.4**	**2**
Petermann Isl. (2010)	Antarctic Peninsula												**0**	**0**
Devil Island (2010)	Weddell Sea	0.7	9.8	0.4					0.7				**11.5**	**4**
Paulet Island (2011)	Weddell Sea		0.5										**0.5**	**1**

* Species recorded in Antarctica for the first time

Table A2. Actinedida. Juveniles not identifiable to species level were only counted as a 'species' for a particular site if no other species of the taxon were determined at that site.

Locality	Paulet Island (2011)	Devil Island (2010)	Petermann Isl. (2010)	Neko Harbour (2011)	Neko Harbour (2010)	Telefon Bay (2011)	Whalers Bay (2011)	Whalers Bay (2010)	Hannah Point (2011)	Halfmoon Island (2011)	Halfmoon Island (2010)	Ardley Island (2011)	Punta Cristian 2 (2010)	Punta Cristian (2010)	Biologenbucht (2010)	Arctowski Station (2010)
Region	Weddell Sea	Weddell Sea	Antarctic Peninsula	Antarctic Peninsula	Antarctic Peninsula	Deception Isl.	Deception Isl.	Deception Isl.	Livingston Isl.	Livingston Isl.	Livingston Isl.	King George Isl.	King George Isl.	King George Isl.	King George Isl.	King George Isl.
Alicorhagia sp. *								0.08								
Apotriophtydeus cf. wilkesi								0.09								0.07
Apotriophtydeus scotia												0.86		11		
Apotriophtydeus sp. juv.				0.04			0.04							4.2		
Bakerdania cf. antarcticus							0.98	0.47	0.06							4.9
Coccotydaeolus cf. krantzii *			0.16	0.60			2.06	0.35	0.10				0.07			
Ereynetes macquariensis							0.04	0.26			0.11	2.4	2.8		0.34	13.1
Eriophyidae Gen. sp.							0.08						0.09			
Eupodes (Protereunetes) sp. juv.				1.10		0.11	0.93			0.06		0.61	0.15	1.17	0.14	1.5
Eupodes exiguus				0.24			0.12		0.03			2.6	3.8	5.7	10.8	10.6
Eupodes minutus							0.04				0.23		0.4	0.08	0.10	2.2
Eupodes parvus ssp. grahamensis												3.98		0.74	0.13	

Taxon																
Heterostigmata juv.	0.22															
'Lorryia' sp.		0.13	0.09			0.06			0.12		0.05		0.04			
Nanorchestes berryi	14.5	23.7	7.6	15.2	17.4				0.16	0.16						
Nanorchestes cf. *antarcticus*										0.06						
Nanorchestes nivalis	0.06	0.43	0.07	0.36					0.62							
Nanorchestes n.sp. *										0.51						
Nanorchestes sp. V			0.07													
Nanorchestes sp. juv.	0.32	11.2	1.00	0.46				0.29	0.42	1.06			0.04			
Meyerellidae/Iolinidae juv.										0.15			0.04			
Pretriophtydeus tilbrooki	0.79		0.11							0.11			0.04			
Pygmephoridae juv.									0.09	0.2						
Rhagidia gerlachei		0.11														
Rhagidia sp.	0.04															
Speleorchestes sp. *	0.52	0.09	0.26				0.05		0.41	0.12		0.16	0.04	0.16		
Stereotydeus villosus	0.13	0.10	0.15	1.71		0.12								0.16		
Stigmaeidae juv.											0.05					
Tarsonemidae juv.	0.22	0.51	0.16	0.58		0.21		0.05	0.04				0.08			0.05
Terpnacarus gibbosus *		0.19	0.09	0.09						0.04			0.12			
Total densities	**49**	**48**	**32**	**26**	**28**	**0.7**	**0.1**	**0.6**	**2.8**	**6.8**	**0.3**	**0.2**	**2.4**	**0.5**	**0**	**0.05**
Total number of species	**12**	**12**	**13**	**10**	**5**	**4**	**2**	**6**	**7**	**14**	**4**	**1**	**9**	**3**	**0**	**1**

* Taxa recorded in Antarctica for the first time.

Table A3. Oribatida & Gamasina.

Locality	Arctowski Station (2010)	Biologenbucht (2010)	Punta Cristian (2010)	Punta Cristian 2 (2010)	Ardley Island (2011)	Halfmoon Island (2010)	Halfmoon Island (2011)	Hannah Point (2011)	Whalers Bay (2010)	Whalers Bay (2011)	Telefon Bay (2011)	Neko Harbour (2010)	Neko Harbour (2011)	Petermann Isl. (2010)	Devil Island (2010)	Paulet Island (2011)
Region	King George Isl.	King George Isl.	King George Isl.	King George Isl.	King George Isl.	Livingston Isl.	Livingston Isl.	Livingston Isl.	Deception Isl.	Deception Isl.	Deception Isl.	Antarctic Peninsula	Antarctic Peninsula	Antarctic Peninsula	Weddell Sea	Weddell Sea
Oribatida																
Alaskozetes antarcticus	16					380	9.1									3.2
Brachychochthonius sp.													1.3			
Globoppia loxolineata	7.1		25													
Halozetes belgicae	9.1															
Liochthonius cf. *mollis*			2.6													
nymphs	69		1.7			868	75	9.1								13.5
Total densities	**85**		**29**			**1247**	**84**	**9.1**					**1.3**			**16.7**
Total number of species	**3**		**2**			**1**	**1**	**1**					**1**			**1**
Gamasina																
Hydrogamasellus racovitzai	72	39	15	45	36	1.5		21								
cf. *Hydrogamasellus* sp. 2	4.4															
Parasitus tarsispinosus										30						
Genus sp. III											1.3					
Total densities	**76**	**39**	**15**	**45**	**36**			**21**		**30**	**1.3**					

Table A4. Nematoda. Also shown are the feeding types of the individual species: al: algivore-omnivore, ba: bakterivore, ca: carnivore, fu: fungivore-radicivore.

Species	Feeding Type	Arctowski Station (2010) King George Isl.	Biologenbucht (2010) King George Isl.	Punta Cristian (2010) King George Isl.	Punta Cristian 2 (2010) King George Isl.	Ardley Island (2011) King George Isl.	Halfmoon Island (2010) Livingston Isl.	Halfmoon Island (2011) Livingston Isl.	Hannah Point (2011) Livingston Isl.	Whalers Bay (2010) Deception Isl.	Whalers Bay (2011) Deception Isl.	Telefon Bay (2011) Deception Isl.	Neko Harbour (2010) Antarctic Peninsula	Neko Harbour (2011) Antarctic Peninsula	Petermann Isl. (2010) Antarctic Peninsula	Devil Island (2010) Weddell Sea	Paulet Island (2011) Weddell Sea
Acrobeloides arctowskii	ba	230								14	209						
Aphelenchoides haguei	fu	688	1433	241	593	0,2			1								
Aphelenchoides helicosoma	fu	14	33	197		2											
Aphelenchoides sp. 1	fu										105					0,3	
Aporcelaimellus sp. juv.	al		6	107	4	48			0,2								
Ceratoplectus armatus	ba		1258			0,5											
Cervidellus cf. vexilliger	ba	36															
Coomansus gerlachei	ca	121	57	1	7		555	124	113								
Diploscapter sp.	ba													0,1			
Ditylenchus parcevivens	fu	1070	212	59	16												
Dorylaimida sp. 1	al			16	16						73						
Dorylaimida sp. 2	al		38	61	2	4											
Enchodelus signyensis	al	73															
Eudorylaimus coniceps	al		374	47	106	54	74										
Eudorylaimus paradoxus	al	4	940	86	22												

Species		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16
Eudorylaimus pseudocarteri	al	165	298	61		110			0,1								
Eumonhystera sp. 1	ba	335	327	36	4	0,1											
Eumonhystera vulgaris	ba	3259	327	7	315												
Filenchus sp. 1	fu		526	268	1	1											
Filenchus sp. 2	fu		91														
Geomonhystera villosa	ba		235	6	456	74			4				0,3				
Heterocephalobus sp.	ba												0,2				
Mesodorylaimus antarcticus	al	616	142	1									0,2				
Mesodorylaimus chipevi	al	348			3												
Mesodorylaimus sp.	al	18		291	4												
Panagrolaimus sp.	ba	472					0,2		20	1166	93	0,2	5			306	0,2
Rhabditis marina-group	ba											354					
Pelodera parateres-group	ba	2953									9						
Pelodera teres-group	ba								5	230	54		0,3				2309
Pelodera strongyloides-group	ba								10				104	0,3		1378	
Plectus antarcticus	ba	41	74							421						0,3	
Plectus cf. *belgicae*	ba	330	505	54	294	51		6		274	0,3				1		
Plectus insolens	ba					42											
Plectus sp. 1	ba	1460	24														
Plectus cf. *tolerans*	ba	64	172	20	312	26			10								
Prismatolaimus sp.	ba	160	9	128													
Rhabditoidea sp. 1	ba						3	0,4									
Teratocephalus rugosus	ba	284	51	4	4	1		4			0,1					0,2	
Teratocephalus tilbrooki	ba	82	935	628	580	126	650		2								
Total densities		11,344	9,429	2,433	2,739	830	1282	129	199	2,109	626	411	112	0,8	1,5	1,686	2,310
Total number of species		22	23	22	17	15	4	4	11	5	8	2	7	1	1	5	2