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Species distribution within the free-living marine nematode genus *Dichromadora* in the Weddell Sea and adjacent areas

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Abstract

Studies of Antarctic, free-living, marine nematodes are mostly restricted to genus level. In the current study, the genus *Dichromadora* (Kreis, H.A., 1929. Capita Zoologica 2(7), 1–98) is analysed to species level. *Dichromadora* is one of the genera that are frequently present along the continental margin of the eastern Weddell Sea. Samples were retrieved from the 1000–2000 m depth line in the eastern Weddell Sea (Halley Bay, Vestkapp and Kapp Norvegia), South Sandwich Trench and the Drake Passage. Eight species are distinguished within the genus *Dichromadora* of which seven are new to science. Out of these seven species, five are described taxonomically: *Dichromadora weddellensis* sp. n., *Dichromadora southernis* sp. n., *Dichromadora parva* sp. n., and *Dichromadora polaris* sp. n. The two other species (*D.* spec A, *D.* spec B) receive, as to the scarcety of available specimens, no scientific name. The distribution of the *Dichromadora* species from Antarctica are discussed in the context of deep-sea (1000–2000 m) observations in Arctic, Atlantic, Pacific and Indian oceans.

1. Introduction

Free-living Nematoda are the most abundant and diverse metazoan component of the meiofauna in many marine environments (Heip et al., 1985). In particular in the deep sea they become increasingly important in terms of abundance and species richness in comparison to other taxa. They represent more than 90% of the metazoans in the

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meiofaunal size class (32–1000 µm) in soft sediments along the continental slope (Vincx et al., 1994), while their species richness increases with water depth from the shelf to bathyal regions (Lambshead and Boucher, 2003). Per sample unit of 10 cm² or per 200 individuals, more than 100 species are estimated to be present at most investigated geographical and bathymetric locations along the continental slope (Soetaert et al., 1991). The high diversification within the dominant genera is especially striking. Typical dominant genera like *Acantholaimus*, *Halalaimus* and *Thalassomonhystera* (and related monhysterids)

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can be represented by more than 10 species within the same sample (of $10\,\mathrm{cm}^2$) in soft deep-sea sediments (Vanreusel et al., 1995). The few studies on deep-sea nematode biodiversity are restricted to estimating total species numbers without providing any information about which species are present since almost all of them are new to science. It would be a tremendous task to describe taxonomically all the unknown deep-sea species within the Nematoda, but giving it a start seems the only way to gain some insight in the distribution ranges of species.

The Antarctic deep sea is interesting as a case study in relation to the distribution of species, since the Southern Ocean is characterized by an extremely constant physical environment with permanent low temperatures, a long polar night, a short summer, an extensive ice cover and a marked seasonality of primary production (Arntz and Gili, 2001; De Broyer et al., 2001). Despite this typical environment, the Antarctic marine fauna is very diverse (Brey et al., 1994; Arntz and Gili, 2001; De Broyer et al., 2001). The richest macrobenthos communities, mostly dominated by sessile suspension feeders, are found on the deeper shelf and slope (Arntz et al., 1997). The knowledge on the meiofauna at these bathyal depths is limited, and generally restricted to higher taxon level (Herman and Dahms, 1992; Fabiano and Danovaro, 1999; Vanhove et al., 1995, 1999; Lee et al., 2001a, b). These studies have confirmed the socalled meiofauna-paradox which says that in completely divergent areas many identical meiofauna taxa are found (Giere, 1993). This paradox strongly contrasts with the trend of a degree of endemism at genus and at species level observed in fish and macrofauna communities (Arntz et al., 1997).

This study will focus on the taxonomy and species distribution of the genus *Dichromadora* from mid-slope depths (1000–2000 m) in the Atlantic part of the Southern Ocean. The 1000–2000 m bathymetric region was chosen because at these depths valuable comparisons can be made with other oceans (e.g., similar depth samples are available); the genus *Dichromadora* was selected because, in contrast to other deep-sea areas in the world, the Weddell Sea slope is

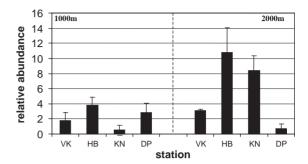


Fig. 1. Relative abundance ($\%\pm$ standard deviation) of the genus *Dichromadora* over the different stations at 1000 and 2000 m water depth.

dominated by this genus *Dichromadora* (Fig. 1) (Vanreusel et al., 1997; Vanhove et al. 1999; Vanreusel et al., 2000; Muthumbi et al., 2004). Unfortunately, only one *Dichromadora* species has been described so far (Timm, 1978). The main objective is to make taxonomic descriptions of the *Dichromadora* species in order to allow estimates of distribution ranges by looking for affinities with comparable nematode communities within and outside the Southern Ocean.

2. Method

2.1. Study material

Material was collected at five sites in the Atlantic part of the Southern Ocean: three sites on the continental slope of the eastern Weddell Sea (i.e. Kapp Norvegia, Vestkapp and Halley Bay), one site in the Drake Passage and one site in the South Sandwich Trench (Table 1 and Fig. 2). Samples were collected during the mid-to-late austral summer at the end and after the bloom period (Fischer et al., 1988, 2000). At each site three replicate samples were taken at 1000 and 2000 m water depth (except at Kapp Norvegia where six samples per depth were taken). Details are given in EPOS (Arntz et al., 1990), EASIZ II (Arntz and Gutt, 1999), LAMPOS (Arntz and Brey, 2003) and ANDEEP-reports (Fütterer et al., 2003). Meiofauna, nematode treatment, methods and observations on the nematode genera are

Table 1 Overview of the stations in the Southern Ocean (MUC: Multi-corer; MG: Multibox-corer)

Station	Campaign	Date	Region	Locality	Depth (m)	Gear
Haller Day (HD)	EDOC (14/252)	07.02.1000	SF Weddell Sea	74°32 S 29°18 W	1102	MUC
Halley Bay (HB)	EPOS (14/252)	06.02.1989	SE weddell Sea	74°32 S 29°18 W	1183	MUC
Halley Bay (HB)	EPOS (14/253)	07.02.1989	SE Weddell Sea	74°08 S 30°04 W	1958	MUC
Vestkapp (VK)	EASIZ 2 (48/092)	04.02.1998	SE Weddell Sea (Drescher Inlet)	73°34 S 22°38 W	993	MG
Vestkapp (VK)	EASIZ 2 (48/131)	08.02.1998	SE Weddell Sea (Drescher Inlet)	73°24 S 22°09W	1985	MG
Kapp Norvegia (KN)	EPOS (14/294)	20.02.1989	SE Weddell Sea	71°06 S 13°04 W	1199	MUC
Kapp Norvegia (KN)	EPOS (14/295)	21.02.1989	SE Weddell Sea	71°08 S 13°48 W	2080	MUC
Drake Passage (DP)	EASIZ 2 (48/334)	19.03.1998	near King George Island	61°27 S 58°07 W	1028	MG
Drake Passage (DP)	EASIZ 2 (48/330)	18.03.1998	near King George Island	61°21 S 58°15 W	2009	MG
South Sandwich Trench (SST)	LAMPOS (PS61-211)	16.04.2002	in the middle of the Scotia Arc	58°16 S 24°54 W	1095	MUC
South Sandwich Trench (SST)	ANDEEP (PS61-141)	23.03.2002	in the middle of the Scotia Arc	58°25 S 25°00 W	2285	MUC

described in Vanhove et al. (1999). All specimens (in total 200) of the genus *Dichromadora* (Kreis, 1929) were identified to species level, except for the juveniles (which are impossible to distinguish).

2.2. Taxonomy

Type specimens are deposited in the collection of UGMD (Zoology Museum, Ghent University).

Drawings were made with a Leica DMLS microscope. All measurements are in micrometers and curved structures are measured along the arc. The abbreviations of the used measurements are: a = body length divided by maximum body diameter, b = body length divided by oesophagal length, c = body length divided by tail length, c' = tail length divided by anal body diameter, V = distance from head to vulva, V% = V divided by body length, L = total body length, cbd = cor-

responding body diameter, M = maximum body diameter, formula: distance from anterior to

 $\frac{\text{Head end of the pharynx } M(\text{vulva}) \text{ anus}}{\text{cbd}}$

Andrassy's formula is used to calculate the individual nematode biomass (Andrassy, 1956).

3. Results

Out of the 200 *Dichromadora* specimens studied in the Southern Ocean, eight different species were distinguished. Seven of these eight species were new to science and five of these are described in detail. Two species are described but not named yet since they were each represented by only two individuals. At most six species were counted per

site (Table 2) although on the average only 3.6 species were found.

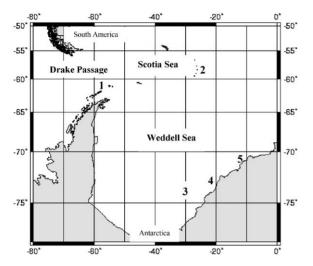


Fig. 2. Map of the Atlantic part of the Southern Ocean with indication of the stations: (1) Drake Passage; (2) South Sandwich Trench; (3) Halley Bay; (4) Vestkapp; (5) Kapp Norvegia.

3.1. Dichromadora weddellensis sp. n.

Type material: Five males and four females on slide numbers 104068 to 104074 in collection UGMD. Holotype male (δ_1) on slide no 104068, allotype female (φ_1) on slide no 104069.

Type locality: Antarctic deep sea, Weddell Sea: Halley Bay, station 252 (sand: 53%, silt: 42%) and station 253 (silt: 61%, clay: 29%).

Kapp Norvegia, station 294 (sand: 36%, silt: 20%) and station 295 (sand: 27%, silt: 54%).

Etymology: Name given because this is the only species present in all the samples of the Weddell Sea (from Kapp Norvegia to South Sandwich Trench area) but not observed in the Drake Passage.

Measurements:

$$\frac{-123 \text{ M } 716}{11 \text{ 17 } 29 \text{ 23}} 841$$
Holotype δ_1 : $a = 29$; $b = 6.9$; $c = 8.1$; $c' = 4.5$; spic = 37.

Table 2 Overview of the distribution of *Dichromadora* species at the 1000-2000 m line in the Weddell Sea, South Sandwich Trench and Drake Passage; each species is represented by its relative abundance (%).

	South Sandwich Trench		Halley Bay		Kapp Norvegia		Vestkapp		Drake Passage	
	1000 m	2000 m	1000 m	2000 m	1000 m	2000 m	1000 m	2000 m	1000 m	2000 m
Number of <i>Dichromadora</i> specimens studied	4	9	14	37	8	110	11	26	26	5
D. quadripapillata		10								
D. specA				5.1						
D. specB			14.3			1.9				
D. weddellensis	100	90	42.9	12.8		42.4		36.4		
D. southernis				74.3	12.5	24.4		0.9	13.3	
D. parva			42.9			1.9	33.3	0.9	6.7	
D. polarsternis				5.1	37.5	40.6	33.3	18.2	40.0	66.7
D. polaris				2.6	50.0	2.8	33.3	27.3	40.0	33.3

$$\frac{-106\ 360\ 641}{11\ 19\ 32\ 22}769$$
 Allotype \mathfrak{P}_1 : $a=24$; $b=7.2$; $c=8.3$; $c'=4.4$; $V\%=46.8$.

Paratypes:

Other &: L: 687–884; a: 27.5–31; b: 6.3–8; c: 7.6–8.7; c': 3.8–4.3; spic: 36–41.

Other $\$: L: 783–951; a: 23.8–25.3; b: 6.7–7.1; c: 7.8–8.8; c': 4.3–5.0; V%: 49.3–56.8.

3.1.1. Description

Holotype: The body has a long, cylindrical shape with a flat head and a cylindrical-conical tail (Fig. 3A). Towards the head, the body becomes only slightly narrower whereas towards

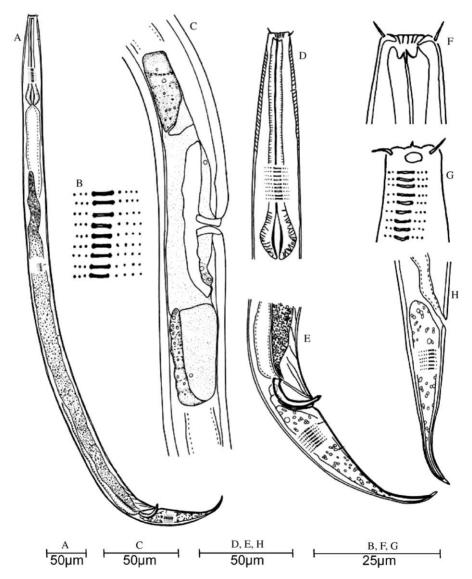


Fig. 3. *D. weddellensis* sp. n.: (A) habitus \eth_1 , (B) cuticle pattern, (C) reproductive system \Im_1 , (D) pharyngeal region \eth_1 , (E) tail \eth_1 , (F) detail head \eth_1 (internal), (G) detail head \eth_1 (external) and (H) tail \Im_1 .

the tail, the width of the body decreases markedly, especially in the second part of the tail. The tail finally ends in a 4 µm long spinneret (Fig. 3E, H). The cuticle of this species consists of transverse, homogeneous rows of distinct and large dots. These dots are more strongly pronounced in the head and tail region and seem to merge together in the head region. Along the complete length of the body the lateral differentiation is clearly visible and is bordered by 2 longitudinal rows of dots. These dots are larger than any of the other dots in a transversal row. The transverse bars over the area of the lateral differentiation connect these two larger dots with each other (Fig. 3B). Somatic setae are present in four longitudinal rows. The head is flattened and possesses four cephalic setae (6 μm long) (Fig. 3F, G). The buccal cavity contains a large dorsal and two smaller ventral teeth (Fig. 3F). The pharynx, surrounding the buccal cavity, is slightly swollen. It is 123 µm long and ends in a distinct bulb of 18 µm length and 17 μm width (Fig. 3D, F). The amphid is round to elliptical and is located at the front of the head, about at the same height of the four cephalic setae (Fig. 3G). The nerve ring and ventral gland are not observed. The reproductive system of the male is monorchic with outstretched testis (Fig. 3A). The spicules are 37 µm long, arcuate (angle of 90°), strongly cuticularised and have a slightly cephalate capitulum. The gubernaculum is 21µm long. It is a rather simple, thin feature lying against the back of the spicules (Fig. 3E,4). Microscopically, there are no precloacal supplements. The tail contains three caudal glands (Fig. 3E).

Allotype: The female strongly resembles the male. The female reproductive system is didelphic, amphidelphic with reflexed ovaries (Fig. 3C). The vulva is located just before the mid body region (V% = 46.8).

3.1.2. Differential diagnosis

Several *Dichromadora* species lack precloacal supplements. Table 3 gives an overview of these species. *Dichromadora abnormis* (Gerlach, 1953), *D. gracilis* (Kreis, 1929) and *D. strandi* (Allgén, 1940) are large nematodes that can be distinguished from the new species by their body length. In addition *D. abnormis* has slightly lower *b*- and *c*-



Fig. 4. D. weddellensis sp. n.: tail with the extended pair of spicules.

values, larger cephalic setae, smaller spicules and a distally enlarged gubernaculum. *D. gracilis* ranges in length from 1108 to 1218 µm and has a rounded head and a double oesophageal bulb. *D. strandi* has slightly higher *b*- and *c*-values and a small gubernaculum with a completely different shape.

On the other hand, D. amphidiscoides (Kito, 1981), D. antarctica (Cobb, 1914), D. acrospiculum (Timm, 1961), D. longicaudata (Muthumbi and Vinex, 1998), D. simplex (Timm, 1961) and D. tobaensis (Schneider, 1937) are nematode species that are smaller than D. weddellensis sp. n. Other differences with the new species are the much lower c-value of D. amphidiscoides, D. antarctica and D. longicaudata. Above this the circular amphid and the larger S-shaped spinneret distinguishes D. amphidiscoides. D. antarctica has smaller spicules and a larger spinneret. D. longicaudata has a higher a-value, short cephalic setae, small spicules, a small gubernaculum, and a long spinneret. D. acrospiculum has a lower b-value, shorter cephalic setae and smaller spicules. D. simplex differs in many characteristics from D. weddellensis sp. n. The three 'de Man' values of D. simplex are lower than of the new species. The cephalic setae are shorter and the spicules and gubernaculum are smaller. D. tobaensis has a sligthly lower b-value and differs in the shape of spicules and buccal cavity.

Table 3 Overview of the *Dichromadora* species without precloacal supplements.

Species	Body length (µm)	Body width (µm)	de Man ratio		V%	Tail length (μm)	Width head (µm)	Cephalic setae (µm)	Spicules (µm)	Gubernaculum (µm)	Spinneret (µm)	
			a	b	c							
D. abnormis	761–1103	28–44	24–34	5,4–6,1	7–7,5	45–47		22–23	15–18	27		
D. amphidiscoides	398–612		18,3–30,6	6,1-7,5	4,5-5,3		88-117	5–7				8
D. antarctica	420-680		22,9–35,8	5,4–7	3,5-5,2	44,7–48		6–8	4	14		5–10
D. apapillata	729–820		15,2–17	5,4–5,5	5,5-7,2	48			6	38	16	
D. acrospiculum	540-578		30-30,4	5,7-6,1	6,3				2	28	18	
D. gathuai	509-817	25–28	26,2–32,7	5,5–7,5	5,3-7,8	43–47	93–109	8–10				
D. geophila	583–958	38–49	13,4–24	5,7–8	5,6–12	44–46,5		13–14	5	28-36	16–18	
D. gracilis	1108-1218	33,8–36,4	29,9-33,2	8,3–8,4	7,3–10,9	44,8–48,7						
D. islandica	764–989		18,3–22,3	6,3-7,2	6,5–7,6	47,30–49,1			10,5–11,5	36,5–40,5	19–21	
D. longicaudata	425–590	13–14	30,4-44,8	6,7–8,6	2,5–4	39–43	107–212	5	2–3	18,4	7	10–16
D. punctata	904	40	22,6	6,90	7,5			20				
D. simplex	480–494		15-20	5–6	6,5–7,5				3	20–24	10	
D. strandi	1700-1875		30,9–31,3	8,1-8,3	10,3–10,4							
D. tobaensis	337–700		15,6–28	4,6–6,5	6,5–9	45,5–46,3						
D. weddellensis	687–951	29–32	23,8–31	6,3–8	7,6–8,7	46,8–56,8		11	6	37	21	4
D. southernis	721–865	27–28	28,6–32,1	6,6–8,5	8,8–10,6	52,5-56,9		9	2	31		5
D. polarsternis	964–1183	41–43	21,4–30,3	6,3-7,4	6,7–9,4	46,7–55,8		12	7	28		
D. spec A	880	37	23.8	5.2	6.3			12	8	26		
D. spec B	568-734	17	33.4–43.2	8.2–10.4	5.6-5.9	42.3	124			18		

D. apapillata (Timm, 1961), D. geophila (de Man, 1876), D. islandica (Kreis, 1963) and D. punctata (Schuurmans Stekhoven, 1950) have a lower avalue than the new species. D. apapillata also has a lower b- and c-value and differs in shape and length of the gubernaculum. D. geophila has a larger body diameter. The spicules of D. weddellensis sp. n. are more strongly curved (angle of 90 $^{\circ}$) than for D. *geophila* (angle of about 126.1 $^{\circ}$). The tail of D. weddellensis sp. n. is also much more slender and ends in a cylindrical part in contrast to the conical tail of D. geophila, a species that is described from fresh and brackish waters. Other differences with D. islandica are the length of cephalic setae, the shape of the amphid and the tailtip. D. islandica has much larger cephalic setae, a spiral amphid and a tail with a rounded tip. D. punctata has larger cephalic setae and differs in the shape of the spicules and gubernaculum. Dichromadra qathuai has slightly lower c-value and differs in the shape of the testis, spicules and gubernaculum.

3.2. Dichromadora southernis sp. n.

Type material: Five males and five females on slide numbers 104075 to 104079 in collection UGMD. Holotype male (δ_1) on slide no 104075, allotype female (φ_1) on slide no 104075.

Type locality: Antarctic deep sea, Weddell Sea. Halley Bay, station 253 (silt: 61%, clay: 29%). *Etymology:* Name given after its present known distribution area, the Southern Ocean

Measurements:

$$\frac{-112 \text{ M} 730}{9 \text{ 19 } 27 \text{ 19}} 865$$
Holotype δ_1 : $a = 32$; $b = 7.7$; $c = 11.1$; $c' = 4.1$; spic = 31.

Allotype
$$\mathfrak{P}_1$$
: $a = 28.6$; $b = 7.2$; $c = 9.1$; $c' = 4.9$; $V\% = 52.7$.

Paratypes:

Other &: L: 780–835; a: 28.9–32.1; b: 6.8–8.5; c: 9.6–10.6; c': 3.8–4.2; spic: 29–30.

Other \mathcal{L} : 721–835; a: 29.8–31.4; b: 6.6–7.1; c: 8.8–9.2; c': 4.5–5.4; V%: 52.5–56.9.

3.2.1. Description:

Holotype: The body has a cylindrical shape with a flattened head and a rather short tail that ends in a 5 µm long spinneret (Fig. 5A). The cuticle pattern consists of homogeneous, transverse rows of dots with four longitudinal rows of slightly larger dots on both sides of the lateral differentiation. Transverse bars over the lateral differentiation area are not observed (Fig. 5B). Somatic setae are observed along the lateral differentiation, these setae are mainly observed in the head and tail region (Fig. 5E, F). The flattened head has four subterminal cephalic setae that are 2 µm long (Figs. 5C and 6B). The buccal cavity is small with small dorsal and ventral teeth (Fig. 5C). The amphid is slit-like and is not visible with the lightmicroscope but can be seen in the SEM (Fig. 6A). The ventral gland and nerve ring are not observed. The pharynx is 112 µm long and ends in a distinct bulb of 22 µm long and 18 µm width (Fig. 5E). The reproductive system is monorchic with outstretched testis (Fig. 5A). The spicules are long and slender with a very weak cephalic capitulum (Fig. 5F). They are 31 μm long. The gubernaculum is a very thin feature lying against the back of the spicules. The precloacal supplements are not observed with the light microscope, but SEM pictures of the species show the presence of seven very small precloacal supplements (detail precloacal supplement: Fig. 6C).

Allotype: The female is very similar to the male, except for the tail. The female has a slightly longer tail then the male (c-ratio female: 8.8–9.2; c-ratio male: 9.6–11.1). The reproductive system is didelphic, amphidelphic with reflexed ovaries. The vulva is positioned in the mid-body region (V% = 52.7%) (Fig. 5G).

3.2.2. Differential diagnosis

Although this new species possesses very small precloacal supplements, for the differential diagnosis a comparison will be made between this new species and the known *Dichromadora* species without precloacal supplements. The reason for this is that these precloacal supplements are only

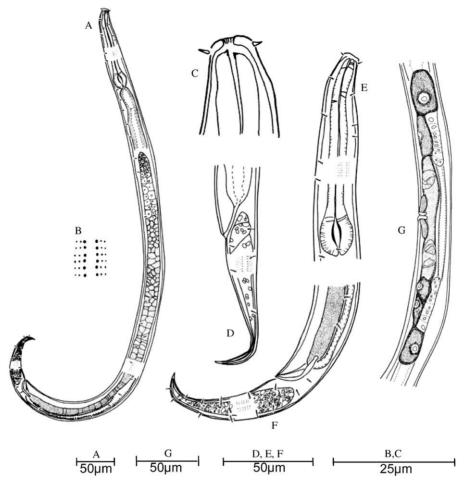
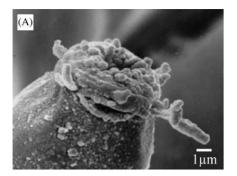


Fig. 5. *D. southernis* sp. n.: (A) habitus \eth_1 , (B) cuticle pattern, (C) detail head \eth_1 (internal), (D) tail \Im_1 , (E) pharyngeal region \eth_1 , (F) tail \eth_1 and (G) reproductive system \Im_1 .

observed in the scanning electron microscope and not by light microscopy, which is the usual way to identifying nematodes. Table 3 gives a list of the *Dichromadora* species without precloacal supplements. *D. abnormis*, *D. acrospiculum*, *D. amphidiscoides*, *D. antarctica*, *D. gathuai* (Muthumbi & Vincx, 1998), *D. islandica*, *D. longicaudata* and *D. simplex* can be clearly distinguished from the new species by their long tail in addition to other characteristics which are different for each species. *D. abnormis* has longer cephalic and somatic setae and a more complex gubernaculum and cuticular ornamentation. Also *D. acrospiculum* has a larger and more complex gubernaculum. *D. amphidis*-

coides has strongly curved spicules and is much smaller in body size. *D. antarctica* has a very long and pointed spinneret on an elongated cylindrical tail. *D. gathuai* looks very similar except for the elongated tail and the striated cuticle. *D. islandica* has much longer cephalic setae and a different cuticular ornamentation. *D. simplex* is only half the size in body length.

D. apappillata and D. geophila have a lower a-ratio than Dichromadora southernis sp. n. D. apappillata is also characterized by the presence of transverse bars over the lateral differentiation. These bars are absent in the new species. D. geophila is much thicker. D. strandi is more





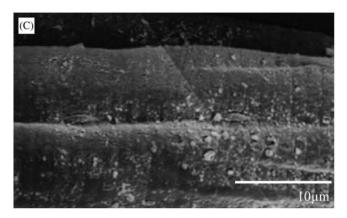


Fig. 6. D. southernis sp. n.: (A) side view of the head, (B) front view of the head and (C) detail of precloacal supplements.

than twice as long and has longer cephalic setae and a higher *b*-ratio than *D. southernis* sp. n. *D. tobaensis* has a lower *a*- and *b*-ratio than *D. southernis* sp. n. and smaller spicules. *D. weddellensis* sp. n. has a slightly lower *c*-value and larger cephalic setae. The spicules are a bit larger but differ in shape. The spicules of *D. weddellensis* are much stronger cuticularised. Also differences are made in the shape of the cuticular punctuations.

3.3. Dichromadora polarsternis sp. n.

Type material: Five males and five females on slide numbers 104077, 104080 to 104085 in collection UGMD. Holotype male (\mathcal{S}_1) on slide no 104077, allotype female (\mathcal{S}_1) on slide no 104080.

Type locality: Antarctic deep sea, Weddell Sea. Halley Bay: station 253 (silt: 61%, clay: 29%). Kapp Norvegia: station 294 (sand: 36%, silt: 20%) and station 295 (sand: 27%, silt: 54%).

Etymology: Named after the research vessel Polarstern.

Measurements:

$$\frac{-160 \text{ M} 1078}{12 31 43 25} 1183$$
Holotype δ_1 : $a = 27.5$; $b = 7.4$; $c = 9.4$; $c' = 4.8$; spic = 40.

$$\frac{-140\ 568\ 863}{12\ 32\ 41\ 22}964$$
 Allotype \mathfrak{P}_1 : $a=30.3;\ b=6.8;\ c=7.9;\ c'=5.3;$ $V\%=55.8.$

Paratypes:

Other &: L: 1012–1087; a: 23–29; b: 6.4–7; c: 8–8.5; c': 4.6–5; spic: 36–43.

Other 9: L = 968-1041; a: 21.4-62.2; b: 6.3-7.1; c: 6.7-9.2; c': 4.5-5.7; V%: 46.7-54.6.

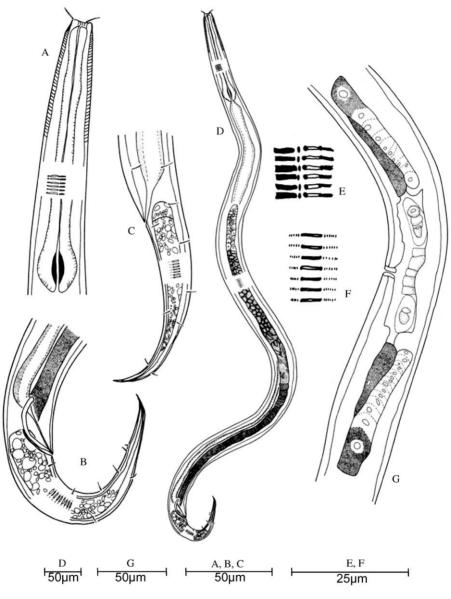
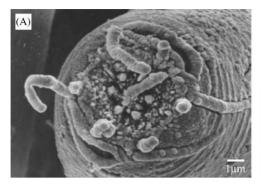


Fig. 7. *D. polarsternis* sp. n.: (A) pharyngeal region δ_1 , (B) tail δ_1 , (C) tail \mathfrak{P}_1 , (D) habitus δ_1 , (E) cuticle pattern of the head region, (F) cuticle pattern at mid-body and tail region and (G) reproductive system \mathfrak{P}_1 .

3.3.1. Description

Holotype: A cylindrical body with a cylindrical-conical tail, ending in a spinneret (Fig. 7D). The cuticle pattern is not fully homogeneous. In the head region, the cuticle is rather heavy (Fig. 7E), whereas the rest of the cuticle patterns consists of transverse rings of dots (Fig. 7E). The dots, present along the sides of the lateral

differentiation, are connected by transverse bars. The cuticle pattern and somatic setae are clearly visible in head and tail region and less in the midbody region (Fig. 7B, C). The head has four cephalic setae (7 µm long) (Fig. 7A) and six external and internal labial sensilla (Fig. 8A). Teeth were not clearly observed. The amphid is not observed by light microscope but a slit-like



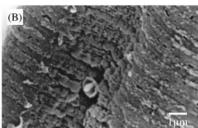


Fig. 8. D. polarsternis sp. n.: (A) frontal view of the head and (B) detail SEM picture of one precloacal supplement.

amphid is visible when viewed in the SEM (Fig. 8A). The nerve ring and ventral gland are not observed. The oesophagus is 160 µm long and ends in a bulb 21 µm long and 21 µm width (Fig. 7A). The reproductive system is monorchic with outstretched testis (Fig. 7D). The testis is positioned ventrally and at the right side of the intestine. The spicules are long, slender and strongly curved. A small, slender gubernaculum is observed (Fig. 7B). The SEM-picture of this new species shows the presence of small, bell-shaped precloacal supplements (Fig. 8B), which have not been observed with the light microscope. In the tail three caudal glands are present (Fig. 7B, C).

Allotype: The female resembles the male. The reproductive system is didelphic, amphidelphic with reflexed ovaria (Fig. 7G). The vulva is positioned just after the mid-body region (V% = 55.8).

3.3.2. Differential diagnosis

As in the case of *D. southernis* sp. n., this new species will be compared with the *Dichromadora* species without precloacal supplements (Table 3). Nine out of the 17 *Dichromadora* species present in Table 3 have a total body length which is smaller than that of the new species. Other observed differences are a lower *a*- and *b*-value for *D. apapillata* and *D. simplex. D. simplex* has smaller cephalic setae than the new species. *D. longicaudata* has a higher *a*-value, a lower *c*-value and smaller cephalic setae. *D. amphidiscoides*, *D. antarctica* have a lower *c*-value meaning that the tail of these two species is longer than the tail of the new species *D. polarsternis*.

In Table 3 three known *Dichromadora* species, *D. abnormis*, *D. gracilis* and *D. strandi* have a total body length which is in the same size-class as the new species. *D. abnormis* has a slightly lower *b*-value, longer cephalic setae and a distally enlarged gubernaculum. *D. gracilis* has a higher *b*-value and a double pharyngeal bulb, very slender spicules and a totally different gubernaculum. *D. strandi* has a higher *b*- and *c*-value.

3.4. Dichromadora parva sp. n.

Type material: Three males and two females on slide numbers 104086 to 104090 in collection UGMD. Holotype male (\mathcal{E}_1) on slide no 104086, allotype female (\mathcal{E}_1) on slide no 104087.

Type locality: Antarctic deep sea, Weddell Sea. Halley Bay, station 252 (sand: 53%, silt: 42%). *Etymology:* The name *parva* refers to the small supplements of the male.

Measurements:

$$\frac{-115 \text{ M } 607}{9 \text{ 16 } 27 \text{ 18}} 696$$
Holotype δ_1 : $a = 25.8$; $b = 6.1$; $c = 8.9$; $c' = 4.3$; spic = 29.

$$\frac{-121\ 403\ 657}{8\ 17\ 36\ 18}730$$
 Allotype \mathfrak{P}_1 : $a=20;\ b=6.1;\ c=8.4;\ c'=4.9;$ $V\%=55.3.$

Paratypes:

Other &: L: 582–783; a: 27.9–29.0; b: 4.9–6.5; c: 7.8–9.8; c': 4.2–4.4; spic: 25–29.

Other \mathcal{P} : L: 760; a: 23; b: 6.3; c: 9; c': 4.7; V%: 51.6.

3.4.1. Description

Holotype: The new species D. parva has a cylindrical body with a flattened head and a cylindrical-conical tail which ends in a 5 μ m long spinneret (Fig. 9A). The body becomes slightly narrower towards the head region. The cuticle consists of transverse rows of small dots. These rows are interrupted by the lateral differentiation but cross this area by transverse bars (Fig. 9G). The distance between two dots in a transverse row is very small. The four longitudinal rows bordering the lateral differentiation have slightly larger dots. Somatic setae are clearly visible in head and tail region, they are $4 \mu m \log$ (Fig. 9D, E). The head

has four cephalic setae of 7 µm long, the external labial sensilla are papilliform (Fig. 9D). In the buccal cavity a small dorsal tooth and small ventral teeth are observed (Fig. 9B). The amphid is small and elliptical and is positioned just above the start of the cuticle pattern (Fig. 9C). The nerve ring, ventral gland and internal labial sensilla are not observed. The pharvnx is 115 um long and ends in a distinct bulb 20 µm long and 16 µm wide (Fig. 9D). The reproductive system consists of one outstretched testis, ventral and right of the intestine (Fig. 9A). The spicules are 29 µm long, slender and strongly curved. A small gubernaculum is present. There are seven or eight small, simple precloacal supplements (Fig. 9E). In the tail 3 caudal glands are observed (Fig. 9E, H).

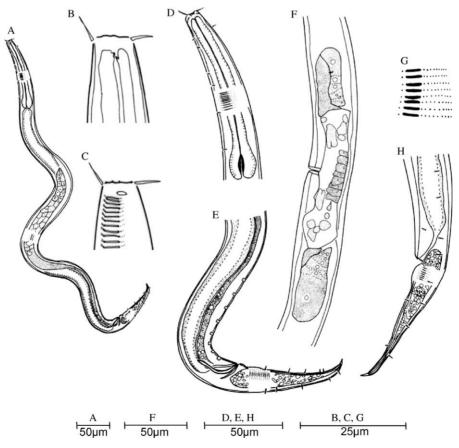


Fig. 9. D. sp. n.: (A) habitus δ_1 , (B) detail head δ_1 (internal), (C) detail head δ_1 (external) (D) pharyngeal region δ_1 , (E) tail δ_1 , (F) reproductive system \mathfrak{P}_1 , (G) cuticle pattern and (H) tail \mathfrak{P}_1 .

Allotype: The female is similar to the male. The reproductive system is didelphic, amphidelphic with reflexed ovaria. The vulva is positioned in the middle of the body (V% = 55.3) (Fig. 9F).

3.4.2. Differential diagnosis

Within the genus Dichromadora three species are described with seven or eight precloacal supplements: Dichromadora cephalata (Steiner, 1916), Dichromadora cucullata (Lorenzen, 1973) and Dichromadora loiseae (Muthumbi and Vincx, 1998). D. cephalata has a rounded head and differs in the shape of spicules, gubernaculum and precloacal supplements. Small differences in band c-value are observed. The b-value of D. cephalata (b: 6.3–8.1) is slightly higher than of D. parva sp. n. (b: 4.9-6.5) whereas the c-value (c: 6.6–7.9) is slightly lower than of D. parva sp. n. (c: 7.8-9.0). D. cucullata has different precloacal supplements and spicules. The species also has a lower c-value (c: 5.8–6.8) than D. parva sp. n. (c: 7.8-9.0). D. loiseae has a double pharyngeal bulb, a raised collar that surrounds the labial rugae and a higher a-value (a: 26.0–36.6) than D. parva sp. n. (a: 20.3–29.0).

3.5. Dichromadora polaris sp. n.

Type material: Four males on slide numbers 104091 to 104094 in collection UGMD. Holotype male (δ_1) on slide no 104091.

Remark: The allotype female is a non-gravid female; it is the only female observed of this *Dichromadora* species.

Type locality: Antarctic deep sea, Weddell Sea:

Kapp Norvegia, station 294 (sand: 36%, silt: 20%) and station 295 (sand: 27%, silt: 54%).

Etymology: The name refers to the polar region. Measurements:

Holotype
$$\hat{\sigma}_1$$
: $a = 20.2$; $b = 6.7$; $c = 10.8$; $c' = 3.7$; spic = 35.

$$\frac{-128\ 373\ 582}{9\ 24\ 32\ 17}667$$
 Allotype \mathfrak{P}_1 : $a=20.9;\ b=5.2;\ c=7.8;\ c'=4.8;$ $V\%=55.9\%.$

Paratypes:

Other &: L:714–848; a:23–33.9; b: 5.4–7.1; c: 7.9–9.9; spic: 28–30.

3.5.1. Description:

Holotype: D. polaris sp. n. has a cylindrical body with a cylindrical-conical tail which ends in a 5 µm long spinneret (Fig. 10C). The cuticle consists of transverse, homogeneous rows of dots connected by transverse bars along the lateral differentiation (Fig. 10H). The transverse rows of dots in the mid-body region are smaller than on both ends of the body. Somatic setae are present along the lateral differentiation, clearly visible in head and tail region (Fig. 10D, E). The head is flattened and has four cephalic setae (Fig. 10A, B). In the buccal cavity a dorsal and two smaller ventral teeth are present (Fig. 10B). The nerve ring, ventral gland and labial sensilla are not observed. The pharynx ends in a bulb of 23 µm long and 20 µm wide (Fig. 10D). The reproductive system is monorchic with outstretched testis (Fig. 10c). The shape of the spicules is very simple: long, slender and strongly curved (angle of about 90°). The gubernaculum is 16 µm long and slender with a curved top. Eight or nine large precloacal supplements are present (Fig. 11). A seta is present between the last precloacal supplement and the cloaca. In the tail, there are three caudal glands (Fig. 10E, G).

Allotype: The female resembles the male. The reproductive system is didelphic, amphidelphic with reflexed ovaria (Fig. 10F).

3.5.2. Differential diagnosis

Dichromadora hyalocheile (Kreis, 1929) is the only other species with nine or 10 precloacal supplements. Four differences distinguish both species from each other:

- 1. the supplements *D. hyalocheile* are smaller and different in shape than the supplements of *D. polaris* sp.n.
- 2. the reversed S-shaped spicules of *D. hyalocheile*,

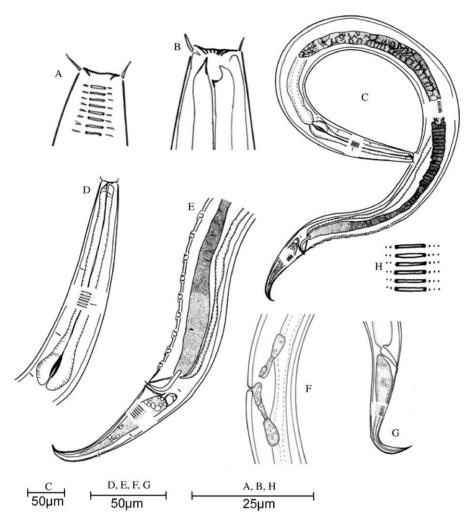


Fig. 10. *D. polaris* sp.n. : (A) head region δ_1 (external), (B) head region δ_1 (internal), (C) habitus δ_1 , (D) pharyngeal region δ_1 , (E) tail δ_1 , (F) reproductive system \mathfrak{P}_1 , (G) tail \mathfrak{P}_1 and (H) detail cuticle pattern.

- 3. the pharynx surrounding the buccal cavity of *D. hyalocheile* is clearly swollen and this is not the case in the new species,
- 4. the cephalic setae of *D. polaris* sp. n. are short and the somatic setae are not so prominent as in *D. hyalocheile*.

3.6. Dichromadora spec. A

Material: Two males from the Antarctic deep sea, Weddell Sea (Halley Bay: station 253; silt: 61%, clay: 29%). Females were not observed.

Measurements:

$$\delta_1$$
:
$$\frac{-170 \text{ M} 740}{12 \text{ 21 } 37 \text{ 23}} 880$$
 $a = 23.8; b = 5.2; c = 6.3; c' = 5.8; \text{ spic} = 39.$

Other &: L: 1032; a: 24.6; b: 7.2; c: 8.7; c': 4.8; spic: 35.

3.6.1. Description

First male: D. spec A has a cylindrical body with a cylindrical-conical tail without spinneret (Fig. 12A). The head is flattened and teeth are not clearly visible. The four cephalic setae are 8 µm



Fig. 11. D. polaris sp. n.: tail with precloacal supplements.

long. Amphid, nerve ring, ventral gland and labial sensilla are not observed. The oesophagus has a bulb of $20\,\mu m$ long and $21\,\mu m$ wide (Fig. 12C). The cuticle pattern consists of homogenous transverse rows of small dots connected by transverse bars (Fig. 12B). Somatic setae are observed, they are $7\,\mu m$ long. The reproductive system is monorchic with outstretched testis. The testis is situated ventrally and at the right side of the intestine. The spicules are long and slender. The gubernaculum is hook-like shape. No precloacal supplements are present (Fig. 12D).

3.6.2. Differential diagnosis

See Table 3 for an overview of the *Dichromadora* species without precloacal supplements. This *Dichromadora* species can be distinguished from other *Dichromadora* species by the shape of the gubernaculum. In addition to *D.* spec A can be distinguished by other features. *D. gracilis*, *D. longicaudata*, *D. strandi* and *D. southernis* differ from *D.* spec A in each of the three 'de Man'-values. *D. amphidiscoides*, *D. punctata* and *D.*

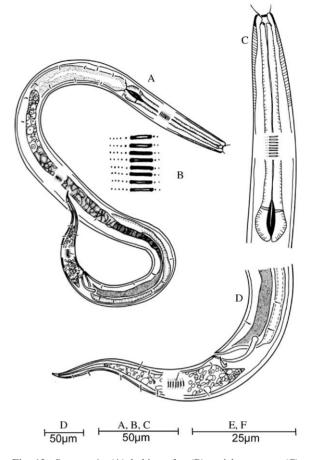


Fig. 12. D. spec A: (A) habitus δ_1 , (B) cuticle pattern, (C) pharyngeal region δ_1 , (D) tail δ_1 .

weddellensis differ in two out of three 'de Man' values and D. abnormis, D. apapillata, D. puncatata, D. simplex and D. polarsternis differ in one 'de Man'-value. D. abnormis has longer cephalic setae.

3.7. Dichromadora spec. B

Material: One male and one female from Antarctic deep sea, Weddell Sea (Halley Bay, station 252; sand: 53%, silt: 42%).

Measurements:

$$\frac{-17 \text{ M} 400}{5 11 17 12} 734$$

$$a = 43.2; b = 10.4; c = 5.9; c' = 9.5; \text{ spic} = 18.$$

$$\begin{array}{c} 9: & \frac{-70\ 240\ 364}{5\ 10\ 17\ 10} \, 568 \\ a = 33.4; \ b = 8.2; \ c = 5.6; \ c' = 10.2; \ V\% = 42.3. \end{array}$$

3.7.1. Description

Male: A cylindrical, thin body with a very long tail (124 μm long), ending in a long, slender spinneret (Fig. 13E). The cuticle pattern is homogenous with transverse rows of dots. No transverse bars are observed (Fig. 13C). Cephalic and somatic setae were not observed nor were the amphid, nerve ring, ventral gland or teeth. The pharyngeal bulb is 13 μm long and 11 μm wide (Fig. 13B, F). The reproductive system is monorchich with outstretched testis. The testis is positioned ventrally and at the right side of the

intestine. The spicules and gubernaculum are slender. No precloacal supplements are observed (Fig. 13D).

Female: The female resembles the male. The nerve ring is observed (Fig. 13F). The reproductive system is didelphic, amphidelphic with reversed ovaria (Fig. 13A). The vulva is positioned just before the mid-body region (V% = 42.3%).

3.7.2. Differential diagnosis

Three known *Dichromadora* species have a long tail: *D. amphidiscoides* (Kito, 1981), *D. antarctica* (Cobb, 1914) and *D. longicaudata* (Muthumbi and Vinex, 1998). *D. longicaudata* has a lower *c*-ratio (*c*: 2.5–4.0) than *D.* spec B (*c*: 5.6–5.9). This means that *D. longicaudata* has a much longer tail than *D.* spec B. *Dichromadora amphidiscoides* has

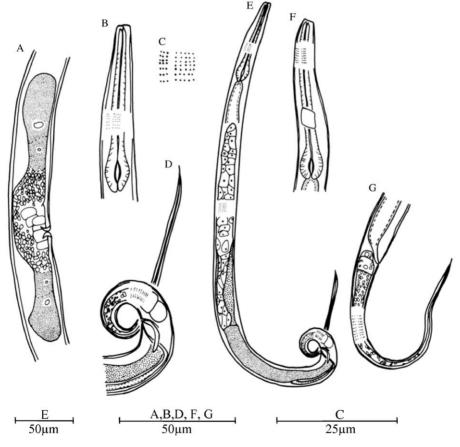


Fig. 13. D. spec B: (A) reproductive system \mathcal{P}_1 , (B) pharyngeal region \mathcal{F}_1 , (C) cuticle pattern, (D) tail \mathcal{F}_1 , (E) habitus \mathcal{F}_1 , (F) pharyngeal region \mathcal{P}_1 , (G) tail \mathcal{P}_1 .

transverse bars and strongly curved, cephalate spicules, this is not the case for *D*. spec B. *Dichromadora antarctica* differs in the shape of the spicules. The capitulum of the spicules is strongly cephalate.

4. Discussion

4.1. Taxonomy

In 58% of all described *Dichromadora* species from all over the world, no male precloacal supplements are observed by means of light microscope (17 species without precloacal supplements and 12 species with precloacal supplements). But scanning electron microscopy of some of the new *Dichromadora* species (*D. southernis* sp. n. and *D. polarsternis* sp. n.) have shown the presence of very small precloacal supplements that cannot be seen with the light microscope. This may mean that all the *Dichromadora* species without precloacal supplements in fact do have these features but they have not been observed with the light microscope.

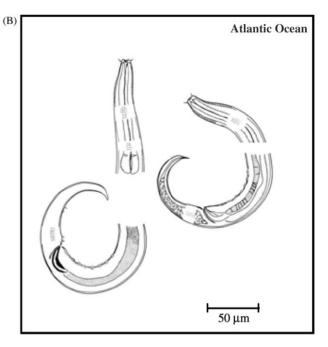
4.2. Distribution and size characteristics of Antarctic bathyal Dichromadora species and comparison with deep-seas worldwide

Despite the fact that the species concept lies at the base of all ecological studies and that the first nematode descriptions date back to 1865 (Bastian, 1865), very few species have been described adequately. Those that have been described tend to be clustered in geographical regions where taxonomists are located (Lambshead and Boucher, 2003). Thus in most species-level ecological studies new species are not taxonomically described but named as spec A, B, C, ... because taxonomy is too time consuming (Godfray, 2002). This makes comparisons between ecological studies from different areas, conducted by different scientists, difficult. It is so far impossible to draw any conclusions or even get an indication about the species distribution patterns of free-living, marine nematodes in the deep sea and in the oceans in general. Therefore, nematode samples from In-

Pacific. Arctic and Atlantic oceans (1000-2000 m), available at the Marine Biology of Ghent University, are reconsidered for identification of Dichromadora, thus allowing valuable comparisons with Antarctic Dichromadora species. In the Indian and Pacific Ocean this genus is not retrieved, whereas in the Atlantic and Arctic Ocean it is represented by 1-3% (Vanaverbeke et al., 1997; Vanreusel et al., 2000). In total more Dichromadora species are observed in the Southern Ocean (8 sp.) than in the Arctic (2 sp.) or Atlantic Ocean (3 sp.) (Fig. 14), probably related to the higher occurrence of Dichromadora in the Southern Ocean. Seven out of nine Antarctic species (ours and the only available earlier description from the Antarctic, e.g. D. antarctica) (Timm, 1978) do not appear in the other deep-sea sites. This might point towards Antarctic endemism (e.g., 30 to 97% of the known macrobenthic species, Arntz et al., 1997 and 16% of the known harpacticoid copepod species; Dahms and Pottek, 1992, Razouls et al., 2000 are endemic), indicative of the long isolation of Antarctica from other land areas and their associated shelf and slope regions. However, the low taxonomic effort undertaken so far in free-living nematodes from the oceans, and especially from the deep sea, does not allow us to make solid conclusions. The Arctic and Atlantic species retrieved in our samples are, for example, also new to science.

This taxo-ecological approach provides a basis for comparison with major distribution patterns of the benthic organisms in Antarctica (Knox, 1994; Brey et al., 1994; Arntz et al., 1997). The Antarctic fauna is considered as being circumpolar, circum-antarctic or circum-subantarctic as a result of constant and similar conditions around Antarctica. Furthermore, three different benthic communities can be distinguished on the shelf and upper slope, (1) the Eastern Shelf Community within the confines of the Antarctic Coastal Current in the east. (2) the Southern Trench Community in the Filchner Trench and in the depression close to the Antarctic Peninsula, and (3) a Southern Shelf Community, in front of the Filchen-Rønne ice shelf and off Halley Bay (Voß, 1988). Our results show that within the Antarctic deep sea five of the eight





Station	Campaign	Date	Region	Locality	Depth (m)	Gear
Arctic Ocean	ARK VIII/3 (7)	01.08.1994	Chukchi Abyssal Plain	76°41 N 173°28 W	2220	MG
Arctic Ocean	ARK VIII/3 (8)	03.08.1994	Arlis Plateau	78°08 N 176°53 W	1000	MG
Arctic Ocean	ARK VIII/3 (16)	08.08.1994	Mendeleev Ridge	80°20 N 178°43 W	1520	MG
Atlantic Ocean	OMEX (B)	10.1993	Celtic Sea	49°22 N 11°48 W	1034	MG
Atlantic Ocean	OMEX (C)	10.1993	Celtic Sea	49°10 N 12°59 W	1961	MG
Atlantic Ocean	OMEX (F)	10.1993	Celtic Sea	49°09 N 13°05 W	2182	MG

Fig. 14. Overview of the *Dichromadora* spp. In (A) Arctic and (B) Atlantic Ocean and (C) table with overview of the stations in the Arctic and Antarctic Ocean.

identified Dichromadora species are observed at four of the five sites (i.e. D. parva, D. polarsternis, D. southernis, D. polaris and D. weddellensis). The three remaining species are only rarely found (i.e. D. spec A, D. spec B and Dichromadora quadripapillata) (Table 2). No species are restricted to a certain region in Antarctica (e.g., South Sandwich Trench, Halley Bay, Kapp Norvegia, Vestkapp, Drake Passage) and two species (D. polaris and D. polarsternis) are not found in the South Sandwich Trench. So, some species tend to be spatially restricted in their distribution; others are widespread in the Atlantic sector of the Southern Ocean. This confirms the observation that nematode species have wide ranges over regional scales in the deep sea (Lambshead and Boucher, 2003).

The Antarctic benthic fauna is also characterized by many eurybathic species (Brey et al., 1996). This is so because the Antarctic ice sheet underwent periodic extensions and contractions, which may have enhanced the speciation processes on the continental shelf, the so-called Antarctic 'diversity pump' (Clarke and Crame, 1992). The Dichromadora species show, accordingly, no distribution constraints within the limited bathymetric range studied here (1000-2000 m) (Table 2). However, at 2000 m more species are observed than at 1000 m (except for Drake Passage). This could mean that the number of 'true' deep-sea species is superimposed by 'shelf' species that have followed the extensions of the ice and stayed in the deep waters until now. More research is needed to illustrate this hypothesis.

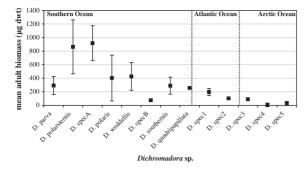


Fig. 15. Mean individual adult nematode biomass (μg dwt±standard deviation) of each species in Southern, Atlantic and Arctic Ocean.

A last characteristic observed within our nematode species deals with size character. A comparison of the mean individual nematode biomass of each Dichromodora species from the Southern, Atlantic and Arctic Ocean shows a significantly higher mean individual nematode biomass of the Antarctic species compared to the Atlantic and Arctic species (Kruskall-Walis test: H(2,N=188) = 51.29, p < 0.001) (Fig. 15). The only exception is D. spec. B $(76+16.1 \mu g dwt)$, an Antarctic species with a mean individual biomass similar to the Arctic species. The pattern in mean individual nematode biomass corresponds to the observed pattern at the community level, with a general tendency of Antarctic nematodes towards the higher individual size classes, compared to counterparts in West Indian, Arctic, Pacific and Atlantic Ocean (De Broyer et al., 2001). The combination of high summer food input and low ambient temperatures may result in a longer availability of organic sources to these detritusfeeders.

5. Conclusion

The taxonomic approach adopted in this paper resulting in the description of seven new *Dichromadora* species from the Antarctic, makes some early conclusions regarding the species distribution of Antarctic bathyal nematodes possible. By extending our identifications of *Dichromadora* to similar depths in other oceans, additional world-

wide comparisons could be started. However, meiobenthic nematode taxonomy in the oceans, and especially the deep seas, is almost non-existing. Any conclusion concerning species distributions, thus far, is heavily dependent on the intensity of research.

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