Polar Biol (2014) 37:1517–1531
DOI 10.1007/s00300-014-1544-4

REVIEW

A review of current Antarctic limno-terrestrial microfauna

Alejandro Velasco-Castrillón · John A. E. Gibson · Mark I. Stevens

Received: 26 December 2013 / Revised: 3 July 2014 / Accepted: 4 July 2014 / Published online: 20 July 2014

Abstract Antarctic arthropods (mites and springtails) have been the subject of numerous studies. However, by far, the most diverse and numerically dominant fauna in Antarctica are the limno-terrestrial microfauna (tardigrades, rotifers and nematodes). Although they have been the focus of several studies, there remains uncertainty of the actual number of species in Antarctica. Inadequate sampling and conserved morphology are the main cause of misclassification of species and underestimation of this diversity. Most species' distributional records are dominated by proximity to research stations or limited opportunistic collections, and therefore, an absence of records for a species may also be a consequence of the limitations of sampling. Limitations in fundamental knowledge of how many species are present and how widespread they are prevents any meaningful analyses that have been applied more generally to the arthropods within Antarctica, such as exploring ancient origins (at least pre-last glacial maximum) and tracking colonisation routes from glacial refugia. In this review, we list published species names and where possible the distribution of microfaunal (tardigrade, rotifer and nematode) species reported for Antarctica. Our current state of knowledge of Antarctic records (south of 60°S) includes 28 bdelloid rotifers, 66 monogonont rotifers, 59 tardigrades and 68 nematodes. In the light of the difficulties in working with microfauna across such geographical scales, we emphasise the need for molecular markers to help understand the 'true levels' of diversity and suggest future directions for Antarctic biodiversity assessment and species discovery.

Keywords Tardigrada · Rotifera · Nematoda · DNA barcoding · Antarctic Conservation Biogeographic Regions (ACBR)

Electronic supplementary material The online version of this article (doi:10.1007/s00300-014-1544-4) contains supplementary material, which is available to authorized users.

A. Velasco-Castrillón (✉)
Australian Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia
e-mail: macalusio@yahoo.com

J. A. E. Gibson
Institute of Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, TAS 7001, Australia

M. I. Stevens
South Australian Museum, GPO Box 234, Adelaide, SA 5000, Australia

M. I. Stevens
School of Pharmacy and Medical Sciences, University of South Australia, Adelaide, SA, Australia

Introduction

Antarctica has one of the most extreme and challenging environments on the planet, experiencing prolonged winters, freezing temperature and lack of liquid water. It spans nearly 30° of latitude (61°–90°S) and covers an area of 14 million km^2 with only 0.3 % of its total area remaining ice- and snow-free year round (British Antarctic Survey 2004). It has been isolated from the other southern continents for around 28 million years by the Southern Ocean (Lawver et al. 1998), since the opening of the South Tasman Rise (32 My) and the Drake Passage (28 My) (Lawver and Gahagan 2003). It has also been covered in a permanent ice sheet for ~34 My (Tripati et al. 2005) and has experienced more than 10 major glacial cycles over the last million years (Hays et al. 1976). Despite this, life has managed to survive. Some of the Antarctic terrestrial arthropods consist of likely descendants of ancestors present in Gondwanan times that have diversified in ice-free isolated locations, such as nunataks, since the completion of glaciation in the late Miocene (~21–11 Mya) (Marshall and Pugh 1996; McInnes and Pugh 1998; Stevens and Hogg 2003; Stevens et al. 2006a). In the case of Antarctic lakes, few studies have dealt with their continuous presence since the break-up of Gondwana. De Smet and Gibson (2008) suggested survival of rotifers in freshwater environments since the last glacial maximum (LGM). Over the last decade, it has become well accepted that several Antarctic localities have remained ice-free throughout the LGM (e.g. Convey and Stevens 2007; Convey et al. 2008, 2009) and some likely to have been ice-free for much longer. Continental regions such as Dronning Maud Land (Marshall and Pugh 1996), Antarctic Peninsula (AP) (Pugh and Convey 2000), southern Victoria Land (Stevens and Hogg 2003, 2006b) and coastal areas (Burgess et al. 1994; Gore et al. 2001; Hodgson et al. 2001) have been suitable for the long-term survival of terrestrial life in ice-free refugia (Cromer et al. 2006; Convey and Stevens 2007) with many terrestrial habitats becoming available for colonisation from refuges within the current inter-glacial period (<17,000 years) (Stevens and Hogg 2003).

The Antarctic limno-terrestrial microfauna is fragmented, patchily distributed and taxonomically restricted, and mostly comprises rotifers, tardigrades and nematodes (e.g. Wharton 2003; Sohlenius et al. 2004; Sohlenius and Boström 2005, 2008; Huiskes et al. 2006). Microfaunal communities have commonly been associated with habitats rich in organic material (algae, moss or lichen), in the vicinity of bird colonies (e.g. Sohlenius et al. 2004; Sohlenius and Boström 2005; Wall 2007), or in lakes or melt pools (e.g. Kirjanova 1958; Suren 1990; Dartnall 2000; Andrássy and Gibson 2007; De Smet and Gibson 2008). The limno-terrestrial microfauna form a vital component of the food web, playing an essential function in soil ecosystem processes, mainly in recycling nutrients and processes of decomposition (Sands et al. 2008). Today fewer than 550 non-marine invertebrate species have been identified from Antarctica (Adams et al. 2006; Convey et al. 2008, 2009). Most of these are endemic (58 %) and can be defined as continental (>25 %) or maritime (>29 %), with only 3 % of species having a pan-Antarctic distribution (Pugh and Convey 2008). Diversity is greatest for the microfauna (rotifers, tardigrades and nematodes) (e.g. Dastych 1984; Andrássy 1998; Convey and McInnes 2005; Adams et al. 2006; Sohlenius and Boström 2008), followed by arthropods, particularly springtails (Collembola) and mites (Acari) (e.g. Hogg and Stevens 2002; Sinclair and Stevens 2006; Stevens and Hogg 2006b). Given these basic statistics, it is surprising that the arthropods have received a disproportionate amount of attention and that there is no single study that provides a complete list of diversity and distribution for the Antarctic microfaunal species of the Phyla Rotifera, Tardigrada and Nematoda. Such an important synopsis of the microfauna may have been seen as a difficult task when it is widely regarded that identification to morpho-species of these minute microfauna are often difficult given the lack of distinctive morphological features (e.g. Andrássy 1998; Floyd et al. 2002; Robeson et al. 2009) resulting in misclassification and underestimation of diversity (Adams et al. 2006; Fontaneto et al. 2009; Stevens et al. 2011).

In order to assess microfaunal diversity in Antarctica (south of 60°S), we have used, for continental Antarctica, the sectors: Maud, Enderby, Wilkes, Scott, Byrd and Ronne (see Pugh 1993). We have also included the AP, and the maritime Antarctica (west of AP, and the sub-Antarctic islands of South Orkney and South Shetland; Fig. 1). The selection of these largely empirical sectors has also been adopted by other studies (e.g. McInnes and Pugh 1998; Convey and McInnes 2005; Pugh and Convey 2008) but do not represent the bioregions as defined by Terauds et al. (2012). The aim here is to compile the current state of knowledge of Antarctic limno-terrestrial microfaunal diversity and distribution based on morphology of rotifers, tardigrades and nematodes (collectively referred to in this review as microfauna) from continental and maritime Antarctica. We then discuss potential dispersal mechanisms and the need to establish diversity by combining molecular methods. We conclude with suggestions for future directions for Antarctic biodiversity assessment and species discovery.

Current state of knowledge

Microfauna community

Tardigrada

The Phylum Tardigrada is divided into three Classes (Heterotardigrada, Mesotardigrada and Eutardigrada), which comprise a total of ~800 species of freshwater, terrestrial and marine tardigrades worldwide (McInnes and Pugh 1998). Most of the limno-terrestrial forms belong to the Class Eutardigrada, and to some extent the Heterotardigrada (which also include marine forms) (Kinchin 1994). To date, 64 published species of tardigrades have been reported for Antarctica and sub-Antarctic islands (including records north of 60°S; McInnes and Pugh 2007), although no species list was included in their work. In the present review, we list 59 records of Antarctic tardigrades

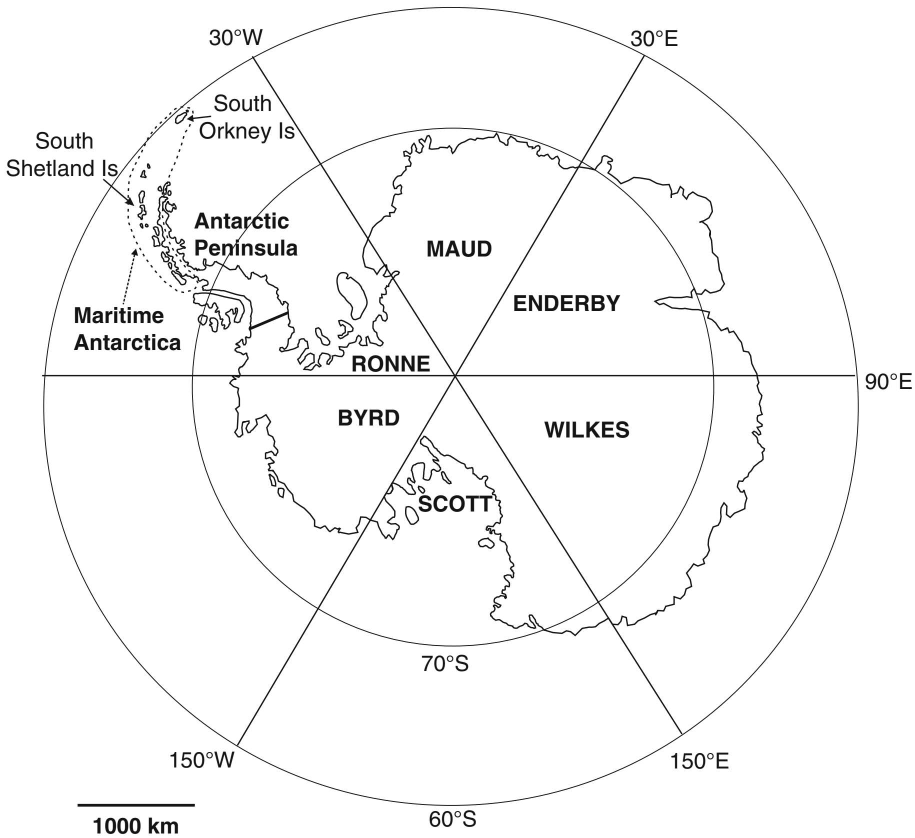

Fig. 1 Map of Antarctica showing the six sectors for continental Antarctica, the Antarctic Peninsula, and the maritime Antarctica

(south of 60°S) from 34 references and compiled a species distribution list for all named Antarctic tardigrades (Table 1). Records for continental Antarctica include 42 species, while for maritime Antarctica, 36 species are reported (19 shared species). We found no records for Byrd sector and only three records for Ronne sector, because of a probable lack of studies in these areas. The most widespread tardigrades in Antarctica are the pan-Antarctic species *Acutuncus antarcticus* Binda and Pilato 2000 and *Milnesium tardigradum* Doyère, 1840 (Table 1). Misidentifications and species synonyms have been included in the online Supplementary Material (Online Resource 1).

Rotifera

The Phylum Rotifera includes the Classes Bdelloidea, Monogononta and Seisonidea, with the former two being most common in Antarctica. Segers (2007) listed 92 rotifer species and assigned them to 'Antarctica' (including sub-Antarctic islands north of 55°S) but without specifying geographical regions. We confirmed, from other references, the presence of 63 of those species (44 monogononts and 19 bdelloids) listed by Segers (2007) to occur in continental and/or maritime Antarctica (south of 60°S) (see Tables 2 and 3). Most records in the literature correspond to the widely known Antarctic endemic *Philodina gregaria* Murray 1910, which has been reported from across Antarctica. Frequently found with *P. gregaria* is another endemic Antarctic rotifer *Adineta grandis* Murray 1910 and two cosmopolitan species *Epiphanes senta* Müller, 1773 and *Cephalodella catellina* Müller, 1786. All four species are usually found in bodies of water that remain frozen in the winter and have a circumpolar distribution similar to other cosmopolitan species from terrestrial habitats (*Adineta gracilis* Janson, 1893) and lake habitats (*Collotheca ornata cornuta* Dobie, 1849 and *Lepadella patella* Müller, 1773) (Dartnall 1983). We have compiled a distribution list (based on published species) of Antarctic limno-terrestrial rotifers that includes 66 monogonont and 28 bdelloid species from 24 different reference sources (Tables 2 and 3). Species records reported by Segers (2007) for Antarctica that were not confirmed by other references can be found in the Supplementary Material (Online Resource 2). For a list of species synonyms, refer to the Online Resource 3.

Nematoda

Nematodes are usually associated with rotifers and tardigrades and generally found in areas where moss, lichens or algae are present (e.g. Timm 1971; Sohlenius et al. 2004; Velasco-Castrillón et al. 2014). Some species (*Plectus*

Table 1 List of Tardigrada species recorded from the Antarctic and their regional distributions

Tardigrade species/sectors	Continental Antarctica					AP—Maritime Antarctica	
	Maud	Enderby	Wilkes	Scott	Ronne	AP	SS-SO
Class Heterotardigrada							
Echiniscus corrugicaudatus (McInnes 2010)					13b		
Echiniscus jenningsi (Dastych 1984)		14, e1				3, 5	4, 3, 13
Echiniscus kerguelensis (Richters 1904)		(28b, 29)					(29)
Echiniscus pseudowendti (Dastych 1984)	24	4, 27				e1	
Echiniscus punctus (McInnes 1995)							3, 13
Testechiniscus meridionalis (Murray 1906)							4, 3, 13
Oreella mollis (Murray 1910)							3
Pseudoechiniscus cf. *suillus* (Ehrenberg 1853)		4, 16	5, 16b				4, 3, 13
Pseudoechiniscus novaezeelandiae (Richters 1903)		21, 15, 16					
Class Eutardigrada							
Acutuncus antarcticus (Binda and Pilato 2000)	23, 24, 25	6, 11, 14, 16, 17, 21, 27, 28, 28b, 29, 30	5, 16b	1, 22, 6		3	3, 12, 29
Amphibolus volubilus Durante Pasa & Maucci, 1975							(29)
Dactylobiotus cf. *ambiguus* (Murray 1907)						11	3, 12,13
Hexapodibius boothi (Dastych and McInnes 1994)							3, 9
Diphascon ongulensis (Morikawa 1962)		17, 27, 28, 29					
Diphascon (Adropion) greveni (Dastych 1984)						3	3, 12, 13
Diphascon (Adropion) maucci Dastych & McInnes, 1996							3
Diphascon (Adropion) tricuspidatum (Binda and Pilato 2000)				1, 2			
Diphascon (Diphascon) alpinum (Murray 1906)							(29)
Diphascon (Diphascon) dastychi (Pilato and Binda 1999)				1, 19			
Diphascon (Diphascon) higginsi (Binda 1971)							(29)
Diphascon (Diphascon) langhovdense (Sudzuki 1964)	23, 24	7, 27, 30					3
Diphascon (Diphascon) mirabilis (Dastych 1984)							3, 12
Diphascon (Diphascon) pingue ('Variety A') (Marcus 1936)			16b			3, 5	3
Diphascon (Diphascon) pingue ('Variety B') (Marcus 1936)	19					5	4
Diphascon (Diphascon) polare (Pilato and Binda 1999)				1, 19			
Diphascon (Diphascon) victoriae (Pilato and Binda 1999)				1, 19			
Diphascon (Diphascon?) puniceum Jennings, 1971	e1	15					3, 13
Diphascon sanae Dastych, Ryan & Watkins, 1990	10	14, 27, e1			3	3	
Hebesuncus mollispinus Pilato, McInnes & Lisi, 2012						20	
Hebesuncus ryani Dastych & Harris, 1994	23, 25, 27				3	3	
Hebesuncus schusteri (Dastych 1984)	24	4				3	3
Hypsibius allisoni Horning, Schuster & Grigarick, 1978		15					
Hypsibius (Diphascon) scoticus Murray, 1905				(1)			
Hypsibius cf. *convergens* (Urbanowicz, 1925)				(1)			
Hypsibius cf. *dujardini* (Doyère, 1840)						3	3, 12,13
Hypsibius cf. *mertoni simoizumii* (Sudzuki 1964)			e1	1			
Isohypsibius asper Murray, 1905						e1	29,3,12, 13

Table 1 continued

Tardigrade species/sectors	Continental Antarctica					AP—Maritime Antarctica	
	Maud	Enderby	Wilkes	Scott	Ronne	AP	SS-SO
Isohypsibius improvisus Dastych 1984		4					4
Isohypsibius laevis (McInnes 1995)							3,13
Isohypsibius papillifer Murray, 1905							29, 3, 12, 13
Isohypsibius saracenus Pilato, 1973		(29)					
Macrobiotus blocki Dastych 1984	23, 24	4, 11, 14, 27					
Macrobiotus cf. *hufelandi* (Schultze, 1833)	23		e1			3, 5	
Macrobiotus cf. *polaris* (Murray 1910)				1, 18			
Macrobiotus harmsworthi coronatus (Utsugi, 1991)		(28b, 29)					
Macrobiotus harmsworthi (Barros, 1942)	e1						(29)
Macrobiotus krynauwi Dastych and Harris 1995	23, 25, 8						12, 13
Macrobiotus meridionalis Richters, 1909				22			
Macrobiotus montanus Murray 1910		(29)					
Macrobiotus mottai Binda & Pilato, 1994				1			
Macrobiotus polaris Dougherty & Harris, 1963				1			
Minibiotus stuckenbergi (Dastych, Ryan & Watkins, 1990)	3, 10	14, e1					
Minibiotus vinciguerrae Binda & Pilato, 1992				1			
Minibiotus weinerorum (Dastych 1984)		4, 11, 16					
Ramajendas frigidus Pilato & Binda, 1990			16b	1			
Ramajendas renaudi Ramazzotti, 1972						3, 4	3, 12
Ramazzottius cf. *oberhäuseri* (Doyère, 1840)	e1	e1		1		3, e1	
Milnesium antarcticum Tumanov 2006				22			26
Milnesium cf. *tardigradum* (Doyère, 1840)	23, 24	16, 27, 30			3	3	3

The numbers in each column refer to reference (see table)

AP Antarctic Peninsula, *SS–SO* South Shetland and South Orkney Islands

Literature source: (1) Adams et al. 2006, (2) Binda and Pilato 2000, (3) Convey and McInnes 2005, (4) Dastych 1984, (5) Dastych 1989, (6) Dastych 1991, (7) Dastych 2003, (8) Dastych and Harris 1995, (9) Dastych and McInnes 1994, (10) Dastych et al. 1990, (11) Gibson et al. 2007, (12) Janiec 1996, (13) McInnes 1995, (13b) McInnes 2010, (14) Miller and Heatwole 1995, (15) Miller et al. 1988, (16) Miller et al. 1994, (16b) Miller et al. 1996, (17) Morikawa 1962, (18) Murray 1910, (19) Pilato and Binda 1999, (20) Pilato et al. 2012, (21) Rounsevell and Horne 1986, (22) Smykla et al. 2012, (23) Sohlenius and Boström 2005, (24) Sohlenius et al. 1995, (25) Sohlenius et al. 2004, (26) Tumanov 2006, (27) Tsujimoto et al. 2014, (28) Utsugi and Ohyama 1989, (28b) Utsugi and Ohyama 1991, (29) Utsugi and Ohyama 1993, (30) Sudzuki 1964, (e1) Australian Antarctic Data Centre (https://data.aad.gov.au/aadc/biodiversity/search_taxon.cfm). References in parenthesis indicate possible misidentifications

frigophilus Kirjanova 1958; *Halomonhystera* spp) have also been recorded from Antarctic lakes (Kirjanova 1958; Andrássy and Gibson 2007) or in highly organic soils adjacent to bird colonies, for example *Panagrolaimus* (Sohlenius 1989; Sinclair 2001). According to Wharton (2003), nematodes are the most diverse and abundant invertebrates in both the maritime and continental Antarctic regions. The Phylum includes the Classes Dorylaimia, Enoplia and Chromadoria (Meldal et al. 2007), which according to Andrássy (2008a) are represented by 54 species from Antarctica, 32 in the maritime region and 22 from continental Antarctica. In the present review, we list 68 published species for Antarctica (Table 4). We identified 34 species occurring in continental Antarctica and 37 species in maritime Antarctica (see Velasco-Castrillón and Stevens 2014). Of particular interest is the geographical overlap of three species (*Plectus murrayi* Yeates 1970; *P. frigophilus* and *Teratocephalus tilbrooki* Maslen, 1979). *P. murrayi* and *P. frigophilus* (commonly known for continental Antarctica) were represented by unconfirmed records for maritime Antarctica. While *T. tilbrooki* known from maritime Antarctica, (Andrássy 1998) was reported for continental Antarctica (Table 4). Unfortunately, no morphological or molecular data were provided in these studies. The overlap of *P. murrayi* with other species could be a result of the difficulties

Table 2 List of Monogononta (Rotifera) species recorded from the Antarctic and their regional distributions

Rotifer species/sectors	Antarctica (unspecified)	Continental Antarctica				AP—Maritime Antarctica	
		Maud	Enderby	Wilkes	Scott	AP	SS-SO
Class Monogononta							
Brachionus angularis Gosse, 1851					10		
Brachionus bidentatus bidentatus Anderson, 1889*	14					10, e1	e1
Brachionus bidentatus inermis Rousselet, 1906						10	
Brachionus calyciflorus Pallas, 1766	14			10, e1			
Brachionus havanaensis trahea Murray, 1913						10, e1	10, e1
Brachionus quadridentatus quadridentatus Hermann, 1783*	14	10		10, e1			
Brachionus urceolaris urceolaris Müller, 1773*	14				10	10	10
Cephalodella auriculata Müller, 1773	14						1, e1
Cephalodella catellina Müller, 1786	14				2, 1	e1	1, 2, 10b, e1
Cephalodella forficata (Ehrenberg, 1832)	14					e1	1, 10b, e1
Cephalodella gibba (Ehrenberg, 1830)	14					e1	1, 2, e1
Cephalodella megalocephala (Glascott, 1893)	14						1, e1
Cephalodella sterea (Gosse, 1887)	14		5				
Cephalodella tenuior (Goose, 1886)	14					e1	
Cephalodella ventripes angustior Donner, 1950			5				
Collotheca gracilipes Edmonson, 1939							1, e1
Collotheca ornata cornuta (Dobie, 1849)	14		4, 5, e1	2, e1	2, 1	e1	1, 2, e1
Colurella colurus colurus (Ehrenberg, 1830)	14					e1	10b, e1
Colurella colurus compressa (Lucks, 1912)	14						1, e1
Dicranophorus permollis giganthea Dartnall and Hollowday 1985					1	e1	1, e1
Dicranophorus uncinatus (Milne, 1886)							1, e1
Encentrum brevifulcrum Dartnall, 1997	14		4				
Encentrum forcipatum Dartnall, 1997	14		4, e1				
Encentrum mustela Milne, 1885	14		4, 5, e1	e1		e1	1, 10b, e1
Encentrum permolle Gosse, 1886							e1
Encentrum salinum Dartnall, 1997	14		4				
Encentrum spatiatum Wulfert, 1936			4, 5, e1				
Encentrum uncinatum (Milne, 1886)	14					e1	e1
Eosphora najas (Ehrenberg, 1832)							1, 2, e1
Epiphanes senta Müller, 1773	14		4, 5, 2, e1	2, 6, e1	1, 2, 13, e1	e1	1, 2, 10b, e1
Euchlanis dilatata dilatata Ehrenberg, 1832	14						1, e1
Euchlanis dilatata parva Rousselet, 1832							e1
Kellicottia longispina (Kellicott, 1879)					10		
Keratella americana Carlin, 1943	14					10, 20, e1	10, 20, e1
Keratella cochlearis Gosse, 1851	14		4, 10		10	10, 20, e1	10, 20, e1
Keratella quadrata Müller, 1786					10		
Keratella valga (Ehrenberg, 1834)	14					e1	e1
Lecane lunaris (Ehrenberg, 1832)	14					e1	1, 2, e1
Lepadella acuminata (Ehrenberg, 1834)	14		5	e1			
Lepadella elliptica (Turner, 1892)	14		e1				
Lepadella intermedia Dartnall and Hollowday 1985	14						1, e1
Lepadella patella Müller, 1773	14		2, 4, 5, e1	2, 6, e1		e1	2, 10b, e1
Lepadella patella oblonga Ehrenberg, 1834	14						1, e1

Table 2 continued

Rotifer species/sectors	Antarctica (unspecified)	Continental Antarctica				AP—Maritime Antarctica	
		Maud	Enderby	Wilkes	Scott	AP	SS-SO
Lepadella rhomboides signiensis Dartnall and Hollowday 1985	14						1, e1
Lepadella triptera (Ehrenberg, 1832)	14				10		10, 1, e1
Lindia torulosa antarctica Dartnall and Hollowday 1985			4				
Lindia torulosa Dujardin, 1841	14		e1			e1	
Notholca foliacea (Ehrenberg, 1838)					10		
Notholca jugosa Gosse, 1887			10				
Notholca salina Focke, 1961	14					10, e1	1, 10, 10b, e1
Notholca verae Kutikova, 1958	14		2, e1	10, 2, 6, e1			2
Notholca walterkostei de Paggi, 1982	14					10, e1	1, 10, 10b, e1
Notholca walterkostei reducta Dartnall and Hollowday 1985	14						1, 10, e1
Paradicranophorus sordidus Donner, 1968	14		e1				
Proales reinhardti (Ehrenberg, 1834)			4, 6				
Ptygura crystallina (Ehrenberg, 1834)	14		4, 5, e1	e1			1, e1
Ptygura melicerta (Ehrenberg, 1832)	14						1, 2, e1
Resticula gelida (Harring & Myers, 1922)	14		4, 5, e1	e1		e1	1, 2, 10b, e1
Resticula nyssa (Harring & Myers, 1924)						e1	10b, e1
Rhinoglena fertoeensis (Varga, 1929)				6, e1			
Rhinoglena kutikovae De Smet, 2007				6			
Scaridium bostjani Daems & Dumont, 1974							1, 2, e1
Scaridium longicaudum Müller, 1786	14						e1
Trichocerca brachyura (Gosse, 1851)	14						1, e1
Trichocerca rattus globosa Dartnall and Hollowday 1985							1, e1
Trichocerca rattus Müller, 1776	14						e1

The numbers in each column refer to reference (see Table 3)

AP Antarctic Peninsula; *SS–SO* South Shetland and South Orkney Islands

encountered in the identification of *Plectus* species and especially of those lacking males (see Boström 2005). Species synonyms have been included in Supplementary Material (Online Resource 4).

Microfaunal dispersal and occurrence

Information on dispersal of Antarctic invertebrates results from casual observations from arthropod collections, which have received comparatively more work in Antarctica (see Convey et al. 2008, 2009). It is believed that air currents are one potential mode of passive dispersal (Miller and Heatwole 1995; Greenslade et al. 1999; Muñoz et al. 2004; Nkem et al. 2006; Hawes et al. 2007). This method of transport may not be as successful for arthropods (springtails, mites, dipterans) due to potential desiccation (see Marshall and Pugh 1996). Other possible dispersal mechanisms are birds (Stevens and Hogg 2002), bubbles carried in water currents (Rounsevell and Horne 1986) or on floating materials in melt-water streams (Moore 2002; Sinclair and Stevens 2006). For nematodes, tardigrades and rotifers, with a specialised dispersal life stage, a far greater potential for dispersal via wind and water has been suggested (Stevens and Hogg 2006a). However, long-range dispersal (inter-oceanic), even during the anhydrobiotic phase, has been questioned by McInnes and Pugh (1998). Dispersal by human activities has also been reported in the literature, particularly for the sub-Antarctic islands and maritime Antarctica (e.g. Burn 1984; Greenslade and Wise 1984; Rounsevell and Horne 1986).

Table 3 List of Bdelloidea (Rotifera) species recorded from the Antarctic and their regional distributions

Rotifer species/sectors	Antarctica (unspecified)	Continental Antarctica				AP—Maritime Antarctica	
		Maud	Enderby	Wilkes	Scott	AP	SS-SO
Class Bdelloidea							
Adineta barbata Janson, 1893	14	16, 17, 18, e1	4		1, 8, 11	e1	1, e1
Adineta gracilis Janson, 1893	14	16, 17, 18, e1	2	2, e1	1, 2, 11	e1	1, 2, 9, e1
Adineta grandis Murray 1910	14	e1	4, 5, e1	2, 3, 12, e1	1, 8, 11, 13, 15, e1	e1	1, 2, 9, e1
Adineta longicornis Murray, 1906	14				11	e1	
Adineta steineri Bartoš, 1951	14	16, 17, 18, e1					
Adineta vaga vaga (Davis, 1873)*	14	16, 17, 18, e1			1, 11, 22	e1	
Habrotrocha angularis (Murray 1910)	14				1, 8, 11	e1	
Habrotrocha constricta (Dujardin, 1841)	14	16, 17, 18, e1	4, 5, e1	3, e1	1, 7, 8, 15, 22	e1	1, e1
Habrotrocha elusa elusa Milne, 1916*	14	16, 17, 18, e1		e1			
Habrotrocha gulosa Milne, 1916				17, 19, e1			
Habrotrocha tridens Milne, 1886	14	16, 17, 18, e1				e1	
Macrotrachela ambigua Donner, 1965		16, 18, e1					
Macrotrachela concinna (Bryce, 1912)	14						1, e1
Macrotrachela constricta Milne, 1886					11	e1	
Macrotrachela insolita De Koning, 1947	14	16, 17, 18, e1		17, 19, e1	1, 7, 15	e1	
Macrotrachela habita (Bryce, 1894)	14	16, 17, 18, e1			1, 8, 11	e1	
Macrotrachela libera Donner, 1949		16, 17, 18, e1					
Macrotrachela cf. *ligulata* Haigh, 1965		16, 18, e1					
Macrotrachela nixa Donner, 1962	14	16, 18, e1		17, 19, e1			
Macrotrachela quadricornifera quadricornifera Milne, 1886*	14		4, e1				
Macrotrachela timida Milne, 1916		16, 17, 18, e1					
Mniobia russeola (Zelinka, 1891)	14		4, e1				
Mniobia symbiotica (Zelinka, 1886)		16, 17, 18, e1					
Otostephanos torquatus (Bryce, 1913)		16, 18, e1					
Philodina alata Murray 1910	14		10	6, 10, e1	1, 8, 10, 11, 21, 22, e1	e1	
Philodina antarctica Murray 1910	14				1, 8, 11, 22, e1	e1	
Philodina gregaria Murray 1910	14	e1	4, 5, e1	2, 3, 12, e1	1, 2, 7, 8, 11, 13, 21, 22	1, e1	2, 1, e1
Rotaria rotatoria (Pallas, 1766)					15		

The numbers in each column refer to reference

AP Antarctic Peninsula; *SS–SO* South Shetland and South Orkney Islands

Species names followed by '*' were recorded as subspecies by Segers (2007). Records from Antarctic Peninsula (AP) include Palmer sector and Graham sector. References from South Shetland and South Orkney Islands (SS-SO) are shown combined. *Literature source*: (1) Dartnall and Hollowday 1985, (2) Dartnall 1983, (3) Dartnall 2005, (4) Dartnall 2000, (5) Dartnall 1995, (6) De Smet and Gibson 2008, (7) Donner 1972, (8) Dougherty and Harris 1963, (9) Fontaneto et al. 2008, (10) Hansson et al. 2012, (10b), Janiec 1996, (11) Murray 1910, (12) Opalinski 1972, (13) Suren 1990, (14) Segers 2007, (15) Smykla et al. 2010 (16) Sohlenius and Boström 2005, (17) Sohlenius et al. 1995, (18) Sohlenius et al. 1996, (19) Sudzuki 1979, (20) Sudzuki 1988, (21) Vincent and James 1996, (22) Webster-Brown et al. 2010, (e1) Australian Antarctic Data Centre (https://data.aad.gov.au/aadc/biodiversity/search_taxon.cfm)

Records of species in some areas could be relicts from a warmer pre-Pleistocene period in Antarctica (McInnes and Pugh 1998), descendants of more recent arrivals from outside the continent (Sohlenius et al. 2004), or simply the result of misidentification (McInnes 1995; Czechowski et al. 2012). Successful colonisation requires suitable conditions for the propagules to survive, establish and reproduce (Miller et al. 1994). Given the isolation of ice-free habitats, we would expect a very low probability of colonisation and the presence of habitat patches lacking microfauna (Sohlenius et al. 2004). For slow, more gradual changes (climate and environmental change) dispersal to

Table 4 List of Nematoda species recorded from the Antarctic and their regional distributions

Nematode species/sectors	Continental Antarctica				Maritime Antarctica
	Maud	Enderby	Wilkes	Scott	
Class Chromadorea					
Acrobeloides arctowskii Holovachov and Boström 2006					15b
Aglenchus agricola (de Man, 1884) Andrássy, 1954	24				
Antarctenchus motililus Ghosh, Chatterjee, Mitra, De, 2005	14b				
Antarctenchus hooperi Spaull, 1972					4, 34, 35, 36, 37
Aphelenchoides haguei Maslen, 1979					4, 20, 35
Aphelenchoides vaughani Maslen, 1979					4, 20, 35
Apratylenchoides joenssoni Ryss et al. 2005	24				
Ceratoplectus armatus (Butschli, 1873) Andrássy, 1984					4, 20, 34, 36
Chiloplacoides antarcticus Heyns 1994	15				
Chiloplectus masleni Boström 1996	4, 10				
Cuticularia firmata Andrássy 1998					4
Ditylenchus parcevivens Andrássy 1998					4
Dolichorhabditis tereticorpus Kito and Ohyama 2008			17		
Eumonhystera vulgaris (de Man, 1880) Andrássy 1981					4, 20, 3
Geomonhystera antarcticola Andrássy 1998				1, 4, 29	
Geomonhystera villosa (Butschli, 1873) Andrássy 1981					4, 20, 34, 35
Halomonhystera antarctica (Cobb, 1914) Andrássy 2006				5*	
Halomonhystera continentalis Andrássy 2006		5, 8			
Halomonhystera disjuncta (Bastian, 1865) Andrássy 2006					5*
Halomonhystera glaciei (Blome & Riemann, 1999) Andrássy 2006					5*
Halomonhystera halophila Andrássy 2006		5, 8			
Halomonhystera uniformis (Cobb, 1914) Andrássy 2006				5*	
Helicotylenchus diagonicus Perry in Perry, Darling & Thorne, 1959	21				
Helicotylenchus dihystera (Cobb, 1893) Sher, 1961	21				
Helicotylenchus exallus Sher, 1966	21				
Hypodontolaimus antarcticus Andrássy and Gibson 2007		8			
Laimaphelenchus helicosoma (Maslen, 1979) Peneva and Chipev 1999					4, 20, 35
Panagrolaimus davidi Timm 1971				1, 26, 29, 34	
Panagrolaimus magnivulvatus Boström 1995	4, 27, 28, 9				
Paratylenchus nanus Coob, 1923	24				
Plectus antarcticus de Man, 1904					4, 20, 34, 35, 36, 37
Plectus belgicae de Man 1904					4, 20
Plectus frigophilus Kirjanova 1958		8, 25, 18	16, 31	1, 4, 29, 34	20
Plectus insolens Andrássy 1998					4
Plectus meridianus Andrássy 1998					4
Plectus murrayi Yeates 1970	4, 27, 28, 9	4, 23, 25, 18	7, 16	1, 4, 13, 29, 30	20
Plectus telekii Mulk & Coomans, 1978	21				
Plectus tolerans Andrássy 1998					4, 20
Pratylenchus andinus Lordello, Zamith & Boock, 1961	24				
Rhabditis krylovi Tsalolikhin, 1989					4
Rotylenchus capensis Van den Berg & Heyns, 1974	4				

Table 4 continued

Nematode species/sectors	Continental Antarctica				Maritime Antarctica
	Maud	Enderby	Wilkes	Scott	
Scottnema lindsayae Timm 1971		25, 2		1, 2, 4, 11, 12, 13, 26, 29	
Teratocephalus pseudolirellus Maslen, 1979					20
Teratocephalus rugosus Maslen, 1979					20, 35
Teratocephalus tilbrooki Maslen, 1979	32, 33				4, 20, 35
Tylenchorhynchus maximus Allen, 1955	24				
Class Enoplea					
Amblydorylaimus isokaryon (Loof, 1975) Andrássy 1998					4, 34
Calcaridorylaimus signatus (Loof, 1975) Andrássy, 1986					4, 20, 34
Coomansus gerlachei (de Man, 1904) Jairajpuri & Khan, 1977					4, 20
Enchodelus signyensis Loof, 1975					4, 20, 34, 35
Eudorylaimus antarcticus (Steiner, 1916) Yeates 1970				1, 4, 6, 13, 29	
Eudorylaimus coniceps Loof, 1975					4, 20, 34, 35
Eudorylaimus glacialis Andrássy 1998		6		1, 6, 30	
Eudorylaimus nudicaudatus Heyns, 1993	4,6				
Eudorylaimus pseudocarteri Loof, 1975					4, 20, 34, 35
Eudorylaimus quintus Andrássy, 2008		6		6	
Eudorylaimus sabulophilus Tijepkema, Ferris & Ferris, 1971	21				
Eudorylaimus sextus Andrássy, 2008		6			
Eudorylaimus shirasei Kito, Shishida and Ohyama 1996	10b	4, 6, 19		1	
Eudorylaimus spauli Loof, 1975					4, 20, 34, 35
Eudorylaimus verrucosus Loof, 1975					4, 20, 34, 35
Eutobrilus antarcticus Tsalolikhin, 1981			4, 14		
Mesodorylaimus antarcticus Nedelchev and Peneva 2000					22
Mesodorylaimus chipevi Nedelchev and Peneva 2000					22
Mesodorylaimus imperator Loof, 1975					4, 20, 34
Mesodorylaimus masleni Nedelchev and Peneva, 2000					22
Paramphidelus antarcticus Tsalolikhin, 1989					4
Rhyssocolpus paradoxus (Loof, 1975) Andrássy, 1986					4, 20, 34, 35

The numbers in each column refer to reference (see table)

References followed by '*' indicate marine inhabitants. Literature source: (1) Adams et al. 2006, (2) Adams et al. 2007, (3) Andrássy 1981, (4) Andrássy 1998 (5) Andrássy 2006, (6) Andrássy 2008a, (7) Andrássy 2008b, (8) Andrássy and Gibson 2007, (9) Boström 1995, (10) Boström 1996, (10b) Boström 2005, (11) Boström et al. 2010, (12) Courtright et al. 2000, (13) Freckman and Virginia 1997, (14) Gagarin 2009, (14b) Ghosh et al. 2005, (15) Heyns 1994, (15b) Holovachov and Boström 2006, (16) Kirjanova 1958, (17) Kito and Ohyama 2008, (18) Kito et al. 1991, (19) Kito et al. 1996, (20) Maslen and Convey 2006, (21) Bohra et al. 2010, (22) Nedelchev and Peneva 2000, (23) Rounsevell and Horne 1986, (24) Ryss et al. 2005, (25) Shishida and Ohyama 1986, (26) Sinclair 2001, (27) Sohlenius et al. 1995, (28) Sohlenius et al. 1996, (29) Timm 1971, (30) Yeates 1970, (31) Yeates 1979, (32) Ingole and Parulekar 1993, (33) Verlecar et al. 1996, (34) Maslen 1979, (35) Maslen 1981, (36) Spaull 1973a, (37) Spaull 1973b

new areas of suitable habitat may be possible provided that the rate of change does not exceed their dispersal ability to find a new alternative habitat. At a larger scale (hundreds of kilometres), the rate of change may occur in conjunction with other changes (soil formation, vegetation growth), although long-distance dispersal between habitats may be limited (Wise 1967; Hogg and Stevens 2002; Stevens and Hogg 2002). Furthermore, several studies have suggested that the time since the last glaciation has been insufficient for successful colonisation of favourable habitats by soil taxa (Convey and Block 1996; Convey and Stevens 2007; Convey et al. 2008), and this is supported by recent data for arthropods (Stevens et al. 2006a; Stevens and Hogg 2006a). Accordingly, the natural dispersal of animals, other than local, seems unlikely to provide an adequate response to any environmental change. Long-term patterns can be useful in determining whether taxa are capable of migrating over large distances, whether they have persisted over long-term environmental change, or if they are the result of exotic introductions either by natural (passive) or by anthropogenic means. Such analyses for the microfauna is, however, currently limited until accurate widespread data for species identifications can lead to informed diversity and distributions.

Establishing diversity and distribution

Rotifera, Tardigrada and Nematoda are the most abundant and diverse microfaunal groups in the Antarctic region, but even greater levels of cryptic diversity are expected. Studies on the arthropods (Collembola and Acari) (e.g. Stevens et al. 2006b) have revealed that several new genetic entities (species) are present in the Antarctic and on sub-Antarctic islands, and this has also been found for the microfauna (Fontaneto et al. 2008; Sands et al. 2008; Czechowski et al. 2012). The species diversity of these ecologically important animals is still unresolved because taxonomic work has been dominated by arthropods (Greenslade and Wise 1984; Greenslade 1995; Stevens et al. 2006b). However, it is apparent that species diagnosis is difficult in many cases due to the conservative morphology of the microfauna (e.g. Andrássy 1998; Floyd et al. 2002; Robeson et al. 2009).

Molecular studies are needed to delineate species boundaries and dispersal patterns (e.g. Stevens et al. 2006b; Sands et al. 2008; Torricelli et al. 2010). It will then be possible to make accurate assessments of the patterns and processes of biodiversity of the microfauna, which will further our knowledge of the evolutionary history throughout the Southern Hemisphere (Convey and Stevens 2007; Convey et al. 2008). These studies are now beginning to explain the significance of glacial events in determining patterns of species' distribution and genetic diversity for terrestrial communities in Antarctica (Courtright et al. 2000; Frati et al. 2001; Stevens and Hogg 2006a). They have revealed that some taxa of little dispersal capability have large-scale biogeographic distributions across Antarctica and the sub-Antarctic islands (e.g. Convey and McInnes 2005; Stevens and Hogg 2006a; Czechowski et al. 2012). Collectively, these studies have revealed a significant effect of glacial and sea–ice barriers to examine the mobility and gene flow of Antarctic taxa across fragmented landscapes over evolutionary time scales.

Future directions in biodiversity assessment and species discovery in Antarctica

With increased access to molecular techniques (Hebert et al. 2003), the diversity of Antarctic invertebrates and the association between organisms and environments can now be estimated to levels previously unimaginable (Peck 2005; Ji et al. 2013). Molecular techniques can be used to test hypotheses related to connectivity (i.e. gene flow) and reveal phylogeographic processes that have moulded the pattern of genetic diversity among populations, as well as their evolutionary history and relationships to other taxa (Stevens and Hogg 2006a). The usefulness of the mitochondrial cytochrome *c* oxidase I (COI) gene as a DNA barcode to determine sequence divergence among invertebrates and discern among morphologically similar (cryptic) species is now well established (e.g. Hebert et al. 2003; Stevens and Hogg 2003; Stevens et al. 2006a). COI records can now be found for Antarctic arthropods (e.g. Stevens and Hogg 2003, 2006a; Stevens et al. 2006a; Stevens and D'Haese 2014) and collectively have revealed patterns of recolonisation from glacial refugia that show far greater diversity than known previously. Most of the success of these data have been due to capturing most of the geographical range for species. Comparatively, molecular data for the microfauna from Antarctica are limited to tardigrades (Sands et al. 2008; Czechowski et al. 2012) and more recently nematodes (Velasco-Castrillón and Stevens 2014) and bdelloid rotifers (Velasco-Castrillón et al. 2014). These studies have tended to have restricted sample sizes and/or geographical coverage limiting their use for biogeographic comparisons beyond diversity and systematics. Despite this, they have revealed greater diversity in Antarctica than has been previously recognised. With an increasing attention of microfauna outside continental Antarctica on bdelloid rotifers (Fontaneto et al. 2008) and nematodes (e.g. Blouin 2000; Derycke et al. 2010; Prosser et al. 2013), the potential for examining the distribution of microfauna throughout Antarctica and its neighbouring landmasses will provide one of the most comprehensive datasets for any group of organisms across the continent.

Rotifera, Nematoda and Tardigrada are critical microfaunal groups given their role in nutrient recycling and their importance in Antarctic limno-terrestrial ecosystems. Unfortunately, we are in our infancy in our understanding of these ecosystems in Antarctica and we highlight below three areas that are fundamental in providing information on diversity, distributional range and type of habitats in which microfauna are found; information that is critical for future conservation and land management, and in detecting new species and species introductions.

(1) Molecular techniques need to be applied to the identification of species. Most of the Antarctic microfauna to date are limited to morphological assessments, and past molecular studies have shown that this has not accurately reflected the biodiversity present, particularly where wide species ranges have been reported. This is fundamental information

necessary for understanding and managing sustainable biodiversity as well as detecting exotic introductions.

(2) Sampling in Antarctica has tended to ignore information linked to abiotic data (e.g. soil chemistry, mineral analyses, and other environmental) which are important in establishing comparisons among biotic communities (i.e. do the same communities occur in similar habitats) and can also be used in predictive modelling of Antarctic biodiversity and habitat requirements (e.g. Convey et al. 2014; Fraser et al. 2014).

(3) Recently, biotic data have been assessed for Antarctica in an attempt to determine biogeographic regions (Terauds et al. 2012). The use of GIS systems to define Antarctic Conservation Biogeographic Regions (ACBR) (see Terauds et al. 2012) is an important step forward, but only with the inclusion of phylogenetically informed biodiversity will we be able to have accurate ACBRs. The implementation of the current knowledge on microfaunal diversity (as shown in this review) with genetic lineages identified by phylogenetic studies combined with abiotic data will help to better delineate ACBRs.

Acknowledgments We thank Dieter Piepenburg for editorial comments and two anonymous reviewers. In particular, we thank Dr. Sven Boström for providing a thorough review of the nematodes and Dr. Sandra McInnes for assisting with the tardigrades. We are grateful to the University of Adelaide (http://www.sciences.adelaide.edu.au/) for a PhD scholarship to AVC and the South Australian Museum Mawson Trust for providing funding for the Sir Douglas Mawson Doctoral Scholarship (http://www.samuseum.sa.gov.au/). This study was partially supported and funded by the Australian Antarctic Division (http://www.antarctica.gov.au/) Project (ASAC 2355 to MIS).

References

Adams BJ, Bardgett RD, Ayres E, Wall DH, Aislabie J, Bamforth S, Bargagli R, Cary C, Cavacini P, Connell L, Convey P, Fell JW, Frati F, Hogg ID, Newsham KK, O'Donnell A, Russell N, Seppelt RD, Stevens MI (2006) Diversity and distribution of Victoria Land biota. Soil Biol Biochem 38:3003–3018

Adams BJ, Wall DH, Gozel U, Dillman AR, Chaston JM, Hogg ID (2007) The southernmost worm, *Scottnema lindsayae* (Nematoda): diversity, dispersal and ecological stability. Polar Biol 30:809–815

Andrássy I (1981) Revision of the order Monhysterida (Nematoda) inhabiting soil and inland waters. Opusc Zool Bp 17–18:13–47

Andrássy I (1998) Nematodes in the Sixth Continent. J Nematode Morph Syst 1:107–186

Andrássy I (2006) *Halomonhystera*, a new genus distinct from *Geomonhystera* Andrássy, 1981 (Nematoda: Monhysteridae). Meiofauna Mar 15:11–24

Andrássy I (2008a) *Eudorylaimus* species (Nematoda: Dorylaimida) of continental Antarctica. J Nematode Morph Syst 11:49–66

Andrássy I (2008b) On the male of the Antarctic nematode species, *Plectus murrayi* Yeates, 1970. J Nematode Morph Syst 11:87–89

Andrássy I, Gibson J (2007) Nematodes from saline and freshwater lakes of the Vestfold Hills, East Antarctica, including the description of *Hypodontolaimus antarcticus* sp. n. Polar Biol 30:669–678

Binda MG, Pilato G (2000) *Diphascon* (*Adropion*) *tricuspidatum*, a new species of eutardigrade from Antarctica. Polar Biol 23: 75–76

Blouin M (2000) Brief communication. Neutrality tests on mtDNA: unusual results from nematodes. J Hered 91:156–158

Bohra P, Sanyal AK, Hussain A, Mitra B (2010) Five new records of nematodes from East Antarctica. J Threat Taxa 2:974–977

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

Boström S (1996) *Chiloplectus masleni* sp. nov. and variability in populations of *Plectus acuminatus* Bastian 1865 (Nematoda: Plectidae) from the nunatak Basen, Vestfjella, Dronning Maud Land, East Antarctica. Polar Biol 17:74–80

Boström S (2005) Nematodes from Schirmacher Oasis, Dronning Maud Land, East Antarctica. Russ J Nematol 13:43–54

Boström S, Holovachov O, Nadler S (2010) Description of *Scottnema lindsayae* Timm, 1971 (Rhabditida: Cephalobidae) from Taylor Valley, Antarctica and its phylogenetic relationship. Polar Biol 34:1–12

British Antarctic Survey (2004) Antarctica, 1:10,000,000 scale map. British Antarctic Survey, Cambridge

Burgess JS, Spate AP, Shevlin J (1994) The onset of deglaciation in the Larsemann Hills, Eastern Antarctica. Antarct Sci 6:491–495

Burn AJ (1984) Life cycle strategies in two Antarctic Collembola. Oecologia 64:223–229

Convey P, Block W (1996) Antarctic Diptera: ecology, physiology and distribution. Eur J Entomol 93:1–13

Convey P, McInnes SJ (2005) Exceptional tardigrade-dominated ecosystems in Ellsworth Land, Antarctica. Ecology 86:519–527

Convey P, Stevens MI (2007) Antarctic biodiversity. Science 317:1877–1878

Convey P, Gibson JAE, Hillenbrand CD, Hodgson DA, Pugh PJA, Smellie JL, Stevens MI (2008) Antarctic terrestrial life—challenging the history of the frozen continent? Biol Rev 83:103–117

Convey P, Stevens MI, Hodgson DA, Smellie JL, Hillenbrand CD, Barnes DKA, Clarke A, Pugh PJA, Linse K, Cary SC (2009) Exploring biological constraints on the glacial history of Antarctica. Quat Sci Rev 28:3035–3048

Convey P, Chown SL, Clarke A, Barnes DK, Bokhorst S, Cummings V, Ducklow HW, Frati F, Green TA, Gordon S et al (2014) The spatial structure of Antarctic biodiversity. Ecol Monogr 84: 203–244

Courtright EM, Wall DH, Virginia RA, Frisse LM, Vida JT, Thomas WK (2000) Nuclear and mitochondrial DNA sequence diversity in the Antarctic nematode *Scottnema lindsayae*. J Nematol 32:143–153

Cromer L, Gibson JAE, Swadling KM, Hodgson DA (2006) Evidence for a lacustrine faunal refuge in the Larsemann Hills, East Antarctica, during the last glacial maximum. J Biogeogr 33: 1314–1323

Czechowski P, Sands CJ, Adams BJ, D'Haese CA, Gibson JAE, McInnes SJ, Stevens MI (2012) Antarctic Tardigrada: a first step in understanding molecular operational taxonomic units (MOTUs) and biogeography of cryptic meiofauna. Invertebr Syst 26:526–538

Dartnall HJG (1983) Rotifers of the Antarctic and subantarctic. Hydrobiologia 104:57–60

Dartnall HJG (1995) Rotifers, and other aquatic invertebrates, from the Larsemann Hills, Antarctica. Pap Proc Roy Soc Tasmania 129:17–23
Dartnall HJG (2000) A limnological reconnaissance of the Vestfold Hills. ANARE Rep 141:1–53
Dartnall HJG (2005) Freshwater invertebrates of subantarctic South Georgia. J Nat Hist 39:3321–3342
Dartnall HJG, Hollowday ED (1985) Antarctic Rotifers. Br Antarct Surv Sci Rep 100:1–46
Dastych H (1984) The Tardigrada from Antarctic with descriptions of several new species. Acta Zool Cracov 27:377–436
Dastych H (1989) An annotated list of Tardigrada from the Antarctic. Entomol Mitt Zool Mus Hambg 9:249–257
Dastych H (1991) Redescription of *Hypsibius antarcticus* (Richters, 1904), with some notes on *Hypsibius arcticus* (Murray, 1907) (Tardigrada). Mitt Hamb Zool Mus Inst 88:141–159
Dastych H (2003) *Diphascon langhovdense* (Sudzuki, 1964) stat. nov., a new taxonomic status for the semi-terrestrial tardigrade (Tardigrada). Acta Biol Benrodis 12:19–25
Dastych H, Harris JM (1995) A new species of the genus *Macrobiotus* from inland nunataks in western Dronning Maud Land, continental Antarctica (Tardigrada). Entomol Mitt Zool Mus Hambg 11:175–182
Dastych H, McInnes S (1994) *Hexapodibius boothi* sp. n., a new species of semi-terrestrial tardigrade from the Maritime Antarctic. Entomol Mitt Zool Mus Hambg 11:111–117
Dastych H, Ryan PG, Watkins BP (1990) Notes on Tardigrada from western Dronning Maud Land (Antarctica) with a description of two new species. Entomol Mitt Zool Mus Hambg 10:57–66
De Smet WH, Gibson JA (2008) *Rhinoglena kutikovae* n. sp. (Rotifera: Monogononta: Epiphanidae) from the Bunger Hills, East Antarctica: a probable relict species that survived Quaternary glaciations on the continent. Polar Biol 31:595–603
Derycke S, Vanaverbeke J, Rigaux A, Backeljau T, Moens T (2010) Exploring the use of cytochrome oxidase c subunit 1 (COI) for DNA barcoding of free-living marine nematodes. PLoS ONE 5:e13716
Donner J (1972) Report on the finding of Rotifera (Rotatoria) from Antarctica. Polskie Arch Hydrobiol 19:251–252
Floyd R, Abebe E, Papert A, Blaxter M (2002) Molecular barcodes for soil nematode identification. Mol Ecol 11:839–850
Fontaneto D, Barraclough TG, Chen K, Ricci C, Herniou EA (2008) Molecular evidence for broad-scale distributions in bdelloid rotifers: everything is not everywhere but most things are very widespread. Mol Ecol 17:3136–3146
Fontaneto D, Kaya M, Herniou EA, Barraclough TG (2009) Extreme levels of hidden diversity in microscopic animals (Rotifera) revealed by DNA taxonomy. Mol Phylogen Evol 53:182–189
Fraser CI, Terauds A, Smellie J, Convey P, Chown SL (2014) Geothermal activity helps life survive glacial cycles. Proc Natl Acad Sci 111:5634–5639
Frati F, Spinsanti G, Dallai R (2001) Genetic variation of mtCOII gene sequences in the collembolan *Isotoma klovstadi* from Victoria Land, Antarctica: evidence for population differentiation. Polar Biol 24:934–940
Freckman DW, Virginia RA (1997) Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. Ecology 78:363–369
Gagarin VG (2009) A revision of the genus *Eutobrilus* Tsalolikhin, 1981 (Nematoda, Triplonchida). Inl Wat Biol 2:205–212
Ghosh SC, Chatterjee A, Mitra B, De J (2005) *Antarctenchus motililus* sp. n. (Nematoda: Tylenchida) from Schirmacher Oasis, East Antarctica. J Interacademica 9:367–371
Gibson JAE, Cromer L, Agius JT, McInnes SJ, Marley NJ (2007) Tardigrade eggs and exuviae in Antarctic lake sediments: insights into Holocene dynamics and origins of the fauna. J Limnol 66(Suppl. 1):65–71
Gore DB, Rhodes EJ, Augustinus PC, Leishman MR, Colhoun EA, Rees-Jones J (2001) Bunger Hills, East Antarctica: ice free at the last glacial maximum. Geology 29:1103–1106
Greenslade P (1995) Collembola from the Scotia Arc and Antarctic Peninsula including descriptions of two new species and notes on biogeography. Pol Pismo Entomol 64:305–319
Greenslade P, Wise KAJ (1984) Additions to the collembolan fauna of the Antarctic. Trans R Soc Aust 108:203–205
Greenslade P, Farrow RA, Smith JMB (1999) Long distance migration of insects to a subantarctic island. J Biogeogr 26:1161–1167
Hansson LA, Hylander S, Dartnall HJG, Lidström S, Svensson JE (2012) High zooplankton diversity in the extreme environments of the McMurdo Dry Valley lakes, Antarctica. Antarct Sci 24:131–138
Hawes TC, Worland MR, Convey P, Bale JS (2007) Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography. Antarct Sci 19:3–10
Hays JD, Imbrie J, Shackleton NJ (1976) Variations in the Earth's orbit: pacemaker of the ice ages. Science 194:1121–1132
Hebert PDN, Ratnasingham S, deWaard JR (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. Proc R Soc Lond 270(Suppl 1):S96–S99
Heyns J (1994) *Chiloplacoides antarcticus* n. gen., n. sp. from western Dronning Maud Land, Antarctica (Nematoda: Cephalobidae). Fundam Appl Nematol 17:333–338
Hodgson DA, Noon PE, Vyverman W, Bryant CL, Gore DB, Appleby P, Gilmour M, Verleyen E, Sabbe K, Jones VJ, Ellis-Evans JC, Wood PB (2001) Were the Larsemann Hills ice-free through the last glacial maximum? Antarct Sci 13:440–454
Hogg ID, Stevens MI (2002) Soil fauna of Antarctic coastal landscapes. In: Beyer L, Bolter M (eds) Geoecology of Antarctic ice-free coastal landscapes. Ecol Stud 154:265–282
Holovachov O, Boström S (2006) Description of *Acrobeloides arctowskii* sp. n. (Rhabditida: Cephalobidae) from King George Island, Antarctica. Russ J Nematol 14:51–56
Huiskes AHL, Convey P, Bergstrom DM (2006) Trends in Antarctic terrestrial and limnetic ecosystems. In: Bergstrom DM, Convey P, Huiskes AHL (eds) Trends in Antarctic terrestrial and limnetic ecosystems: Antarctica as a global indicator. Springer, Dordrecht, pp 1–13
Ingole BS, Parulekar AH (1993) Limnology of freshwater lakes of Schirmacher Oasis, East Antarctica. Proc Indian Natl Sci Acad B 59:589–600
Janiec K (1996) The comparison of freshwater invertebrates of Spitsbergen (Arctic) and King George Island (Antarctic). Pol Polar Res 17:173–202
Ji Y et al (2013) Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. Ecol Lett 16:1245–1257
Kinchin IM (1994) The biology of tardigrades. Portland Press Ltd, London, p 186
Kirjanova ES (1958) Antarctic specimens of freshwater nematodes of the genus *Plectus* Bastian (Nematoda, Plectidae). Sov Antarct Exped Inf Bull 3:101–103
Kito K, Ohyama Y (2008) Rhabditid nematodes found from a rocky coast contaminated with treated waste water of Casey Station in East Antarctica, with a description of a new species of *Dolichorhabditis* Andrássy, 1983 (Nematoda: Rhabditidae). Zootaxa 1850:43–52
Kito K, Shishida Y, Ohyama Y (1991) *Plectus antarcticus* de Man, 1904 and *P. frigophilus* Kirjanova, 1958 (Nematoda: Plectidae), with emphasis on the male, from the Soya Coast, East Antarctica. Nematologica 37:252–262

Kito K, Shishida Y, Ohyama Y (1996) New species of the genus *Eudorylaimus* Andrassy, 1959 (Nematoda: Qudsianematidae) from East Antarctica. Polar Biol 16:163–169

Lawver LA, Gahagan LM (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeogr Palaeoclim Palaeoecol 198:11–37

Lawver LA, Gahagan LM, Dalziel IWD (1998) A tight fit-Early Mesozoic Gondwana, a plate reconstruction perspective. Mem Natl Inst Polar Res Spec 53:214–229

Marshall DJ, Pugh PJA (1996) Origin of the inland Acari of continental Antarctica, with particular reference to Dronning Maud Land. Zool J Linn Soc 118:101–118

Maslen NR (1979) Additions to the nematode fauna of the Antarctic region with keys to taxa. Br Antarct Surv Bull 49:207–229

Maslen NR (1981) The Signy Island terrestrial reference sites: XII. Population ecology of nematodes with additions to the fauna. Br Antarct Surv Bull 53:57–75

Maslen NR, Convey P (2006) Nematode diversity and distribution in the southern maritime Antarctic—clues to history? Soil Biol Biochem 38:3141–3151

McInnes SJ (1995) Taxonomy and ecology of Tardigrades from Antarctic lakes. M Phil, Open University: 248

McInnes SJ (2010) *Echiniscus corrugicaudatus* (Heterotardigrada; Echiniscidae) a new species from Ellsworth Land, Antarctica. Polar Biol 33:59–70

McInnes SJ, Pugh PJA (1998) Biogeography of limno-terrestrial Tardigrada, with particular reference to the Antarctic fauna. J Biogeogr 25:31–36

McInnes SJ, Pugh PJA (2007) An attempt to revisit the global biogeography of limno-terrestrial Tardigrada. J Limnol 66:90–96

Meldal BHM, Debenham NJ, De Ley P, De Ley IT, Vanfleteren JR, Vierstraete AR, Bert W, Borgonie G, Moens T, Tyler PA, Austen MC, Blaxter ML, Rogers AD, Lambshead PJD (2007) An improved molecular phylogeny of the Nematoda with special emphasis on marine taxa. Mol Phylogen Evol 42:622–636

Miller WR, Heatwole H (1995) Tardigrades of the Australian Antarctic Territories: the Mawson Coast, East Antarctica. Invertebr Biol 114:27–38

Miller JD, Horne P, Heatwole H, Miller WR, Bridges L (1988) A survey of the terrestrial Tardigrada of the Vestfold Hills, Antarctica. Hydrobiologia 165:197–208

Miller WR, Heatwole H, Pidgeon RWJ, Gardiner GR (1994) Tardigrades of the Australian Antarctic Territories: the Larsemann Hills, East Antarctica. Trans Am Microsc Soc 113: 142–160

Miller WR, Miller JD, Heatwole H (1996) Tardigrades of the Australian Antarctic Territories: the Windmill Islands, East Antarctica. Zool J Linn Soc 116:175–184

Moore PD (2002) Biogeography: springboards for springtails. Nature 418:381

Morikawa K (1962) Notes on some Tardigrada from the Antarctic region. Biol Res Jpn Ant Res Exp 17:3–6

Muñoz J, Felicisimo AM, Cabezas F, Burgaz AR, Martinez I (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science 304:1144–1147

Murray J (1910) Part III. Antarctic Rotifera. British Antarctic Expedition 1907–9, under the command of Sir EH Shackleton, cvo reports on the scientific investigations 1:41–65

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

Nkem JN, Wall DH, Virginia RA, Barrett JE, Broos EJ, Porazinska DL, Adams BJ (2006) Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. Polar Biol 29:346–352

Opalinski K (1972) Freshwater fauna and flora in Haswell island (Queen Mary Land, Eastern Antarctica). Pol Arch Hydrobiol 19:377–381

Peck LS (2005) Prospects for survival in the Southern Ocean: vulnerability of benthic species to temperature change. Antarct Sci 17:497–507

Peneva V, Chipev N (1999) *Laimaphelenchus helicosoma* (Maslen, 1979) n. comb. (Nematoda: Aphelenchida) from the Livingston Island (the Antarctic). Bulg Antarct Res 2:57–61

Pilato G, Binda MG (1999) Three new species of *Diphascon* of the *pingue* group (Eutardigrada, Hypsibiidae) from Antarctica. Polar Biol 21:335–342

Pilato G, McInnes SJ, Lisi O (2012) *Hebesuncus mollispinus* (Eutardigrada, Hypsibiidae), a new species from maritime Antarctica. Zootaxa 3446:60–68

Prosser SWJ, Velarde-Aguilar MG, León-Règagnon V, Hebert PDN (2013) Advancing nematode barcoding: a primer cocktail for the cytochrome c oxidase subunit I gene from vertebrate parasitic nematodes. Mol Ecol Resour 13:1108–1115

Pugh PJA (1993) A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. J Nat Hist 27:323–421

Pugh PJA, Convey P (2000) Scotia Arc Acari: antiquity and origin. Zool J Linn Soc 130:309–328

Pugh PJA, Convey P (2008) Surviving out in the cold: Antarctic endemic invertebrates and their refugia. J Biogeogr 35: 2176–2186

Robeson MS, Costello EK, Freeman KR, Whiting J, Adams B, Martin AP, Schmidt SK (2009) Environmental DNA sequencing primers for eutardigrades and bdelloid rotifers. BMC Ecol 9:25

Rounsevell DE, Horne PA (1986) Terrestrial, parasitic and introduced invertebrates of the Vestfold Hills. In: Pickard J (ed) Antarctic Oasis. Terrestrial environments and history of the Vestfold Hills. Academic Press Australia, Sydney, pp 309–331

Ryss A, Boström S, Sohlenius B (2005) Tylenchid nematodes found on the nunatak Basen, East Antarctica. Ann Zool 55:315–324

Sands CJ, Convey P, Linse K, McInnes SJ (2008) Assessing meiofaunal variation among individuals utilising morphological and molecular approaches: an example using the Tardigrada. BMC Ecol 8:7

Segers H (2007) Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. Zootaxa 1564:1–104

Shishida Y, Ohyama Y (1986) A note on the terrestrial nematodes around Syowa station, Antarctica (extended abstract). Mem Natl Inst Polar Res, Spec Issue 44:259–260

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

Sinclair BJ, Stevens MI (2006) Terrestrial microarthropods of Victoria Land and Queen Maud Mountains, Antarctica: implications of climate change. Soil Biol Biochem 38:3158–3170

Smykla J, Porazinska DL, Iakovenko N, Janko K, Weiner WM, Niedbala W, Drewnik M (2010) Studies on Antarctic soil invertebrates: preliminary data on rotifers (Rotatoria), with notes on other taxa from Edmonson Point (Northern Victoria Land, Continental Antarctic). Acta Soc Zool Bohem 74:135–140

Smykla J, Iakovenko N, Devetter M, Kaczmarek Ł (2012) Diversity and distribution of tardigrades in soils of Edmonson Point (Northern Victoria Land, continental Antarctica). Czech Polar Rep 2:61–70

Sohlenius B (1989) Interactions between two species of *Panagrolaimus* in agar cultures. Nematologica 34:208–217

Sohlenius B, Boström S (2005) The geographic distribution of metazoan microfauna on East Antarctic nunataks. Polar Biol 28:439–448

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

Sohlenius B, Boström S, Hirschfelder A (1995) Nematodes, rotifers and tardigrades from nunataks in Dronning Maud Land, East Antarctica. Polar Biol 15:51–56

Sohlenius B, Boström S, Hirschfelder A (1996) Distribution patterns of microfauna (nematodes, rotifers and tardigrades) on nunataks in Dronning Maud Land, East Antarctica. Polar Biol 16:191–200

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

Spaull V (1973a) Distribution of nematode feeding groups at Signy Island, South Orkney Islands, with an estimate of their biomass and oxygen consumption. Br Antarct Surv Bull 37:21–32

Spaull V (1973b) Qualitative and quantitative distribution of soil nematodes of Signy Island, South Orkney Islands. Br Antarct Surv Bull 33:177–184

Stevens MI, D'Haese CA (2014) Islands in ice: isolated populations of *Cryptopygus sverdrupi* (Collembola) among nunataks in the Sør Rondane Mountains, Dronning Maud Land, Antarctica. Biodiversity. doi:10.1080/14888386.2014.928791

Stevens MI, Hogg ID (2002) Expanded distributional records of Collembola and Acari in southern Victoria Land, Antarctica. Pedobiologia 46:485–495

Stevens MI, Hogg ID (2003) Long-term isolation and recent range expansion from glacial refugia revealed for the endemic springtail *Gomphiocephalus hodgsoni* from Victoria Land, Antarctica. Mol Ecol 12:2357–2369

Stevens MI, Hogg ID (2006a) 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 Biol Biochem 38: 3171–3180

Stevens MI, Hogg ID (2006b) The molecular ecology of Antarctic terrestrial and limnetic invertebrates and microbes. In: Bergstrom DM, Convey P, Huiskes AHL (eds) Trends in Antarctic terrestrial and limnetic ecosystems: Antarctica as a global indicator. Springer, Dordrecht, pp 177–192

Stevens MI, Fjellberg A, Greenslade P, Hogg ID, Sunnucks P (2006a) Redescription of the Antarctic springtail *Desoria klovstadi* using morphological and molecular evidence. Polar Biol 29:820–830

Stevens MI, Greenslade P, Hogg ID, Sunnucks P (2006b) Southern Hemisphere springtails: could any have survived glaciation of Antarctica? Mol Biol Evol 23:874–882

Stevens MI, Porco D, D'Haese CA, Deharveng L (2011) Comment on "Taxonomy and the DNA barcoding enterprise" by Ebach (2011). Zootaxa 2838:85–88

Sudzuki M (1964) On the microfauna of the Antarctic region. 1. Moss-water community at Langhovde. JARE Sci Rep 19:1–41

Sudzuki M (1988) Comments on the antarctic Rotifera. Hydrobiologia 165:89–96

Suren A (1990) Microfauna associated with algal mats in melt ponds of the Ross Ice Shelf. Polar Biol 10:329–335

Terauds A, Chown SL, Morgan F, Peat HJ, Watts DJ, Keys H, Convey P, Bergstrom DM (2012) Conservation biogeography of the Antarctic. Divers Dist 18:726–741

Timm RW (1971) Antarctic soil and freshwater nematodes from the McMurdo Sound region. Proc Helminthol Soc Wash 38:42–52

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

Tripati A, Backman J, Elderfield H, Ferretti P (2005) Eocene bipolar glaciation associated with global carbon cycle changes. Nature 436:341–346

Tsujimoto M, McInnes SJ, Convey P, Imura S (2014) Preliminary description of tardigrade species diversity and distribution pattern around coastal Syowa Station and inland Sør Rondane Mountains, Dronning Maud Land, East Antarctica. Polar Biol. doi:10.1007/s00300-014-1516-8

Tumanov DV (2006) Five new species of the genus *Milnesium* (Tardigrada, Eutardigrada, Milnesiidae). Zootaxa 1122:1–23

Utsugi K, Ohyama Y (1989) Antarctic tardigrada. Proc NIPR Symp Polar Biol 2:190–197

Utsugi K, Ohyama Y (1991) Antarctic Tardigrada II. Molodezhnaya and Mt. Riiser-Larsen areas. Proc NIPR Symp Polar Biol 4:161–170

Utsugi K, Ohyama Y (1993) Antarctic Tardigrada III. Fildes Peninsula of King George Island. Proc NIPR Symp Polar Biol 6:139–151

Velasco-Castrillón A, Stevens MI (2014) Morphological and molecular diversity at a regional scale: a step closer to understanding Antarctic nematode biogeography. Soil Biol Biochem 70: 272–284

Velasco-Castrillón A, Schultz MB, Colombo F, Gibson JAE, Davies KA, Austin AD, Stevens MI (2014a) Distribution and diversity of microfauna from East Antarctica: assessing the link between biotic and abiotic factors. PLoS ONE 9:e87529

Velasco-Castrillón A, Page TJ, Gibson JAE, Stevens MI (2014b) Surprisingly high levels of biodiversity and endemism amongst Antarctic rotifers uncovered with mitochondrial DNA. Biodiversity 15:1–13

Verlecar XN, Dhargalkar VK, Matondkar SGP (1996) Ecobiological studies of the freshwater lakes at Schirmacher Oasis, Antarctica. Sci Rep: Twelfth Indian Exp Antarct, Techn Publ 10: 233–257

Vincent WF, James MR (1996) Biodiversity in extreme aquatic environments: lakes, ponds and streams of the Ross Sea sector, Antarctica. Biodivers Conserv 5:1451–1471

Wall DH (2007) Global change tipping points: above-and below-ground biotic interactions in a low diversity ecosystem. Phil Trans R Soc B 362:2291–2306

Webster-Brown J, Gall M, Gibson J, Wood S, Hawes I (2010) The biogeochemistry of meltwater habitats in the Darwin Glacier region (80 S), Victoria Land, Antarctica. Antarct Sci 22:646–661

Wharton DA (2003) The environmental physiology of Antarctic terrestrial nematodes: a review. J Comp Physiol B 173:621–628

Wise KAJ (1967) Collembola (springtails). Antarct Res Ser 10: 123–148

Yeates GW (1970) Two Terrestrial Nematodes from the McMurdo Sound Region, Antarctica, with a Note on *Anaplectus arenicola* Killick, 1964. J Helminthol 44:27–34

Yeates GW (1979) Terrestrial nematodes from the Bunger Hills and Gaussberg, Antarctica. NZ J Zool 6:641–643