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Diversity gradients of rotifer species richness in Antarctica

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Abstract

We gathered taxonomic information regarding the occurrence of rotifers in Antarctica and Subantarctica, producing a database of more than 1100 records from all 93 papers published on the region since the start of research expeditions in the far South. From this literature review, we outline a history of rotifer research in Antarctica. Then, using this database, we address specific questions on biogeographic patterns in species richness in rotifers in Antarctica and Subantarctica. We highlight a complex scenario of differences between areas and latitudinal gradients, differentially affected by problems in sampling bias. The number of species of monogonont rotifers seems to decrease with increasing absolute latitudes, whereas the number of species of bdelloid rotifers generally increases with increasing absolute latitudes.

Keywords

Bdelloidea; biodiversity; biogeography; latitudinal gradients; Monogononta.

Introduction

Research on Antarctica started with the first European expeditions to explore the Antarctic continent and conquer the South Pole. Although microscopic, rotifers were among the first animals that have been studied (Murray, 1910a). Indeed, the famous explorer Ernest Shackleton mentioned the ability of rotifers to survive freezing and drying as an important discovery: “The most important event of the winter months was the discovery by the biologist of microscopical life in the frozen lakes [...] The microscope showed that rotifers, water-bears, and other forms of minute animal-life existed” (Shackleton, 1909b). Shackleton even reported rotifers as an example of animals that are much better adapted to Antarctica than people: “It became a contest between rotifers and scientist, and generally the rotifers seemed to triumph” (Shackleton, 1909a).

Here we collate all 93 studies that recorded Rotifera at the genus and species level from Continental Antarctica, Maritime Antarctica, and Subantarctica into a database. Our aims were to (1) outline a brief history of rotifer research in the Antarctic regions; (2) make the database available online; (3) investigate biogeographic issues on species richness in the Antarctic regions. Thus, we address whether (1) rotifer species richness is different between Antarctica and Subantarctica, (2) there are hotspot of biodiversity with biogeographic sectors that are richer than others, and (3) there is a latitudinal gradient in species richness. To account for potential bias in our knowledge of rotifer diversity, we performed explicit tests accounting for sampling effort.

39 *A history of rotifer research in Antarctica*

40 The first record of rotifers from the Antarctic continent (Gaussberg, 66°50' S,
41 89°12'E, Kaiser Wilhelm II Land) and the Subantarctic regions (Possession Island,
42 Kerguelen Islands, Heard Island) was by Richters (1904, 1907) who reported the
43 presence of several bdelloid individuals often outnumbering other
44 microinvertebrates, and attributed them to the collective genus *Callidina*. This is
45 currently not considered a valid genus (Donner, 1965; Fontaneto & De Smet,
46 2015); thus, we do not know what these bdelloid rotifers could be. The earliest
47 detailed reports on rotifers with accurate species identification from Antarctica
48 were by Murray (1910a, b) who found 17 species: 13 bdelloids (five of which
49 new to science) and 4 monogononts among mosses and in the lakes and ponds at
50 Ross Island (77°30'S, 168°00'E), McMurdo Sound. He stated: "I have never
51 anywhere seen Bdelloid rotifers so plentiful as are the two dominant species at
52 Cape Royds (*Philodina gregaria* and *Adineta grandis*). Among the higher
53 Invertebrata the Rotifera are easily first in numbers, both of individuals and
54 species" (Murray, 1910a: 18). Murray (1910b) also pioneered field studies
55 observing that in the dormant state adult *P. gregaria* and *A. grandis* were
56 remarkably tolerant to adverse conditions. He observed the dormant stages
57 surviving repeated freezing and thawing at weekly intervals for several months,
58 and surviving temperatures as low as -40°C (*P. gregaria*) or -78°C (*A. grandis*);
59 some anhydrobiotic *A. grandis* also survived a short exposure to 100°C. Both
60 species remained alive after a month in seawater and a much more saline
61 solutions (Murray, p.53); they became active quickly after being transferred to
62 fresh water. After being held in the dry state for about a year, they revived within

one hour after rehydration. *Philodina gregaria* and *A. grandis* are now recognized as Antarctic endemics, and are the two most frequently reported bdelloids in limno-terrestrial studies. Kutikova (1958a, b, 1991) also contributed to our knowledge of the rotifer fauna of the Vestfold, Bunger, and Obruchev Hills (East Antarctica), and described *Notholca verae*, another Antarctic endemic. The studies by Sudzuki (e.g. 1964, 1979) on rotifers from the moss-water community and terrestrial interstices at Langhovde (69°13'S, 39°45'E), the Vestfold Hills (68°34'S, 78°11'E), Gaussberg (66°48'S, 89°12'E), and the Bunger Hills (66°10'S, 101°00'E) yielded up to 3 monogononts and 10 bdelloids; however, the species were poorly documented, and identifications may not be reliable. Dartnall (1995b, 1997, 2000) reported on rotifers obtained from mosses and benthos and plankton of water bodies in the Larsemann (69°24'S, 76°20'E) and Vestfold Hills (68°30'S, 78°44'E), and found about 12 identifiable species: 3 species of bdelloid and 9 of monogononts. The fauna was essentially similar in the two regions, comprising both cosmopolitan species and the endemic bdelloids *A. grandis* and *P. gregaria*. A new monogonont species, *Encentrum forcipatum*, to date only known from its type locality, was described from the Vestfold Hills (Dartnall, 1997). The study of soil habitats by Smykla et al. (2010) at Edmonson Point, Northern Victoria Land (74°20'S, 65°08'E) revealed that the invertebrate communities were dominated by bdelloids (9 species), with monogononts lacking. The greatest diversity of planktonic rotifers on the Antarctic continent was reported in Lake Hoare in the Taylor Valley (77°38'S, 162°55'E), one of the Dry Valleys of the McMurdo Sound region (Hansson et al. 2012). A total of nine rotifer taxa, including the bdelloid *Philodina alata*, and the monogononts *Filinia* sp., *Lepadella triptera*, and 6 Brachionidae were found. Of these, six were new to

the Antarctic continent. Except for the Antarctic endemic *P. alata*, records of monogononts were explained as anthropogenic introductions, but this seems questionable. Rather the explanation may be that the sample was contaminated; the illustrations show mostly empty and damaged loricae, potential indications of contamination. Recently, Velasco-Castrillón et al. (2014b) studied bdelloid rotifers from soil samples, bacterial mats, and plankton from the Continental Antarctic sectors (Wilkes, Enderby, Maud and Scott) and the Maritime Antarctica (Francis Island, Antarctic Peninsula) using DNA sequencing of mitochondrial cytochrome oxidase subunit I (COI). They found that the number of COI lineages and putative species largely surpassed the number of known morphospecies in the area: DNA taxonomy applied to sequences of 514 individuals suggested 40 species within *Philodina*, *Adineta*, and other unidentified bdelloids. Comparison of the Antarctic lineages with those from outside the continent indicated that the bdelloid fauna of continental Antarctica comprises mainly endemic species, with only one lineage (*Adineta* cf. *gracilis*) being present also in the Maritime Antarctic.

Minor taxonomical studies and distributional data on the rotifer fauna of continental Antarctica are provided by Russell (1959), Korotkevich (1964), Thomas (1965, 1972), Donner (1972), Opaliński (1972a, b), Everitt (1981), Dartnall (2005b), and De Smet & Gibson (2008). Thomas (1965, 1972) studied meltwater pools near the American base of Wilkes Station, Clark Peninsula, Wilkes Land (66°06'S, 110°37'E) and found two bdelloids (*Philodina* sp., *Habrotrocha* sp.) and the monogononts *Brachionus quadridentatus* and *B. calyciflorus*. The presence of the *Brachionus* species, predominantly inhabiting the temperate region, was explained through dispersal by birds (Antarctic skua)

from New Zealand. Dartnall (2005b), sampling close to the Australian Antarctic station of Casey and nearby Wilkes Station, failed to demonstrate the presence of the *Brachionus* species found by Thomas (1965, 1972). He suggested that both species were introduced during the construction of the American base of Wilkes Station but failed to become permanently established. An alternative explanation could be that contamination of Thomas' samples occurred at Christchurch, New Zealand, during the rotifer identification process by C. R. Russell. De Smet & Gibson (2008) described the monogonont *Rhinoglena kutikovae* from plankton of a freshwater lake in the Bunger Hills (66°16'S, 100°31'E); this species is probably an endemic relict species that survived Quaternary glaciations in glacial lacustrine refugia.

Studies on rotifers from continental Antarctic have dealt with limno-terrestrial habitats (soil, mosses, lichens), algal mats, and water of lakes, ponds, etc., from the ice-free areas of the coastal zone and adjacent islands. A peculiar ice-free habitat of continental Antarctica is formed by inland nunataks, mountain peaks penetrating the ice sheet. Rotifers occur in ~67% of the samples of soil, mosses, lichens or algae collected at nunataks (e.g. Sohlenius & Boström, 1996, 2005), with bdelloid rotifers usually forming the most frequent and most diverse (about 20 species) animal group of the microfauna of nunataks.

Another peculiar habitat is represented by cryoconite holes: i.e., water filled holes in glaciers. The biotic communities of cryoconite holes have been studied mostly in the McMurdo Dry Valley region. Porazinska et al. (2004) identified the bdelloid *P. gregaria* and the monogonont *Cephalodella catellina* from morphology and Christner et al. (2003) demonstrated the presence of

bdelloids by sequencing small subunit (18S) rDNA. The high similarity of the sequences to *Philodina acuticornis* reported by Christner et al. (2003) cannot be used as a reliable identification, given that this marker is highly conserved in bdelloids (Tang et al., 2012), and is thus unable to discriminate between species and genera. Metagenomic/metatranscriptomic analyses of accretion ice of subglacial Lake Vostok (77°50'S, 106°00'E), covered by a ~4000 m ice-sheath, revealed a diverse set of sequences of Bacteria and Eukaryotes, and indicated that viable organisms are present, amongst which a sequence closest to the rotifer *Adineta* sp. (98% identity level) (Shtarkman et al., 2013).

Information on rotifers from the Maritime Antarctic covers the South Shetland and South Orkney Islands, and the Antarctic Peninsula. Studies on rotifers from the South Shetland Islands are limited to King George Island (62°02'S, 58°21'W). José de Paggi (1982) carried out an extensive investigation of freshwater lagoons and a lake at the Potter Peninsula (62°15'S, 58°40'W). She found ten species of monogonont of which eight with widespread distribution, one, *Keratella americana*, originally restricted to N and S America but now also introduced in the Palaearctic and Africa, and a new species, *Notholca walterkosteï*. This new species has also been found in the South Orkney Islands, the Antarctic Peninsula, the Falklands Islands, and the Andean-Patagonian subregion of S. America. Kuczynski (1987) reported the widespread *Brachionus bidentatus*, and the originally American *B. havanaensis* from plankton of a freshwater lagoon near the Argentinian base Jubany (62°14'S, 58°38'W). Freshwater plankton and submerged moss sampled for monogononts in the vicinity of the Polish station Arctowski (62°09'S, 58°30'W) in the area of Admiralty Bay, yielded about 13

160 species, all with widespread distribution, except for *N. walterkosteii*, limited to
161 Antarctica and the surrounding regions (Janiec, 1993, 1996a, b; Janiec &
162 Salwicka, 1996). A year-long investigation of the freshwater plankton of Lake
163 Wujka (Admiralty Bay) by Pocięcha (2008) yielded five species of rotifers, all
164 previously reported for the area.

165 A first mention of rotifers from the South Orkney Islands was by Murray
166 (1906) who reported the bdelloid *Rotifer* sp. from Laurie Island (60°43'S,
167 44°31'W), but later on stated that the *Rotifer vulgaris* (sic) recorded in that paper
168 was probably a contamination (Murray, 1910b). Jennings (1976) performed
169 ecological studies on tardigrades and rotifers from moss carpets of Signy Island
170 (60°43'S, 45°38'W). Identification of rotifers from these samples was done by
171 Donner (1980) who incorrectly reported the samples to be from the Falkland
172 Islands (see Dartnall & Hollowday, 1985); altogether 14 bdelloids and 2
173 monogononts were identified. In their study on pools and lakes of Signy Island,
174 Dartnall & Hollowday (1985) added 5 species of bdelloid and 23 of monogononts,
175 with no species showing common to both habitats. They also described
176 *Dicranophorus permollis giganthea*, now known as *Encentrum permolle*
177 *gigantheum*, and *Lepadella rhomboides signiensis* and *Trichocerca rattus globosa*
178 (both currently considered *species inquirendae*). Fontaneto et al. (2008)
179 sequenced COI from *Adineta gracilis* and *A. grandis* from Signy. Priddle &
180 Dartnall (1978) studied the epiphytic algal and associated invertebrate
181 communities along aquatic moss stems and observed six rotifer species (2
182 bdelloids and 4 sessile monogononts) more or less permanently attached to the
183 moss. The majority of all rotifers reported for Signy Island are cosmopolitan or

184 widespread, except for *N. walterkosteï*, the Antarctic endemics *A. grandis*, *P.*
185 *gregaria*, *E. permolle giganteum*, and the species inquirendae *L. rhomboides*
186 *signiensis* and *T. rattus globosa*.

187 Rotifer research of the Antarctic Peninsula started with de Beauchamp
188 (1913) who found unidentifiable contracted bdelloids in moss samples from
189 several islands of the Palmer Archipelago (64°15'S, 62°50'W). He reported the
190 bdelloid genus *Mniobia* and the monogononts *Lindia torulosa*, *Colurella adriatica*
191 (Jenny Island, 67°44'S, 68°24'W), and *Colurella colurus* (Petermann Island,
192 65°10'S, 64°10'W). Few other observations exist for the Peninsula: Schmitt
193 (1945) reported the bdelloid *P. gregaria* from a freshwater pond at Red Rock
194 Ridge, Palmer Land (68°17'S, 67°13'W); Heywood (1977) identified the bdelloids
195 *Philodina antarctica* and *P. gregaria*, and the monogononts *Lindia torulosa*, *N.*
196 *walterkosteï* (misidentified as *N. verae*), and *Colurella* sp. in ponds and pools at
197 the Ablation Point area, Alexander Island, Graham Land (70°49'S, 67°25'W); at
198 Rothera Point (67°34'S, 68°07'W) in the Adelaide Islands, Dartnall (1980) only
199 found 4 species in benthic vegetation of pools (the bdelloid *Philodina* sp. and the
200 monogononts *C. colurus*, *Encentrum* sp., and *Resticula gelida*); Kuczynski (1987)
201 reported the widespread monogonont *Brachionus bidentatus* f. *inermis* at Barry
202 Islet, Marguerite Bay (68°07'S, 67°08'W); and Hollowday (1993) mentioned *N.*
203 *walterkosteï* from Alexander Island, Graham Land.

204 Information on the rotifers from the Subantarctic region is available for
205 South Georgia, Marion, Crozet, Kerguelen, Heard, and Macquarie Islands.
206 Twenty-eight species of cosmopolitan or widespread species (6 bdelloids, 22
207 monogononts) were found in freshwater habitats of Marion Island (46°45'S,

208 37°44'E) (Dartnall & Smith, 2012). They were rather uncommon, especially in
209 waters with high densities of crustaceans, and restricted to the weedy littoral of
210 lakes and to very shallow waters.

211 The first contribution to the rotifer fauna of the Kerguelen Islands
212 (49°15'S, 69°10'E) was by Richters (1904, 1907) who mentioned 6 unidentified
213 bdelloids belonging to the genus *Callidina*. de Beauchamp (1940) described the
214 bdelloid *Philodina jeanneli*, now considered endemic to Antarctica, and identified
215 the monogonont *Encentrum permolle* from unspecified habitats. Russell (1959)
216 recorded 11 monogonont species from damp vegetation and 'slime'. Lair & Koste
217 (1984) reported 3 species of monogononts in plankton from Lake Studer 2, and
218 De Smet (2001b) found 39 taxa (1 bdelloid, 38 monogononts) in plankton of
219 lentic freshwaters (lakes, ponds, pools). Of the species found, *Notholca*
220 *hollowdayi* is restricted to Subantarctica (Kerguelen and Heard Islands),
221 *Keratella sancta* is known only from South Island, New Zealand, and
222 Subantarctica (Macquarie Island), and the others have a widespread distribution.
223 A species originally reported as *incertae sedis* was afterwards described as
224 *Pourriotia carcharodonta* by De Smet (2003). It is a gall-forming endoparasite
225 infesting the xanthophyte alga *Vaucheria* (De Smet, 2009). From Possession
226 Island (46°24'S, 51°45'E, Crozet Islands) only *Callidina* spp. (Richters, 1904,
227 1907) and 3 common monogononts (De Smet, 2001a) have been reported.

228 Dartnall (1995a, 2003) visited Heard Island (53°04'S, 73°00'E) twice, and
229 studied plankton of different water bodies (lakes, lagoons, pools, tarns, streams,
230 wallows). This resulted in 7 bdelloid taxa and 21 monogononts of widespread
231 distribution, except one described as a new species, *Notholca hollowdayi*, which

further research showed to be a Subantarctic endemic also present at the Kerguelen Islands (De Smet, 2001b).

Russell (1959) reported a single monogonont, *Trichocerca bidens*, from a boggy creek at Macquarie Island (54°38'S, 158°52'E). Investigations by Dartnall (1993) and Dartnall et al. (2005) on plankton of miscellaneous water bodies resulted in 41 rotifer taxa (9 bdelloids, 32 monogononts); the monogonont species described and figured (Dartnall, 1993) as *Epiphanes senta* comprises two species: the correctly identified *E. senta* but also *E. cf. daphnicola*, an epibiont of anomopods, formerly known as *Proales daphnicola* (see Wilts et al., 2012). Most of the rotifers were common cosmopolitan species, except *Encentrum permolle giganthum* and *Keratella sancta*.

A preliminary note on the rotifer fauna of benthic vegetation from South Georgia (54°30'S, 37°00'W) was presented by Dartnall & Heywood (1980). Investigations were later on extended to plankton, benthos, and benthic vegetation of lakes, pools, streams and wallows, and mosses from flooded carpets (Hansson et al., 1996; Dartnall & Hollowday, 1985; Dartnall, 2005a, c). Altogether, 59 taxa (12 bdelloids, 47 monogononts) were recorded. The majority are common widespread species, except for *N. walterkoste*i and the newly described taxa (Dartnall & Hollowday, 1985) *Mytilina mucronata longicauda*, to date only known from the type locality (Maiviken Lake), and *Trichocerca rattus globosa*, apparently restricted to South Georgia, Signy, and the Falkland Islands (Dartnall & Hollwedel, 2007). *Keratella heywoodi* described by Dartnall (2005c) from the Tonsberg Peninsula is synonymous to *K. kostei* described from

255 Patagonia (Paggi, 1981), and also recorded from the Falkland Islands (Dartnall,
256 2005a; Dartnall & Hollwedel, 2007).

257

258 **Methods**

259 *Literature search*

260 Checklist of rotifers from Antarctica and Subantarctica were previously compiled
261 by José de Paggi & Koste (1984), Dartnall & Hollowday (1985), Sudzuki (1988),
262 Kutikova (1991), and Vekhov (1993); Antarctic records are also to be found in
263 Segers (2007) and Jersabek & Leitner (2013). The 'Antarctic Region' in Segers
264 (2007, 2008) and Jersabek & Leitner (2013), however, also included the cool-
265 temperate, Ocean-temperate biogeographic provinces (South Atlantic, South
266 Indian and South Pacific islands) and part of the Indian South subtropical
267 province. Vellasco-Castrillón et al. (2014a) listed the species found south of 60°S,
268 inclusive Maritime Antarctic records from the Antarctic Peninsula and the South
269 Shetland and South Orkney Islands. We started our literature review from the
270 above checklists but, in order to minimize inaccuracies as much as possible, we
271 expanded the literature search through available reference databases (e.g.
272 Google Scholar, Scopus, Web of Science, Zoological Record), and consulted each
273 of the 93 references used in this study.

274 A major problem to identify valid species and verifiable species records
275 was the often undocumented or poorly documented nature of the records. In
276 order not to lose information, both the names used in the publications, and the
277 currently valid names are provided in Supplementary File S1. The valid names in

278 use are those that have been reported by the List of Available Names (LAN) for
279 phylum Rotifera (Segers et al., 2012, but see also Jersabek & Leitner, 2013).
280 Another problem was that some species could represent contamination, as
281 previously explained in the chapter on the history of rotifer research: our
282 decision was to keep these records in the database, but adding a note on their
283 status of potential contaminations.

284

285 *Hypotheses testing*

286 To answer the first of our question – whether the number of species of rotifers
287 was different between Antarctica and Subantarctica – we grouped all the records
288 in three major geographic units generally accepted for the area (Stonehouse,
289 1982; Lewis-Smith, 1984; Ochyra, 1998; Van der Putten et al., 2012): (1)
290 Subantarctica, representing all the islands at latitudes between 45° and 60° S,
291 including the South Atlantic Ocean Province (South Georgia), the South Pacific
292 Ocean Province (Macquarie Island) and the South Indian Ocean Province (Prince
293 Edward Islands, Iles Crozet, Iles Kerguelen and the Heard Island group); (2)
294 Maritime Antarctica, including the other islands and archipelagos in the South
295 Atlantic (namely South Shetlands, South Orkneys, South Sandwich and
296 Bouvetøya) and the Antarctic peninsula (Palmer Land and Graham Land); (3)
297 Continental Antarctica, representing all the rest of the continent and the
298 surrounding islands (Figure 1). Our question was to assess whether species
299 richness in these areas was significantly different, controlling for sampling bias.
300 Differential sampling effort may produce strong biases in our views on biological
301 diversity, especially in understudied organisms such as rotifers (Fontaneto et al.,

2012a). Thus, we explicitly included sampling bias in our models in two ways, either as the number of papers published in each area, or as the number of records for each area. In the results section of the manuscript, for this and all the other analyses, we report the results of sampling effort estimated as the number of papers, whereas we report the results of sampling effort estimated as the number of records in Supplementary File S2. We tested species richness (1) of all rotifers, (2) of only bdelloids, and (3) of only monogononts. We used chi-squared tests, but when expected counts were below five, p-values were obtained from Fisher's exact test, which is less biased by low sample size than chi-squared test; Yates' continuity correction was applied in cases with only one degree of freedom (Crawley, 2013). The rationale for the tests is that non-significant results would suggest species richness being proportional to the number of papers in the contingency tables; thus, indicating sampling bias. On the other hand, significant differences indicate that differences in species richness are unrelated to sampling intensity.

To answer the second question – whether some biogeographical sector was richer than the other sectors in continental Antarctica, regardless of the differences in sampling efforts – we divided all the records in Antarctica (excluding Subantarctica) into the seven traditional biogeographical sectors (Pugh, 1993; McInnes & Pugh, 1998; Velasco-Castrillón et al., 2014a, b) of (1) Maud (between 30° W and 30° E), (2) Enderby (between 30° and 90° E), (3) Wilkes (between 90° and 150° E), (4) Scott (between 150° E and 150° W), (5) Byrd (between 90° and 150° W), (6) Ronne (between 30° and 90° W, including only Continental Antarctica), and (7) Peninsula (between 30° and 90° W,

including only Maritime Antarctica) (Figure 1). As in the previous question, we tested species richness of all rotifers, of only bdelloids, and of only monogononts, controlling for either the number of papers or the number of records. We used chi-squared tests, with p-values obtained from Fisher's exact test when sample size was too low.

To answer the third question – whether a latitudinal gradient of species richness existed in rotifers – we implemented Generalized Linear Models (GLMs) with species richness (of all rotifers, only of bdelloids, or only of monogononts) as response variable. Data were grouped in latitudinal bins of 5 degrees and the median value of each bin used as a measure of latitude for the bin. Such values of latitude were entered as explanatory variable both as linear and quadratic terms in order to detect possible hump-shaped distributions, common in latitudinal gradients of biological diversity (Rahbek, 2005). The number of papers (or of records) was entered in the models as a way to control for spurious results due to sampling efforts correlating with latitude (Fontaneto et al., 2012a), for example if fewer papers were published in more remote areas further South. The models assumed a Poisson distribution, appropriate for count data as species richness (Crawley, 2013). To assess the effects of latitude, quadratic latitude and sampling bias, we started with the simplest model (only latitude as explanatory variable), and then tested whether inclusion of the squared term of latitude, and of sampling bias (number of papers or number of records) significantly improved the fit of the model. Such step was performed explicitly through analysis of variance (ANOVA) with chi-squared statistics for hierarchical models, and also qualitatively by comparing the improvement in model fit calculated by

the pseudo-R-squared of all the GLMs (Crawley, 2013). Pseudo-R-squared values are a measure of model fit for GLMs, similar, but not fully equivalent, to R-squared values in linear models (Faraway, 2006).

All statistical analyses were performed in R 3.1.2 (R Core Team, 2014). The geographical representation of Antarctica and the records of rotifers were obtained with the R package *ggplot2* version 1.0.0 (Wickham, 2009).

Results

Database

The dataset contained 1165 records of rotifers published in 93 papers, for a total of 897 records identified to species level, 217 to genus level, and 51 to family or higher taxonomic level (Supplementary File S1).

Overall, 33 species of bdelloids and 120 species of monogononts were found in Antarctica and Subantarctica. The proportion of species of bdelloids and monogononts known overall for Antarctica and Subantarctica well represent the global proportion of all rotifers, with 461 species known worldwide for bdelloids and 1570 for monogononts (Segers, 2007; Fontaneto & De Smet, 2015) (chi-squared test with Yates' continuity correction = 0.069, $p = 0.792$).

The third group of rotifers, seisonaceans, was also reported in the region, with an undetermined species (Leung & Mohr, 1966). Only four species of this group are known worldwide (Fontaneto & De Smet, 2015).

Biogeographical patterns

372 Three main biogeographic regions are present in the far South (Figure 1): the
373 number of rotifer species was higher in Subantarctica (n=103), compared to the
374 number of species in Continental (n=59) and Maritime Antarctica (n=55).
375 Significantly more species were found in Subantarctica, regardless of sampling
376 effort estimated as the number of papers published in each area (chi-squared
377 test= 18.8, $p = 0.00008$). The same scenario was supported when estimating
378 sampling efforts as the number of records (Supplementary File S2). Such
379 significant difference was all due to the higher number of monogononts in
380 Subantarctica (n = 96) than in Continental (n=32) and Maritime Antarctica
381 (n=39) (Supplementary Figure S1), significantly higher regardless of the number
382 of published papers (chi squared test = 12.9, $p = 0.001$). On the other hand, the
383 number of species in bdelloids, even if higher in Continental Antarctica (n=27)
384 than in Maritime Antarctica (n=16) and Subantarctica (n=7), was proportional to
385 the number of published papers (chi-squared test = 3.1, $p = 0.206$)
386 (Supplementary Figure S1).

387 Seven main biogeographic areas are usually identified in Mainland
388 Antarctica (Figure 1). The Peninsula, with 19 papers, was the most studied area,
389 followed by the Scott area around the Ross Sea, with 16 papers. Scott
390 represented the most studied area in Continental Antarctica. No studies on
391 rotifers exist yet for Byrd and Ronne area. The number of rotifer species found in
392 the different sectors varied between 18 (Maud) and 55 (Peninsula), and was not
393 proportionally different to the number of published papers (chi-squared test =
394 3.9, $p = 0.406$). Regarding only monogononts, no study has been performed yet
395 in Maud either; the richest area, with 39 species, was Peninsula, which was also

the most intensively studied, with 15 papers (Supplementary Figure S2). The number of species found in each area was proportional to the number of published papers (chi-squared test = 1.8, $p = 0.613$). For bdelloids, the richest area was Maud, with 18 species, whereas the most studied area was Scott, with 15 papers (Supplementary Figure S2). Nevertheless, the number of species known in the different areas was not significantly different from the expectations based on the number of published papers (chi-squared test = 4.5, $p = 0.336$).

Regardless of the biogeographic subdivisions, latitudinal gradients in diversity are present in Antarctic rotifers: the best model explaining species richness in latitudinal bins of five degrees of latitude contained only the absolute value of latitude as an explanatory factor (GLM: estimate $\pm$ standard error = -0.04 ± 0.005 , $p < 0.00001$) with a high fit (Pseudo R-square = 0.927). When including the quadratic term of latitude and/or sampling bias expressed as the number of published papers, no significant improvements in the model fit could be found (ANOVA chi-square tests not significant).

The best model for monogononts included both latitude and the confounding factor of sampling bias measured as the number of published papers per latitudinal bin (Table 1, Figure 2). Including the squared term of latitude did not improve model fit (anova: $p = 0.72$), whereas not including the number of papers significantly diminished model fit (anova: $p = 0.0019$). A completely different picture appeared for bdelloids: the best model included latitude in both its linear and quadratic terms, with an increase in species richness at higher latitudes (Table 1, Figure 2). Including the confounding factor of published papers did not improve model fit (ANOVA, chi-square test: $p =$

0.277). The same qualitative results were present when using the number of records instead of the number of papers as a proxy for sampling bias (Supplementary File S2).

Discussion

Antarctic rotifers

The history of research on Antarctic rotifers is long and growing and has clearly revealed rotifers as one of if not the main faunistic component of the region. Rotifers have been known to be common and abundant in Antarctic regions since the time of Shackleton's explorations (Murray, 1910a; Dartnall & Hollowday, 1985). Our review provides the first detailed quantitative assessment of their diversity in the area, up-dating and refining previous surveys of total rotifer species numbers (Convey, 2005; Pocięcha, 2010) in the three Antarctic biogeographical zones. Overall, out of more than 2,000 known species of rotifers (Segers, 2007; Fontaneto & De Smet, 2015), at least 154 species are present in the Antarctic region, including Continental (59 spp.) and Maritime Antarctica (55 spp.), and the Subantarctic islands (103 spp.). Thus, about 8% of rotifer diversity is found in the Southern polar region. The number of species in the three groups of rotifers, bdelloids (n=461), monogononts (n~1,570) and seisonaceans (n=4), is also represented with similar relative proportions in Antarctica (33, 120, and 1, respectively).

Rotifers are abundant in almost every habitat that has been sampled in the Antarctic regions, including permanent water bodies in freshwater, brackish

and marine waters, but also mosses, lichens, soils, and peculiar habitats such as glaciers, meltwater pools, algal mats, and cryoconite holes (Sohlenius & Boström, 2005; Zawierucha et al., 2015). Together with nematodes and tardigrades, rotifers represent an ubiquitous presence in Antarctica (Convey & McInnes, 2005).

Sampling bias

The number of records of Antarctic rotifers is not very high, 1165, from 93 published papers. With this relatively low number in comparison to the large geographical area, the expectation to have some sort of bias in sampling efforts is plausible.

An important bias could be taxonomic, specifically the propensity to sample and report mostly monogononts or mostly bdelloids but not both. Experts usually work only on one of the two groups: this is the case in most studies on freshwater habitats in temperate or tropical areas (Wallace et al., 2006; Fontaneto & De Smet, 2015), whereas in our review of Antarctic studies such bias seems to be negligible: out of 93 consulted papers, 5 reported only “Rotifera” without any clear identification, and, among the other 88 papers, more than half, 47 (53%), reported both groups, 22 (25%) only bdelloids, and 19 (22%) only monogononts. Thus, apparently, sampling effort is not biased towards bdelloids or monogononts; this seems to be the case notwithstanding the major differences in ecology between the two groups: bdelloids and monogononts have rather different desiccation and freezing tolerance (Ricci,

2001), so that samples with bdelloids can be kept frozen or dry for long time
(Fontaneto et al., 2012b), and animals brought to the lab when quiescent.

A second kind of bias is ecological: monogononts are present mostly in
aquatic environments (i.e. water bodies), whereas bdelloids also, and
predominantly, live in limno-terrestrial environments (i.e. mosses, lichens, soils)
(Wallace et al., 2006; Fontaneto & De Smet, 2015). Our literature survey points to
a large variety of habitats that have been sampled and analysed, and we cannot
find any evidence of such bias, or any way to quantitatively assess its influence.

Another type of bias is geographic: some areas may receive more
attention than others. This is especially true in Antarctica (Peat et al., 2007),
where most sampling campaigns are limited to the ice-free localities that could
be reached from permanent research stations (Frenot et al., 2005). Moreover, a
strong effect of geographic sampling bias is already known in monogononts
(Dumont, 1983; Fontaneto et al., 2012a). Such kind of bias was surely present in
our dataset: some biogeographic areas in Continental Antarctica have not been
sampled at all. Moreover, especially for monogononts, we could estimate the
effect of bias in our statistical models on latitudinal gradients in diversity;
nevertheless, we acknowledge that we did it in a rather rudimentary way. Yet,
without more data and more accurate studies on rotifer diversity in Antarctica,
our explicit assessment into statistical models was the only reliable approach.
Moreover, for bdelloids such bias seems not to be relevant in the analysis of
latitudinal gradients of biodiversity.

Latitudinal gradients

If we assume that our statistical models correctly accounted for sampling biases, two different scenarios appear. Species diversity of monogononts diminishes at higher latitudes, according to a general trend in biogeographical studies at large scale (Hillebrand, 2004; Rahbeck, 2005); such pattern for monogononts is robust even after controlling for sampling bias.

The latitudinal gradient for bdelloids is not so straightforward, it has a hump-shaped relationship, and seems to be unaffected by sampling bias. If the pattern is accurate, it means that bdelloids are very diverse at high latitudes, between 60° and 75° S, slightly less diverse at latitudes between 75° and 80° S, whereas they have the lowest diversity at lower absolute latitudes in Subantarctica, between 45° and 55° S. We can only speculate on the potential drivers of such unusual pattern. It is possible that bdelloids become better competitors or are less affected by predation in conditions less suitable for other microscopic fauna, for example when high doses of ionising radiation (Gladyshev & Meselson, 2008) or repeated cycles of thawing or desiccation appear (Ricci et al., 2007). Alternatively, the effect of parasites, known to limit the survival of bdelloids (Wilson & Sherman, 2010; Wilson, 2011), could be relieved at higher absolute latitudes if parasites cannot survive well under harsher conditions. We have anecdotal indications of higher prevalence of endoparasites in monogononts in Subantarctica than in Antarctica (De Smet, personal observation), but we cannot quantify this statement. Overall, using data gathered from the literature in this review, we cannot assess any clear and supported driver to explain the unusual latitudinal gradient in diversity of bdelloids. Only

further studies, specifically devoted to test explicit hypotheses on the pattern we observed, will be able to suggest the mechanisms that could account for the peculiar biological and ecological features of bdelloids that may act on their biodiversity pattern in the Southern regions.

Antarctic biogeography

There are significant differences in species richness among the biogeographic areas: at the large scale between Subantarctica, Continental, and Maritime Antarctica; and at the smaller scale between the biogeographic sectors. Yet, any discussion on potential mechanisms underlying those differences may be premature due to insufficient data. What seems to be a consistent pattern is that the Scott sector is poorer in bdelloids than the Peninsula sector, even if more papers and more records are available for the former than the latter sector. Thus, we posit the general conclusion of a broad-scale biogeographic difference between the Antarctic Peninsula and the area around the Ross Sea (Peat et al., 2007; McGaughan et al., 2010). Surely, given the feasibility of sampling rotifers in remote areas and their extreme abundance and ubiquity in the Antarctic regions, our hope is that research on these organisms would find a boost and more data will become available in the near future for more accurate analyses.

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844

845 Figure caption

846

847 Figure 1. Map of Antarctica with a representation of the sites where the
848 rotifer records at species level were reported: red circles represent those in
849 Continental Antarctica, blue triangles those in Maritime Antarctica, and yellow
850 squares those in Subantarctica. The seven biogeographic subdivisions of
851 Continental (Maud, Enderby, Wilkes, Scott, Byrd, Ronne) and Maritime
852 Antarctica (Peninsula) are marked on the map.

853

854

855 Figure 2. Species richness of monogononts and bdelloids in relationship to
856 latitude. Size of the circles is proportional to the number of papers. The
857 regression lines represent the best model fit between linear and/or quadratic
858 relationships (see the text for details).

859 Table 1. Results of the selected Generalized Linear Models on the influence of
860 latitude (linear and quadratic term) and sampling bias (number of published
861 papers) on the number of known species of monogononts (Pseudo R-squared =
862 0.933) and bdelloids (Pseudo R-squared = 0.930).

863

	Monogononta		Bdelloidea	
variable	estimate ± s.d.	p	estimate ± s.d.	p
(intercept)	7.28 ± 0.44	<0.00001	-14.79 ± 6.20	0.017
latitude	-0.07 ± 0.01	<0.00001	0.51 ± 0.19	0.009
latitude^2	-	-	-0.00 ± 0.00	0.015
papers	0.06 ± 0.02	0.0025	-	-

864

865 Supplementary File S1. The database

866 ID valid_name original_name group level
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870 300 Philodina gregaPrihailodina gregaBridaelloidea species
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872 353 Cephalodella spC.ephadolella spM. onogononta genus
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910 Supplementary File S1
911 Click here to download attachment to manuscript: Suppl File S1.xlsx
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1110	<u>903 Reticula gelidaReticula gelidaMonogononta species</u>
1111	<u>904 Reticula nyssaReticula nyssaMonogononta species</u>
1112	<u>905 Rotaria rotatoria Rotaria rotatoria Bdelloidea species</u>
1113	<u>906 Adineta barbataAdineta barbataBdelloidea species</u>
1114	<u>907 Adineta gracilisAdineta gracilisBdelloidea species</u>
1115	<u>908 Adineta sp. Adineta sp. Bdelloidea genus</u>
1116	<u>909 Bryceella stylataBryceella stylataMonogononta species</u>
1117	<u>910 Cephalodella auCreicpuhlaltoadella auMriocunloagtoanonta species</u>
1118	<u>911 Cephalodella deCleicpahtalodella deMlicoantoagononta species</u>
1119	<u>912 Cephalodella foCrefipcahtaalodella foMrfiocnaotagononta species</u>
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1121	<u>914 Cephalodella mCceegpahloacleopdheallala mMegoanloocgeopnhoanltaa species</u>
1122	<u>915 Cephalodella spC. ephalodella spM. onogononta genus</u>
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1127	<u>920 Encentrum sp. Encentrum salinMuomnogononta genus</u>
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1130	<u>923 Euchlanis sp. Euchlanis dilataMtao pnaorgvoanonta genus</u>
1131	<u>924 Habrotrocha coHnastbrriocctarocha coBndsetrilcotiadea species</u>
1132	<u>925 Habrotrocha spH. abrotrocha spB. delloidea genus</u>
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1135	<u>928 Lecane flexilis Lecane flexilis Monogononta species</u>
1136	<u>929 Lecane latissimaLecane latissimaMonogononta species</u>
1137	<u>930 Lecane lunaris Lecane lunaris Monogononta species</u>
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1142	<u>935 Lepadella triptelreapadella tripteMraonogononta species</u>
1143	<u>936 Lindia torulosa Lindia torulosaMonogononta species</u>
1144	<u>937 Macrotrachela Mcoanccriontnraachela Bcdnedclionindaea species</u>
1145	<u>938 Macrotrachela Mspa. crotrachela Bspd.elloidea genus</u>
1146	<u>939 Monommata spM. onommata spM. onogononta genus</u>
1147	<u>940 Mytilina mucroMnayttai llinna gmicuacurdoaMnaotna olognogniocnautadaspecies</u>

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1704 [620 Lepadella patelLlaepadella patelMlaonogononta species](#)
1705 [621 Lepadella patelLlaepadella patelMlaonogononta species](#)
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1707 [735 Proales reinharPdrtoi ales reinharMdtoi nogononta species](#)
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1750 [2 Rotifera Rotifera unknown phylum](#)
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1775	282 Philodina antarPcthicilaodina antarBctdicealloidea species
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1777	295 Philodina gregaPrihailodina gregaBridaelloidea species
1778	296 Philodina gregaPrihailodina gregaBridaelloidea species
1779	297 Philodina gregaPrihailodina gregaBridaelloidea species
1780	403 Cephalodella teCneupiohralodella teMnuoinoorgononta species
1781	420 Collotheca ornaCtoallotheca ornaMtao cnoorgnountoanta species
1782	421 Collotheca ornaCtoallotheca ornaMtao cnoorgnountoanta species
1783	466 Encentrum sp. Encentrum sp. Monogononta genus
1784	527 Epiphanes sentaEpiphanes sentaMonogononta species
1785	22 Rotifera Rotifera unknown phylum
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1787	318 Philodina gregaPrihailodina gregaBridaelloidea species
1788	184 Macrotrachela Mspa. crotrachela Bspd.elloidea genus
1789	622 Lepadella patelLlaepadella patelMlaonogononta species
1790	5 Rotifera Rotifera unknown phylum
1791	374 Cephalodella caCteepllihnaalodella caMteollninoagononta species
1792	551 Epiphanes sentaEpiphanes sentaMonogononta species
1793	639 Lepadella patelLlaepadella patelMlaonogononta species
1794	687 Notholca salinaNotholca salinaMonogononta species
1795	706 Notholca walteNrkooshtoeleica walteMrkosntoegiononta species
1796	585 Lecane closteroLceecracnae closteroMceorncaogononta species
1797	812 Rotifera Rotifera unknown phylum
1798	813 Philodina gregaPrihailodina gregaBridaelloidea species
1799	814 Philodina gregaPrihailodina gregaBridaelloidea species
1800	815 Philodina gregaPrihailodina gregaBridaelloidea species
1801	816 Philodina gregaPrihailodina gregaBridaelloidea species
1802	817 Cephalodella caCteepllihnaalodella caMteollninoagononta species
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1807	416 Collotheca camCpoalnoutlahteaca gracMilipoensogononta species
1808	434 Collotheca ornaCtoallotheca ornaMtao cnoorgnountoanta species
1809	520 Eosphora najasEosphora najasMonogononta species
1810	555 Euchlanis dilataEtuachlanis dilataMtaonogononta species
1811	695 Notholca walteNrkooshtoeleica walteMrkosntoegiononta species
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1813	752 Ptygura melicerPttaygura melicerMtaonogononta species
1814	773 Scardium longiSccaurdiduimum longiMcaoundougmononta species
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1816	129 Callidina sp. Callidina sp. Bdelloidea genus
1817	130 Callidina sp. Callidina sp. Bdelloidea genus
1818	131 Callidina sp. Callidina sp. Bdelloidea genus
1819	351 Cephalodella spC.ephadella spM. onogononta genus
1820	365 Cephalodella caCteepllihnaalodella caMteollninoagononta species
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1822	449 Colurella coluruCsolurella coluruMs onogononta species
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1824	570 Keratella sanctaKeratella sanctaMonogononta species
1825	596 Lecane sp. Lecane mawsonMi onogononta genus
1826	605 Lepadella acumLinepataadella acumMinoantaogononta species
1827	608 Lepadella elliptLiceapadella elliptMicaonogononta species
1828	616 Lepadella patelLlaepadella patelMlaonogononta species
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1891	<u>170 Habrotracha coHnastbrriocctarocha coBndsetrlilcotiadea species</u>
1892	<u>176 Habrotracha eluHsaabrotracha eluBsdaelloidea species</u>
1893	<u>181 Habrotracha triHdaebnrsotrocha triBddeensloidea species</u>
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1896	<u>211 Macrotrachela Mhaabcirtoatrachela Bhdabeliltoidea species</u>
1897	<u>218 Macrotrachela Minsaocriotatrachela Bindseolliotaidea species</u>
1898	<u>221 Macrotrachela Mlibaecrraotrachela Blibderllaoidea species</u>
1899	<u>226 Macrotrachela Mtimacidroatrachela Btidmeildloidea species</u>
1900	<u>234 Mniobia sp. Mniobia sp. Bdelloidea genus</u>
1901	<u>235 Mniobia sp. Mniobia sp. Bdelloidea genus</u>
1902	<u>240 Mniobia symbioMtinciaobia symbioBtdicealloidea species</u>
1903	<u>64 Adineta barbataAdineta barbataBdelloidea species</u>
1904	<u>74 Adineta gracilisAdineta gracilisBdelloidea species</u>
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1911	<u>114 Adineta steineriAdineta steineriBdelloidea species</u>
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1914	<u>117 Adineta steineriAdineta steineriBdelloidea species</u>
1915	<u>125 Adineta vaga Adineta vaga Bdelloidea species</u>
1916	<u>126 Adineta vaga Adineta vaga Bdelloidea species</u>
1917	<u>127 Adineta vaga Adineta vaga Bdelloidea species</u>
1918	<u>143 Habrotracha spH. abrotracha spB. delloidea genus</u>
1919	<u>144 Habrotracha spH. abrotracha spB. delloidea genus</u>
1920	<u>171 Habrotracha coHnastbrriocctarocha coBndsetrlilcotiadea species</u>
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1923	<u>177 Habrotracha eluHsaabrotracha eluBsdaelloidea species</u>
1924	<u>178 Habrotracha eluHsaabrotracha eluBsdaelloidea species</u>
1925	<u>182 Habrotracha triHdaebnrsotrocha triBddeensloidea species</u>
1926	<u>190 Macrotrachela Mamabcrigoutraachela Bamdebllioguidaea species</u>
1927	<u>191 Macrotrachela Mamabcrigoutraachela Bamdebllioguidaea species</u>
1928	<u>212 Macrotrachela Mhaabcirtoatrachela Bhdabeliltoidea species</u>
1929	<u>213 Macrotrachela Mhaabcirtoatrachela Bhdabeliltoidea species</u>
1930	<u>214 Macrotrachela Mhaabcirtoatrachela Bhdabeliltoidea species</u>
1931	<u>215 Macrotrachela Mhaabcirtoatrachela Bhdabeliltoidea species</u>
1932	<u>219 Macrotrachela Minsaocriotatrachela Bindseolliotaidea species</u>
1933	<u>220 Macrotrachela Minsaocriotatrachela Bindseolliotaidea species</u>
1934	<u>222 Macrotrachela Mlibaecrraotrachela Blibderllaoidea species</u>
1935	<u>223 Macrotrachela Mligaclarotatrachela Bcfd. elilglouildaetaa species</u>
1936	<u>225 Macrotrachela Mnixaacrotrachela Bndixealloidea species</u>
1937	<u>227 Macrotrachela Mtimacidroatrachela Btidmeildloidea species</u>
1938	<u>236 Mniobia sp. Mniobia sp. Bdelloidea genus</u>
1939	<u>237 Mniobia sp. Mniobia sp. Bdelloidea genus</u>
1940	<u>238 Mniobia sp. Mniobia sp. Bdelloidea genus</u>
1941	<u>241 Mniobia symbioMtinciaobia symbioBtdicealloidea species</u>
1942	<u>242 Otostephanos tOotroqsutaetpuhsanos tBodrgeulloatidues species</u>
1943	<u>97 Adineta grandisAdineta grandisBdelloidea species</u>
1944	<u>98 Adineta grandisAdineta grandisBdelloidea species</u>
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1946 [319 Philodina gregaPrihailodina gregaBridaelloidea species](#)
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2003 | [882 Adineta gracilisAdineta gracilisBdelloidea species](#)
 2004 | [883 Adineta sp. Adineta sp. Bdelloidea genus](#)
 2005 | [884 Adineta sp. Adineta sp. Bdelloidea genus](#)
 2006 | [885 Philodina gregaPrihailodina gregaBridaelloidea species](#)
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 2009 | [888 Philodina gregaPrihailodina gregaBridaelloidea species](#)
 2010 | [892 Adineta gracilisAdineta gracilisBdelloidea species](#)
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 2015 | [990 Adineta sp. Adineta sp. Bdelloidea genus](#)
 2016 | [991 Philodina gregaPrihailodina gregaBridaelloidea species](#)
 2017 | [992 Philodina sp. Philodina sp. Bdelloidea genus](#)
 2018 | [840 Adineta barbataAdineta barbataBdelloidea species](#)
 2019 | [843 Philodina alataPhilodina alataBdelloidea species](#)
 2020 | [858 Adineta grandisAdineta grandisBdelloidea species](#)
 2021 | [859 Habrotricha coHnastbrrioccttarocha coBndsetrlilcotiadea species](#)
 2022 | [860 Philodina alataPhilodina alataBdelloidea species](#)
 2023 | [861 Philodina gregaPrihailodina gregaBridaelloidea species](#)
 2024 | [334 Philodina gregaPrihailodina gregaBridaelloidea species](#)
 2025 | [803 Philodina antarPcthicilaodina antarBctdicealloidea species](#)
 2026 | [804 Philodina antarPcthicilaodina antarBctdicealloidea species](#)
 2027 | [805 Philodina gregaPrihailodina gregaBridaelloidea species](#)
 2028 | [806 Habrotricha coHnastbrrioccttarocha cf.B cdoenllsotirdicetaa species](#)
 2029 | [807 Adineta vaga Adineta vaga Bdelloidea species](#)
 2030 | [808 Adineta sp. Adineta sp. Bdelloidea genus](#)
 2031 | [809 Philodina alataPhilodina alataBdelloidea species](#)
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4208 [Velasco-Castrillon A, Page TJ, Gibson JAE & Stevens MI. 2014a. Surprisingly high levels of biodiversity](#)
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4265 [erroneously reported as from Falkland Islands by Donner \(1980\) according to Dartnall & Hollowday](#)
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1 Supplementary File S2. Results of the analyses when sampling bias was
assessed
2 as the number of records instead of as the number of papers.
3 Comparing Subantarctica, Continental, and Maritime Antarctica, significantly
4 more species were found in Subantarctica in comparison to sampling effort
5 estimated as the number of records in each area (chi-squared = 36.6, $p <$
6 0.00001). The number of species of monogononts in the three areas was
7 proportional to the number of records (chi squared = 3.9, $p = 0.141$). The
8 number of species of bdelloids was significantly higher in Continental
Antarctica
9 than in Maritime Antarctica and Subantarctica ($n=7$), irrespective of the
number
10 of records (chi-squared = 27.5, $p < 0.00001$).
11 The number of species found in the different sectors of mainland
12 Antarctica was not proportional to the number of known records (chi-
squared =
13 19.1, $p = 0.0007$) with Peninsula significantly richer and Scott significantly
14 poorer than expected. Regarding monogononts, the number of species found
in
15 each area was proportional to the number of records (chi-squared = 1.8, $p =$
16 0.612). For bdelloids, the number of species known in the different areas was
not
17 proportional to the number of records (chi-squared = 14.9, $p = 0.0048$), with
18 Scott significantly poorer than expected.
19 Regarding latitudinal gradients in diversity, the best model explaining
20 species richness in latitudinal bins of five degrees of latitude contained only
the
21 absolute value of latitude as an explanatory factor (GLM: estimate $\pm$ standard
22 error = -0.04 ± 0.005 , $p < 0.00001$); including sampling bias expressed as the
23 number of records did not provide a significant improvement in the model fit
24 (anova: $p = 0.896$). Considering only monogononts, the best model included
both
25 latitude and the number of records (Supplementary Table S1). Including the
26 squared term of latitude did not improve model fit (anova: $p = 0.363$),
whereas
27 not including the number of records significantly diminished model fit
(anova: p
28 = 0.031). Considering only bdelloids, the best model included latitude in both
its
29 linear and quadratic term (Supplementary Table S1). Including the number of
30 records did not improve model fit (anova: $p = 0.458$).
31 Supplementary Table S1. Results of the selected Generalized Linear Models on
32 the influence of latitude (linear and quadratic term) and sampling bias
(number
33 of records) on the number of known species of monogononts (Pseudo R-
squared
34 = 0.891) and bdelloids (Pseudo R-squared = 0.930).
Monogononta Bdelloidea
variable estimate $\pm$ s.d. p estimate $\pm$ s.d. p

4369 [\(intercept\) 5.55 ± 1.06 <0.00001 -14.79 ± 6.20 0.017](#)
 4370 [latitude -0.04 ± 0.01 0.00096 0.51 ± 0.19 0.009](#)
 4371 [latitude^2 - -0.00 ± 0.00 0.015](#)
 4372 [records 0.01 ± 0.00 0.0317 - -](#)
 4373 [35](#)
 4374 [Supplementary File S2](#)
 4375 [Click here to download attachment to manuscript: Suppl File S2.docx](#)
 4376 [Continental Maritime Subantarctica](#)
 4377 [Bdelloidea](#)
 4378 [richness](#)
 4379 [0 5 10 15 20 25](#)
 4380 [Continental Maritime Subantarctica](#)
 4381 [Monogononta](#)
 4382 [0 20 40 60 80](#)
 4383 [Continental Maritime Subantarctica](#)
 4384 [number of records](#)
 4385 [0 50 100 150 200 250](#)
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 4387 [0 50 100 150 200 250](#)
 4388 [Continental Maritime Subantarctica](#)
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 4390 [0 5 10 15 20 25 30 35](#)
 4391 [Continental Maritime Subantarctica](#)
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 4393 [Supplementary Figure S1](#)
 4394 [Click here to download attachment to manuscript: Suppl Figure S1.pdf](#)
 4395 [Enderby Maud Peninsula Scott Wilkes](#)
 4396 [Bdelloidea](#)
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 4399 [Enderby Maud Peninsula Scott Wilkes](#)
 4400 [Monogononta](#)
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4403 Supplementary File S2. Results of the analyses when sampling bias was assessed
 4404 as the number of records instead of as the number of papers.

4405

4406 Supplementary Figure S1. Number of species, records and published papers for
 4407 bdelloids and monogononts in Continental Antarctica, Maritime Antarctica, and
 4408 Subantarctica.

Supplementary Figure S2. Number of species, records and published papers for bdelloids and monogononts in the five biogeographic areas where records are known: Enderby, Maud, Peninsula, Scott, and Wilkes.

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