



## Taxonomy and species distribution of the genus *Manganonema* Bussau, 1993 (Nematoda: Monhysterida)

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**Abstract:** Different deep-sea sites are frequently characterized by a high number of species belonging to the same genus. In addition, some deep-sea genera (e.g. *Acantholaimus*, *Monhystera*, *Halalaimus*) seem to be dominant and present worldwide. The genus *Manganonema* is present in all oceans in low to medium densities (< 2%) and, apparently, restricted to the deep sea (600 m and deeper). The present study deals with a revision of the genus *Manganonema* based upon known species and nine new species, where only 5 were named due to the lack of males (*M. media* sp. nov., *M. pitilica* sp. nov., *M. robustus* sp. nov., *M. antarctica* sp. nov., *M. bussauensis* sp. nov.). For the species identification, important characters are summarized in a pictorial key. The material studied was collected from six different sites: two in the North Atlantic (Europe), two in the Southern Ocean (Antarctic), one in the South-western Atlantic (Brazil), and one in Western Indian Ocean (Kenya). The species distribution suggests a high turnover of species between sites. Only one *Manganonema* species is recorded from two different sites in the Atlantic Ocean. These results suggest a high degree of endemism of species within the genus.

**Résumé :** *Taxonomie et distribution des espèces du genre Manganonema Bussau, 1993 (Nematoda : Monhysterida).* Les différentes régions des mers profondes sont fréquemment caractérisés par un nombre élevé d'espèces appartenant au même genre. En plus, certains de ces genres (par exemple *Acantholaimus*, *Monhystera*, *Halalaimus*) semblent être dominants et présents au niveau mondial. Le genre *Manganonema* est présent dans tous les océans à faible et moyenne densités (< 2%) et limité à la mer profonde (600 m et plus profond). La présente étude propose la révision du genre *Manganonema* fondé sur les espèces déjà répertoriées et sur la description de neuf espèces nouvelles, dont seulement 5 ont été nommées en raison de l'absence de mâles (*M. media* sp. nov., *M. pitilica* sp. nov., *M. robustus* sp. nov., *M. antarctica* sp. nov., *M. bussauensis* sp. nov.). Pour l'identification d'espèce, les caractères importants sont résumés dans une clef illustrée. Le matériel étudié provient de six localités différentes : deux dans l'Atlantique Nord (Europe), deux dans l'Océan Austral (Antarctique), un dans l'Atlantique du Sud-ouest (Brésil), et un dans l'ouest de L'Océan indien (Kenya). La distribution des espèces suggère un remplacement important des espèces entre les sites. Seulement une espèce du genre *Manganonema* est signalée dans deux sites différents dans l'Atlantique. Ces résultats suggèrent un degré d'endémisme élevé des espèces de ce genre.

**Keywords:** Biogeography; Deep sea; Species turnover; Pictorial identification key; Xyalidae

## Introduction

During the 1980's and even more in the 90's numerous studies have illustrated the increasing importance of free-living marine nematodes in terms of densities, relative abundance and diversity towards bathyal, abyssal and even hadal water depths (e.g. Bussau, 1995; Vanaverbeke et al., 1997; Bussau & Vopel, 1999; Etter et al., 1999). In general nematodes in the deep-sea (from 200 m to below 6000 m) can represent more than 90% of the total metazoan meiofauna community. Moreover, nematode densities can rise up to more than 6000 individuals per 10 cm<sup>2</sup> in organically enriched hadal regions such as the Atacama trench (Gambi et al., 2003) and 60 species and more may be counted in a single core (Vanreusel et al., 1997). Thus nematode communities from deep-sea sediments are characterized by a high local ( $\alpha$ ) diversity (Soetaert et al., 1991; Gray, 1994). The most common and dominant deep-sea nematode genera, for example *Acantholaimus*, *Halalaimus* and *Monhystera*, do not possess relative abundances higher than 15% (Vanreusel et al., 1995). In addition, each of these genera is often represented by more than one and sometimes up to 20 different morphologically recognizable species on the same spot (Tietjen, 1984).

Deep-sea nematode genera are well known to be cosmopolitan. For instance, Vanhove et al. (1999) describe nematode communities from transect towards the deep-Antarctic Sea sharing many similarities in terms of generic composition with communities identified along a Mediterranean slope transect. The apparent homogeneity of the silty sediment (Vanhove et al., 1999) and the absence of marked dispersal barriers has been one of the proposed explanations for such similarities through out the large deep-sea environment (Lambhead & Boucher, 2003). Based on these observations at the generic level plus the remarkable local number of species, speculations on regional to global diversity have been discussed by several authors (Grassle & Maciolek, 1992; Lambhead & Boucher, 2003).

Most of the studies on deep-sea nematodes covering different regions provide information at the species level without any complementary taxonomic study. As far as is known, the present study is the first to deal with a worldwide distribution of deep-sea species within a single taxon (genus); most previous studies are regional (e.g. Soetaert & Decraemer, 1989; Decraemer & Gourbault, 1997; Muthumbi & Vincx, 1998; Bussau & Vopel, 1999; Muthumbi & Vincx, 1999). Actually, nematodes species from the deep-sea are poorly known, taxonomic studies are rare and in general deep-sea species seem to differ from those from estuaries and coastal environments. The lack of basic taxonomic studies hampers the estimation of the spatial species turnover of deep-sea nematodes and conse-

quently of their wider (regional to global) distribution and realistic extrapolations from local biodiversity estimates to regional and even global biodiversity values.

This study deals with the re-description of the genus *Manganonema* (Bussau, 1993) and contributes to the description of nine new species, collected at the different deep-sea locations from the North and the South-western Atlantic Ocean, the Western Indian Ocean, the Weddell Sea and the adjacent South Sandwich Trench. In addition, this study aims to compare the species distribution and to contribute to preliminary insights into the species turnover of different regions from the deep sea.

## Materials and methods

### *Study area and sample processing*

Specimens were collected at different deep-sea sites from the Atlantic, Indian, and Southern Ocean. Details on the southern stations are given by Fonseca et al. (2006), Vermeeren et al. (2004), Vanhove et al. (2004), and by the reports EPOS (Vanhove et al., 1997), EASIZ (Dahms et al., 1990), LAMPOS (Bohlman et al., 2003) and ANDEEP (Vanreusel & De Mesel 2003), while from the Western Indian Ocean by Muthumbi & Vincx (1998), from South-western Atlantic Ocean by Netto et al. (2005), and from the Northern Atlantic Ocean by Vanaverbeke et al. (1997). Briefly, all samples were fixed in formalin 4%; later nematodes were extracted by floatation (LUDOX TM50 specific gravity 1.18) and transferred to permanent glycerine slides according to De Grisse (1969).

Type material is deposited in the nematode collection of Ghent University slides number 104101-104109 where Dominick Verschelde is currently the curator.

### *Species descriptions*

Due to the difficulty to have sufficient material, species were only named when at least one male was present. Species represented only by females were considered as putative species and were named as spec. *a*, *b*, *c* and *d*. Drawings were made with a Leica DMLS microscope. All measurements were carried out with the software Q 500+ and are given in micrometers. The curved structures were measured along the arch. The Cobb formula, showing the distance of each character from the anterior end is presented at the beginning of each species description:

$$\frac{\text{Head} \quad \text{End of the pharynx} \quad \text{Vulva} \quad \text{Anus} \quad \text{total Length}}{\text{Corresponding body diameters}}$$

The abbreviations used are: ratios a = body length divided by body maximum width, b = body length divided by the pharynx length, c = body length divided by the tail length (de Man, 1880). L = total body length, Spic =

spicules length, abd = anal body diameter, cbd = corresponding body diameter, ratio  $c'$  = tail length divided by the anal body diameter, V = distance of the vulva from the anterior end divided by the total body length; M = male.

## Systematics

### *Manganonema* Bussau, 1993

In agreement with Lorenzen (1994), the genus *Manganonema* can be classified within the Monhysteroidea de Man, 1876 by the synapomorphy of a single anterior outstretched ovary and within the family Xyalidae by the synapomorphy of the anterior gonad constantly to the left of the intestine. Additional characters supporting the classification are: the transversally striated cuticle, the 6 outer labial and 4 cephalic sensilla arranged in a single crown; the outer labial setiform sensilla mostly longer than the cephalic sensilla (papilliform or setiform); buccal cavity surrounded by pharyngeal tissue.

#### Diagnosis (adapted)

**Xyalidae.** Conspicuous narrow dummy-like anterior end, head diameter at least one third smaller than the body diameter at level of amphidial fovea, and marked or set off from the rest of the body by a narrowing region. Anterior sensilla arranged in two circlets: an anterior crown of six inner labial papillae (which sometimes are difficult to observe by light microscopy), and a second crown of six outer setiform labial sensilla and the 4 cephalic sensilla (papilliform or setiform). Stoma minute, surrounded by pharyngeal musculature. Amphideal fovea round, and relatively large (40-90% cbd). Tail pointed, curved dorsally upon fixation. Body cuticle transversely striated; somatic setae short more or less papilliform (1  $\mu$ m) and difficult to recognize by light microscopy, arranged in four longitudinal rows (two latero-ventral and two latero-dorsal). No ventral gland of secretory-excretory system present. Male reproductive system monorchic with an anterior outstretched testis to the left of the intestine, a long and narrow vas deferens, two small straight spicules and a weak gubernaculum without apophysis. Sperm cells small, globular, with a very dense nucleus. Female reproductive system monodelphic with an anterior outstretched ovary to the left of the intestine, and a simple vulva located at mid-body. No differentiation of uterus, no spermatheca observed.

### *Manganonema media* sp. nov.

(Fig. 1)

#### Material studied

Two males and three females; slide number 104101.

#### Locality

South-western Atlantic Ocean, Brazil - S22°20' W42°00' (1000 m); North East Atlantic - N49°09' W13°05'4" (Goban Spur, 1250 m).

#### Measurements

Holotype Male:  $\frac{- 114}{2.5}$  M  $\frac{659}{18}$   $\frac{740}{18}$   $\frac{740}{11}$   $\mu$ m

a = 44; b = 7; c = 9;  $c'$  = 8. Spic = 8  $\mu$ m

Allotype Female:  $\frac{- 111}{3}$   $\frac{442}{19}$   $\frac{668}{19}$   $\frac{740}{15}$   $\mu$ m

a = 38; b = 7; c = 10;  $c'$  = 5, V = 60%

Paratypes Male<sub>1</sub>: L = 605  $\mu$ m; a = 36; b = 5; c = 10;  $c'$  = 5, Spic = 9  $\mu$ m

Females<sub>2,3</sub>: L = 670-715  $\mu$ m; a = 39-46; b = 6; c = 8-9;  $c'$  = 5-8, V = 59%

#### Description

Body slim, cylindrical. Small rounded head, set off from the rest of the body by a distinct anteriorly narrowing cylindrical region. Body posteriorly tapered towards the tail region. Tail dorsally bent, largely conical with posterior fourth narrow cylindrical. Inner labial sensilla not visible by light microscopy. 6 outer labial and the 4 cephalic sensilla short setiform, 2  $\mu$ m long. Amphidial fovea, 7  $\mu$ m in diameter or 80% of cbd, located at 20  $\mu$ m from anterior end. Pharynx narrow anteriorly, enlarged/wider at the level of the amphidial fovea and posteriorly ends with terminal bulb. Nerve ring located at mid-pharynx (52%). Intestine formed by cylindrical cells which distinctly border a narrow but pronounced lumen in optical section.

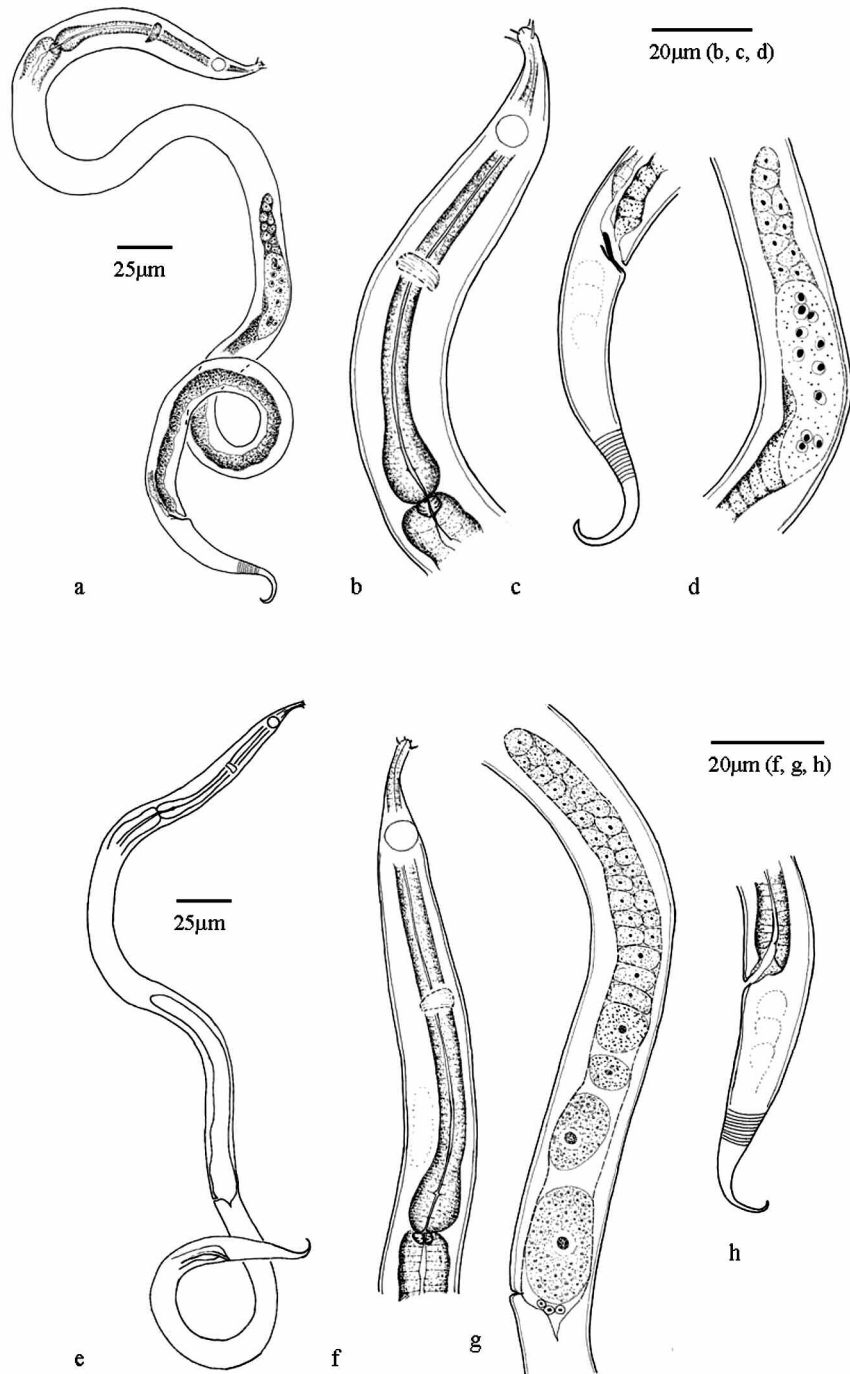
Male reproductive system typical of genus; single anterior testis with a long germinal zone. Spicules needle-like structures, i.e. thin, straight and small. No precloacal supplements observed.

Female reproductive system typical of genus i.e. monodelphic, prodelpic; ovary with long germinal zone, comprising more than half the gonad length.

#### Diagnosis

*Manganonema media* sp. nov. is characterized by a relatively small body length (600-740  $\mu$ m), amphidial fovea wide, rounded, 80% of corresponding body diameter wide and a conical dorsally bent tail with a relatively short cylindrical posterior fourth.

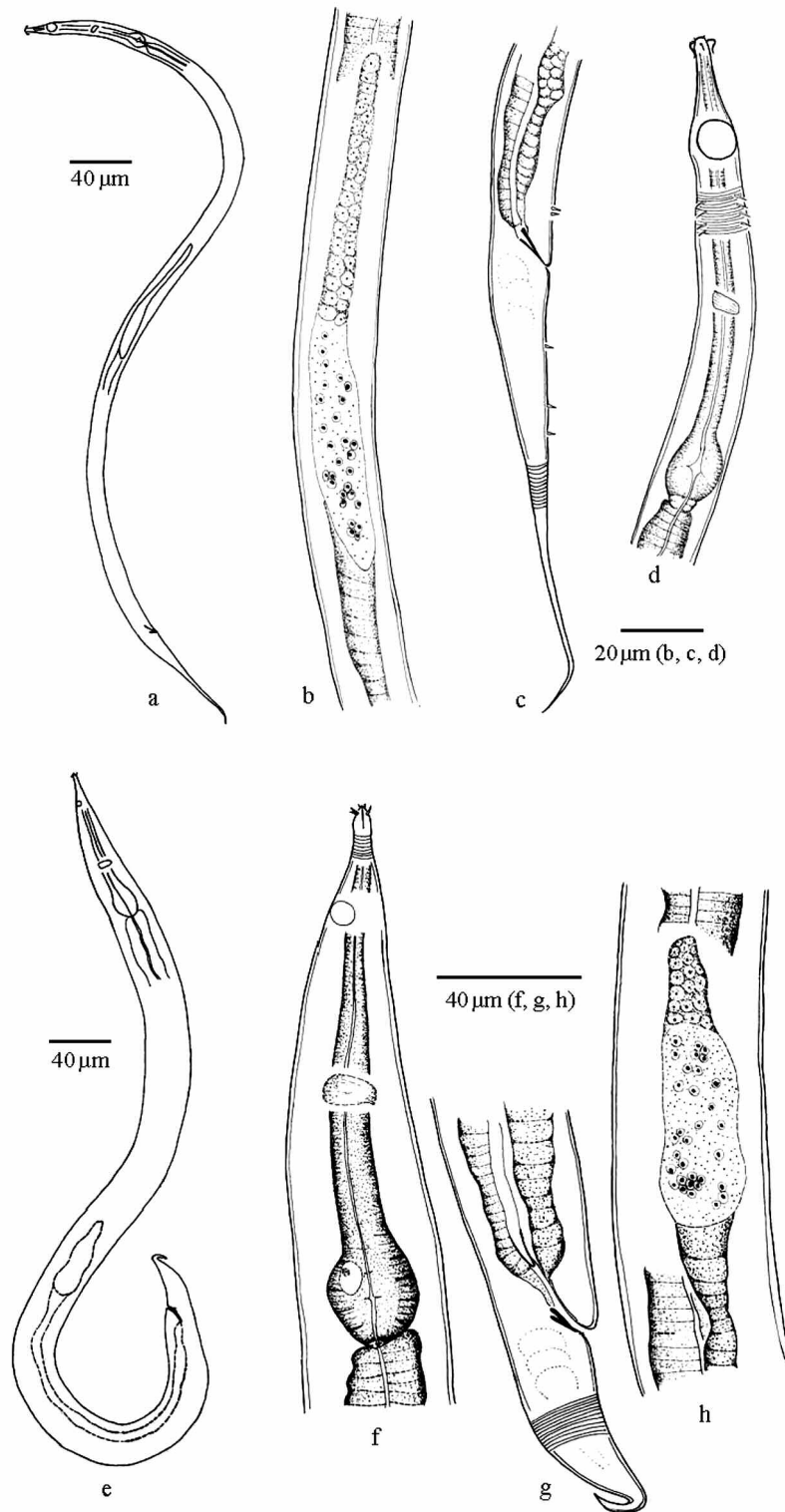
The new species resembles *M. pitilica* sp. nov. and *M. microcephalum* (Bussau, 1993) but can be easily distinguished from former species by the conical tail with a short cylindrical part ( $1/4$ ), vs. the long, thin tail and its shorter body (600-700  $\mu$ m vs. 950-1100  $\mu$ m).



**Figure 1.** *Manganonema media* sp. nov. a-d: male; a) total body; b) anterior end; c) posterior end; d) testis; e-h: female; e) total body; f) anterior end; g) anterior genital branch; h) posterior end.

**Figure 1.** *Manganonema media* sp. nov. a-d : mâle ; a) corps total ; b) extrémité antérieure ; c) extrémité postérieure ; d) testicule ; e- h : femelle ; e) corps total ; f) extrémité antérieure ; g) branche génitale antérieure ; h) extrémité postérieure.





**Figure 2.** *Manganonema pitilica* sp. nov. a-d: male; a) total body; b) testis; c) posterior end; d) anterior end; *Manganonema robustus* sp. nov. e-h: male; e) total body; f) anterior end; g) posterior end; h) testis.

**Figure 2.** *Manganonema pitilica* sp. nov. a-d : mâle ; a) corps total ; b) testicule ; c) extrémité postérieure ; d) extrémité antérieure ; *Manganonema robustus* sp. nov. e-h : mâle ; e) corps total ; f) extrémité antérieure ; g) extrémité postérieure ; h) testicule.

***Manganonema pitilica* sp. nov.**

(Fig. 2)

*Material studied*

One male; slide number 104102.

*Locality*

South-western Atlantic Ocean, Brazil - S22°20' W42°00' (1000 m)

*Measurements*Holotype Male:  $\frac{-}{3} \frac{115}{16} \frac{M}{18} \frac{758}{15} 875 \mu\text{m}$ a = 47; b = 8; c = 8; c' = 8; Spic = 12  $\mu\text{m}$ *Description*

Body slim and long, tapered anteriorly into a narrow cylindrical region ending in a slightly swollen rounded head. Tail relatively long (115  $\mu\text{m}$ ) and thin narrowing gradually six inner labial papillae difficult to distinguish by light microscopy. Six outer and 4 cephalic sensilla situated in at the same level, the outer labial setae are longer (3  $\mu\text{m}$ ) than the papilliform cephalic setae (1  $\mu\text{m}$ ). Amphidial fovea located at 21  $\mu\text{m}$  from the anterior end, wide rounded, 9  $\mu\text{m}$  in diameter or 90% of cbd. Nerve ring located at mid-pharynx at 64  $\mu\text{m}$  from the anterior end.

Male testis with a relatively long germinal zone. Spicules thin and relatively short (11.5  $\mu\text{m}$ ) or 70% of abd. Two pre-cloacal setae, 2  $\mu\text{m}$  long, present.

Females not observed.

*Diagnosis*

*Manganonema pitilica* sp. nov. is characterized by the relatively long (875  $\mu\text{m}$ ) thin body (a = 47), the large amphidial fovea (90% cbd), the difference in length of the anterior sensilla of the second crown (outer labial setae, 3  $\mu\text{m}$  long, cephalic sensilla papilliform), the long tail (115  $\mu\text{m}$ ) tapering gradually to a filliform tip and presence of two small pre-cloacal setae in male. The characteristics of the anterior sensilla, amphidial fovea and tail are unique within the genus.

***Manganonema robustus* sp. nov.**

(Fig. 2)

*Material studied*

One male; slide number 104103.

*Locality*

South-western Atlantic Ocean, Brazil - S22°20' W42°00' (1000 m).

*Measurements*Holotype Male:  $\frac{-}{3} \frac{148}{38} \frac{M}{42} \frac{910}{22} 980 \mu\text{m}$ a = 23; b = 7; c = 15; c' = 3; Spic = 11  $\mu\text{m}$ *Description*

Body large and cylindrical, narrowing towards both extremities. Anterior end pointed. Tail with pointed tip, relatively wide (22  $\mu\text{m}$  at abd) and short (67  $\mu\text{m}$  long); proximal tail part conical and distal portion cylindrical corresponding to  $\frac{1}{5}$  of its length. Head small. Inner labial sensilla not recognizable at light microscopy. Six outer labial and 4 cephalic sensilla setiform and equally long (2  $\mu\text{m}$ ). Amphidial fovea 5.5  $\mu\text{m}$  in diameter (= 40% cbd) located at 26  $\mu\text{m}$  from anterior end. Cardia small.

Male testis characterized by a short germinal zone representing one third of its length. Spicules relatively small, 11  $\mu\text{m}$  long or 50% of abd. Apophysis and precloacal supplements lacking.

No females observed.

*Diagnosis*

*Manganonema robustus* sp. nov. is characterized by a relatively large body (L = 980  $\mu\text{m}$  and a = 23), small amphidial fovea (40% of cbd) and a short tail (c' = 3). Whilst this species is the largest and widest within the genus, it has the smallest amphidial fovea (40% of cbd), setiform cephalic setae, and the shortest tail (67  $\mu\text{m}$ ; c = 15; c' = 3).

***Manganonema antarctica* sp. nov.**

(Fig. 3)

*Material studied*

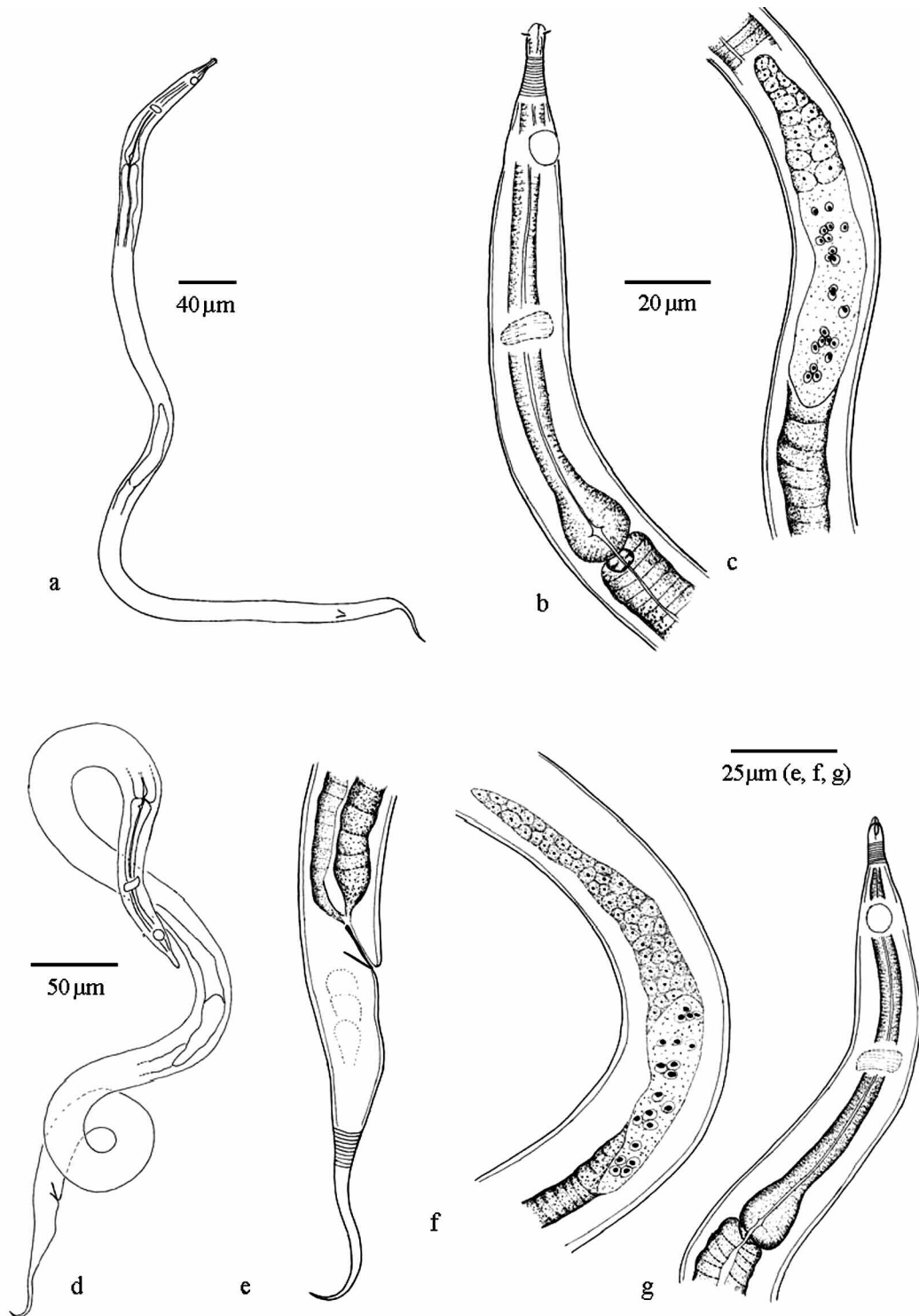
One male; slide number 104104.

*Locality*

Southern Ocean - S70°52' W10°29' (600 m).

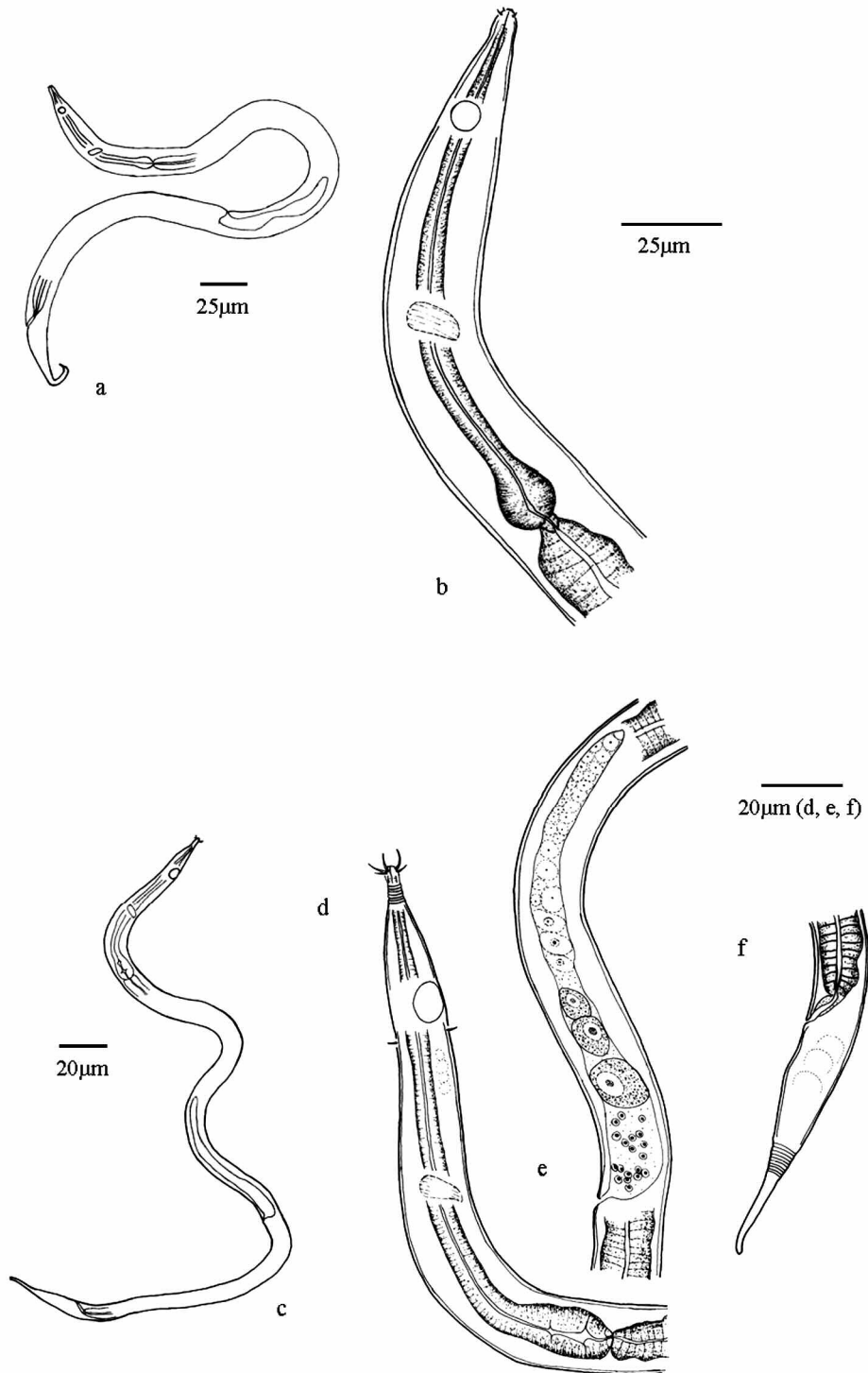
*Measurements*Holotype Male:  $\frac{-}{3} \frac{125}{21} \frac{M}{21} \frac{785}{15} 880 \mu\text{m}$ a = 48; b = 7; c = 9; c' = 6; Spic = 8  $\mu\text{m}$ *Description*

Body long and thin, tapered towards both ends. Anterior end characterized by a long narrowing portion towards a round head. Tail long (95  $\mu\text{m}$ ) and thin. Posterior cylindrical part of the tail  $\frac{1}{3}$  of the tail length. Inner labial sensilla not recognizable. Outer labial and the cephalic setae equally



**Figure 3.** *Manganonema antarctica* sp. nov. a-c: male; a) total body; b) anterior end; c) testis. *Manganonema bussauensis* sp. nov. d-g: male; d) total body; e) posterior end; f) testis; g) anterior end.

**Figure 3.** *Manganonema antarctica* sp. nov. a-c : mâle ; a) corps total ; b) extrémité antérieure ; c) testicule. *Manganonema bussauensis* sp. nov. d-g : mâle ; d) corps total ; e) extrémité postérieure ; f) testicule ; g) extrémité antérieure.



**Figure 4.** *Manganonema* spec. a. a-b: female; a) total body; b) anterior end. *Manganonema* spec. b. c-f: female; c) total body; d) anterior end; e) anterior genital branch; f) posterior end.

**Figure 4.** *Manganonema* spec. a. a-b : femelle ; a) corps total ; b) extrémité antérieure. *Manganonema* spec. b. c-f : femelle ; c) corps total ; d) extrémité antérieure ; e) branche génitale antérieure ; f) extrémité postérieure.



long (2  $\mu\text{m}$ ). Amphidial fovea at 24  $\mu\text{m}$  from anterior end, wide (12  $\mu\text{m}$ ) corresponding to 50% cbd. Pharynx relatively short and narrow, measuring  $1/7$  of the total body length. Pharyngeal-intestinal junction with a distinct round cardia.

Male reproductive system typical of genus. Single anterior testis with short germinal zone; vas deferens long and narrow. Spicules relatively small (8  $\mu\text{m}$  long). No gubernaculum nor supplements observed.

#### Diagnosis

*Manganonema antarctica* sp. nov. is characterized by a relatively long body (880  $\mu\text{m}$ ), long narrowing anterior portion (24  $\mu\text{m}$ ), a long tail (95  $\mu\text{m}$ ) with a long cylindrical part ( $1/3$  of its length) and a round cardia.

*M. antarctica* sp. nov. can be distinguished from the others by the long narrow anterior portion, short outer labial setae (2  $\mu\text{m}$ ), a set off cardia, and a tail with a long cylindrical part ( $1/3$ ). This new species resembles *M. bussauensis* sp. nov., but differs by spicules length (8  $\mu\text{m}$  vs. 13  $\mu\text{m}$ ), somewhat shorter body, tail shape with a longer cylindrical portion and setiform outer labial and cephalic sensilla.

#### *Manganonema bussauensis* sp. nov. (Fig. 3)

#### Material studied

One male; slide number 104105.

#### Locality

North Atlantic - N43°15' W13°05'4" (Eumeli, 2000 m).

#### Measurements

Holotype Male: -  $\frac{135}{3}$   $\frac{M}{26}$   $\frac{659}{26}$   $\frac{980}{18}$   $\mu\text{m}$

a = 37; b = 7; c = 9; c' = 6; Spic = 13  $\mu\text{m}$

#### Description

Body relatively long and wide. Anterior end narrowing towards the slightly swollen head. Tail cylindrical proximally tapering evenly towards the pointed tip. Labial and cephalic sensilla not observed. A refractive oval structure situated laterally to the head resembling the second amphidial fovea of the family Thoracostomopsiidae, however much simpler. Amphidial fovea 7  $\mu\text{m}$  in diameter or 60% of cbd, situated 25  $\mu\text{m}$  from anterior end. Somatic setae (2  $\mu\text{m}$  long), arranged in four longitudinal rows along the body (2 latero-ventral; 2 latero-dorsal). Pharyngeal-intestinal junction characterized by a triangular/conical cardia.

Male testis with a long germinal zone corresponding to  $1/2$  of its length. Spicules 13  $\mu\text{m}$  long and straight, corresponding to 70% abd.

#### Diagnosis

*Manganonema bussauensis* sp. nov. is characterized by the long (980  $\mu\text{m}$ ) and wide body (a = 37), a testis with a long germinal zone ( $1/2$  of its length), relatively long spicules (70% of abd) and tail with an anterior conical part and a posterior narrowing portion tapering continuously to a pointed tip.

This new species is morphologically close to *M. antarctica* sp. nov. but differs at the spicules length, body and tail shape, and on the length of cephalic sensilla (see former description).

#### *Manganonema* spec. a (Fig. 4)

#### Material studied

One female, slide number 104106.

#### Locality

South-western Atlantic Ocean, Brazil - S22°20' W42°00' (1000 m).

#### Measurements

Female: -  $\frac{125}{4}$   $\frac{426}{25}$   $\frac{668}{25}$   $\frac{735}{18}$   $\mu\text{m}$

a = 30; b = 6; c = 9; c' = 5; V = 58%

#### Description

Body cylindrical, medium-sized and relatively stout. Anterior end strongly tapered gradually towards a rounded relative robust head (4  $\mu\text{m}$ ). Tail largely conical, posterior fourth narrow cylindrical. Outer labial and cephalic sensilla papilliform (1  $\mu\text{m}$ ). Amphidial fovea 5  $\mu\text{m}$  in diameter or about 50% of cbd, located at 22  $\mu\text{m}$  from anterior end. Pharynx narrow cylindrical, ending with a small terminal bulb. Cardia small and round.

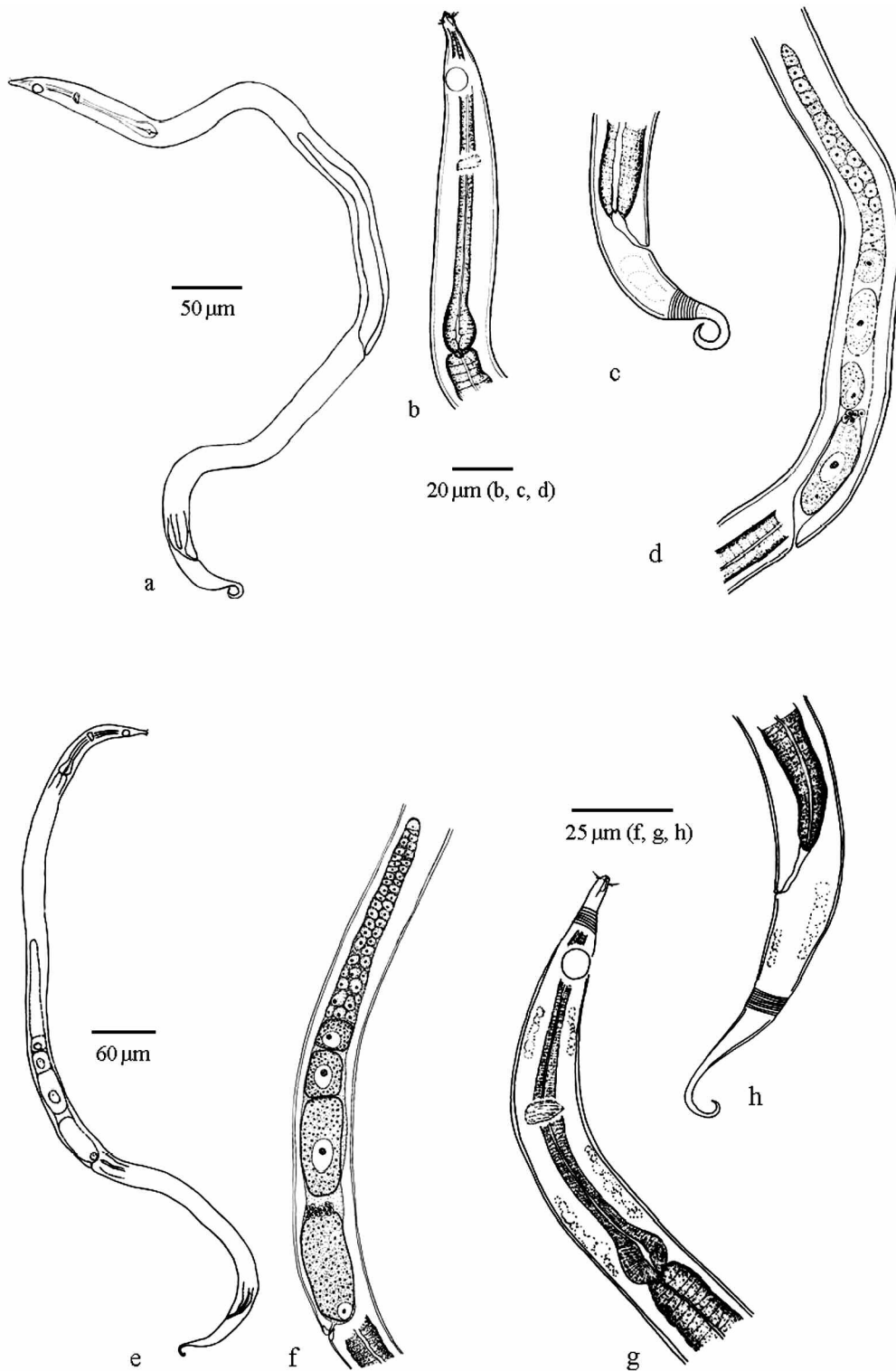
Female reproductive system typical of genus; anterior gonad short, germinal zone corresponding to half of its length.

Males not observed.

#### Diagnosis

*Manganonema* spec. a is characterized by a relatively stout body (a = 30), a short narrowing anterior part ending towards a rather broad head (4  $\mu\text{m}$ ), small amphidial fovea (50% of cbd), and papilliform anterior sensilla of the second crown.

*M. spec. a* can be distinguished from most other *Manganonema* species by the short narrow anterior part ending towards a large head diameter and the presence of papillae at the second circlet. In addition it is characterized by a relatively robust appearance (a = 30) and a tail with short pronounced cylindrical terminal part.



**Figure 5.** *Manganonema* spec. c. a-d: female; a) total body; b) anterior end; c) posterior end; d) anterior genital branch. *Manganonema* spec. d. e-h: female; e) total body; f) anterior genital branch; g) anterior end; h) posterior end.

**Figure 5.** *Manganonema* spec. c. a-d : femelle ; a) corps total ; b) extrémité antérieure ; c) extrémité postérieure ; d) branche génitale antérieure. *Manganonema* spec. d. e-h : femelle ; e) corps total ; f) branche génitale antérieure ; g) extrémité antérieure ; h) extrémité postérieure.

*Manganonema* spec. *b*  
(Fig. 4)

*Material studied*

One female; slide number 104107.

*Locality*

South Sandwich Trench - S58°50'85" W26°27'57" (4000 m).

*Measurements:*

Female:  $\frac{-}{3} \frac{143}{17} \frac{420}{17} \frac{641}{14} \frac{725}{14} \mu\text{m}$   
a = 45; b = 5; c = 9; c' = 6; V = 58%

*Description*

Body medium-sized and relatively slender (a = 45). Head narrow round, separated from the rest of the body by a narrowing region. Tail tapering towards the tip. Inner labial sensilla not observed. Six outer labial setae 5  $\mu\text{m}$  long, and longer than the four cephalic setae (3  $\mu\text{m}$ ). Amphidial fovea located at 32  $\mu\text{m}$  from anterior end, relatively wide (8  $\mu\text{m}$ ) or 60% of cbd. Posterior to the amphid fovea two short somatic setae, 3  $\mu\text{m}$  long. Pharynx with elongated end bulb.

Reproductive system typical of genus; vulva shortly posterior to mid-body (V = 58%). Although no males were found, small globular spermatozooids were present in the uterus.

Males not observed.

*Diagnosis*

This species is characterized by the relatively long outer labial setae (5  $\mu\text{m}$ ) and slightly shorter cephalic setae (3  $\mu\text{m}$ ), the amphidial fovea with a relatively posterior position (at 32  $\mu\text{m}$  from anterior end), the presence of two somatic setae just posterior to the amphidial fovea, the long tail (84  $\mu\text{m}$ ) and the elongated pharyngeal bulb.

*Manganonema* spec. *b* is unique in possessing long outer labial setae (5  $\mu\text{m}$ ) when compared with the others species and by a more elongated pharyngeal end bulb. It resembles *M. pitilica* sp. nov. in the more posterior position of the amphidial fovea but differs by the fovea being smaller in relation to cbd (60% vs. 90%). It also possesses a relatively long tail though rather shorter than *M. pitilica* sp. nov. (c' = 6 vs. c' = 8).

*Manganonema* spec. *c*  
(Fig. 5)

*Material studied*

One female, slide number 104108.

*Locality*

Western Indian Ocean - S04°21'83" W13°05'4" (2000 m).

*Measurements*

Female:  $\frac{-}{3} \frac{91}{14} \frac{304}{19} \frac{506}{12} \frac{555}{12} \mu\text{m}$   
a = 40; b = 7; c = 9; c' = 6; V = 60%

*Description*

Body slender and short, tapering towards both extremities. Anterior end tapering gradually to a short and slightly pointed set off head. Tail short (49  $\mu\text{m}$  long) with a cylindrical portion corresponding to  $\frac{1}{3}$  of its length. Inner labial sensilla difficult to recognize with the light microscope. Outer labial and cephalic sensilla papiliform. At the head an indistinct structure drop-shaped resembling the second amphidial fovea in the family Thoracostomopsidae, however much simpler. Amphids corresponding to 50% cbd and placed at 14  $\mu\text{m}$  from the anterior end. Pharyngeal-intestinal junction characterized by a small cardia.

Reproductive system with a vulva located at shortly posterior to mid-body (V = 58%). Germinal zone of anterior gonad as long as the uterus.

Males not observed.

*Diagnosis*

*Manganonema* spec. *c* is characterized by the short body length (555  $\mu\text{m}$ ), the pointed head, the relatively small amphidial fovea, 50% of cbd, and the tail with a cylindrical posterior third.

This species can be distinguished from the other species of the genus mainly by the short body length and the pointed head. The head region resembles the head of *M. spec. d*, but *M. spec. c* is half the size of *M. spec. d*.

*Manganonema* spec. *d*  
(Fig. 5)

*Material studied*

Three females and three juveniles; slide number 104109.

*Locality*

North Atlantic Deep site-Eumeli.

*Measurements*

Female<sub>1</sub>:  $\frac{-}{3} \frac{132}{23} \frac{530}{23} \frac{971}{18} \frac{1065}{18} \mu\text{m}$   
a = 46; b = 8; c = 11; c' = 5; V = 51%  
Female<sub>2</sub>:  $\frac{-}{3} \frac{111}{20} \frac{536}{20} \frac{920}{17} \frac{1025}{17} \mu\text{m}$

a = 51; b = 9; c = 10; c' = 6; V = 52%

Female<sub>3</sub>: - 105 465 860 920 μm  
                   3 15 15 11

a = 52; b = 7; c = 12; c' = 6; V = 51%

Juveniles stage (n= 3): L = 500–576 μm; a = 42-54; b = 6-7; c = 9-13; c' = 5-7

#### *Description female*

Body long and cylindrical, tapered towards both ends. Tail pointed and long (93 μm), proximal part conical and distal fourth cylindrical. Inner labial sensilla difficult to recognize by light microscopy. Six outer labial and the four cephalic setae measuring 3 and 2 μm, respectively. A refractive drop-shaped structure located at the level of the cephalic setae Amphidial fovea 63 % of cbd and located at 23 μm from the anterior end, or about eight times the head diameter. Pharyngeal-intestinal junction characterized by a triangular cardia.

Female reproductive system typical of genus; germinal zone corresponding to half of the total ovary length. Vulva at mid-body (V = 52%).

Males not observed.

#### *Diagnosis*

*Manganonema* spec. *d* is characterized by the long and slender body length (longer than 1 mm), the pointed head, and the conical tail with short cylindrical anterior portion. *M. spec. d* resembles *M. spec. c* at the anterior end, but has larger amphidial fovea and longer anterior sensilla. In addition, *M. spec. d* is easily distinguished from the other species of the genus by the long thin body (920-1065 μm; a = 46-52).

### **Pictorial Key to species of the genus**

#### ***Manganonema***

Since a small number of species were recorded, and most of them in low densities, the simplest way to show their diversity and proportions as easy identification guide is with a pictorial key coupled with tabulated descriptions of the most important diagnostic characters (Table 1). This type of illustration has proved to be very useful for the generic identification of marine nematodes (Warwick et al., 1998).

### **Genus and species distribution**

Small numbers of specimens hampers the proper taxonomic description of new species. However, this is a typical situation for deep-sea studies, made more difficult by the small size of many adult specimens and the low proportion of males present in samples. This situation is a consequence of

the large number of rare species commonly encountered in this environment (Gray et al., 1997; Gambi et al., 2003; Lamshead et al., 2003). Hence, even with a larger quantity of mud or more numerous samples it remains difficult to collect several individuals from the same species.

The genus *Manganonema* is recorded in many oceans in sediments deeper than 1000 m, in low to intermediate densities, usually representing less than 2% of the nematode community (e.g. Southern Ocean, Vanhove et al., 1999; South west Atlantic, Netto et al., 2005) and never exceeding 2% (Lamshead et al., 2003). Like the genera *Bathyeurystomina* and *Bathychaetosoma*, the genus *Manganonema* is probably restricted to deep waters. All other genera typical from deep-sea sediments (e.g. *Acantholaimus*, *Monhystera*, *Halalaimus*) are also present, although mostly represented by different species, in shallow water and coastal habitats. The only species recorded at shallower depths (600 m) was *M. antarctica* sp. nov. at the Weddell Sea. This observation can be supported by the abiotic conditions of the Weddell Sea sediments, which are comparable to deeper sites in other oceans (Arntz et al., 1994; Vanhove et al., 1999).

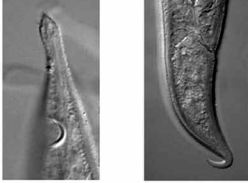
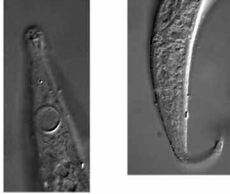
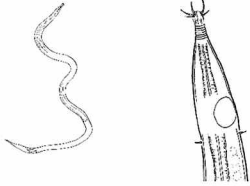
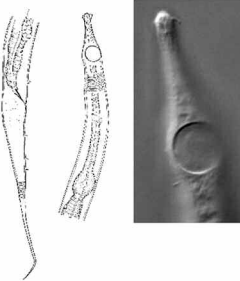
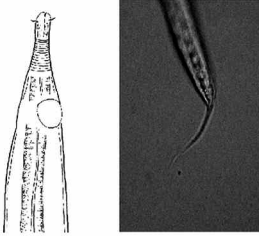
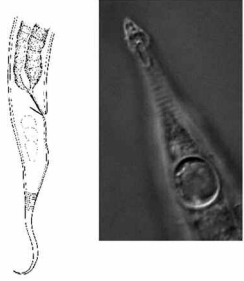
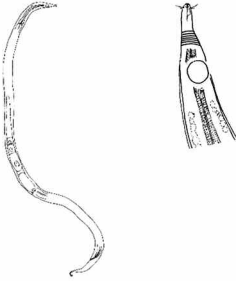
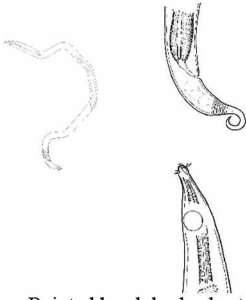
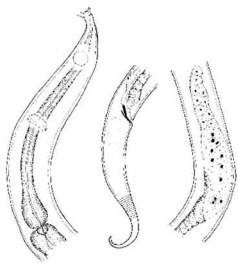
Most dominant deep-sea nematode genera are considered as cosmopolitan, leading consequently to a low generic turnover within and even between ocean basins supporting a relatively low increase in regional (β)-diversity compared to local biodiversity estimates at generic level (Vanhove et al., 1999; Lamshead & Boucher, 2003). At the species level little is known about the geographic distribution ranges of species, and thus also the species-turnover between areas is unknown (Lamshead et al., 2003; Lamshead & Boucher, 2003; Vermeeren et al., 2004). Although limited, the actual distribution of known *Manganonema* species shows a high turnover of species between the different areas and, therefore, rather suggests a certain degree of endemism within oceans, since almost all deep-sea site analyzed showed the presence of different species (Table 2). Nevertheless, an exception was observed. Two males from the new species *M. media* sp. n. were observed at different places, one at the south-western Atlantic deep sea and other in the North Atlantic samples (Table 2). There is no doubt that the genetic flow between these populations is restricted. The distance between the two sites is larger than 8000 km. Therefore, they probably are an example of non-equilibrium meta-populations that were separated somewhere in the past and at present there is no immigration between the different populations. However, it is also important to remember that the identification was done by light microscopy and most likely they could be considered as cryptic species, which could be confirmed by molecular studies.

At some sites more than one species was observed (Table 2). At the south-western Atlantic Ocean deep-sea site



**Table 1.** Pictorial-key for all the species of the genus *Manganonema*, with a short differential diagnosis and place of occurrence with the respective depth.

**Tableau 1.** Image illustrée pour toutes les espèces du genre *Manganonema*; avec un court diagnostic différentiel et endroit d'occurrence avec la profondeur respective

Type species <i>Manganonema microcephalum</i> (Bussau, 1993) - Pacific Ocean 4000 m depth Diagnosis : Tail tapering gradually ( $c = 10$ ; $c' = 5$ ), body length of 660-1000 $\mu\text{m}$ ( $a = 39$ -42), amphids 50%, head width $> 4 \mu\text{m}$ ; spicule = 10 $\mu\text{m}$ .			
<b>Species</b>	<i>M. robustus</i> sp. nov.	<i>M. spec. a</i>	<i>M. spec. b</i>
<b>Pictures</b>			
<b>&amp;</b>			
<b>Diagnosis</b>	Pointed head, small amphids (40%); body wide and long 980 $\mu\text{m}$ , tail short ( $c = 15$ ; $c' = 3$ )	Large head (4 $\mu\text{m}$ ); wide and stout body ( $a = 30$ ); cylindrical part of the tail of 1/4	Long outer labial and cephalic setae, amphids 60% cbd and posterior (amp ant=32 $\mu\text{m}$ )
<b>Occurrence (depth)</b>	SW Atlantic Ocean- (1000m)	SW Atlantic Ocean - (1000m)	Weddell Sea (3000 m)
<b>Species</b>	<i>M. pitilica</i> sp. nov.	<i>M. antarctica</i> sp. nov.	<i>M. bussauensis</i> sp. nov.
<b>Pictures</b>			
<b>&amp;</b>			
<b>Diagnosis</b>	Large amphids (90%); elongated anterior region; thin tail ( $c' = 8$ ), slender body ( $a = 47$ ).	Outer labial and cephalic setae 2 $\mu\text{m}$ ; amphids 50% cbd; tail with a long cylindrical part (1/3)	Long body (980 $\mu\text{m}$ ); low a value (37); tail tapering in the second half; relative long spicules (13 $\mu\text{m}$ )
<b>Occurrence (depth)</b>	SW Atlantic Ocean - (1000m)	Weddell Sea (4000 m)	Northern Atlantic Ocean (1250 m)
<b>Species</b>	<i>M. spec. d</i>	<i>M. spec. c</i>	<i>M. media</i> sp. nov.
<b>Pictures</b>			
<b>&amp;</b>			
<b>Diagnosis</b>	Long body length ( $> 980 \mu\text{m}$ ), pointed head and amphids about 65% cbd	Pointed head, body short (555 $\mu\text{m}$ ), tail with a long cylindrical tip ( $c = 9$ ; $c' = 6$ ); amphids 50% cbd	Round head, body length 605-740 $\mu\text{m}$ , amphids 60%, tail conical with a short cylindrical part ( $c = 10$ , $c' = 5$ )
<b>Occurrence (depth)</b>	Northern Atlantic Ocean (1250 m)	Western Indian Ocean (2000 m)	SW Atlantic -(1000m) & Northern Atlantic Ocean (1250 m)



**Table 2.** Occurrence of all described species from the genus *Manganonema* in the different oceans.**Tableau 2.** Occurrence de l'espèce du genre *Manganonema* dans les différents océans

Locality	<i>M. microcephalum</i>	<i>M. pitilica</i> sp. nov.	<i>M. robustus</i> sp. nov.	<i>M. spec a</i>	<i>M. media</i> sp. nov.	<i>M. spec d</i>	<i>M. bussauensis</i> sp. nov.	<i>M. spec c</i>	<i>M. spec b</i>	<i>M. antarctica</i> sp. nov.
Southern Ocean:										
1. South Sandwich Trench										x
2. Wedell Sea									x	x
Western Indian Ocean (Kenya)								x		
South-western Atlantic Ocean (Brazil)		x	x	x	x					
North-eastern Atlantic Ocean:										
1. Goban Spur					x	x				
2. Eumeli						x	x			
Central Pacific Ocean (Bussau, 1993)	x									

(at 1000 m water depth), for example, four different species of the genus *Manganonema* were found in the same location, although from four different samples. This phenomenon of high local species richness within genera has already been observed and discussed by different authors (Tietjen, 1984; Vanreusel et al., 1997; Vanhove et al., 1999; Lamshead et al., 2000). The high number of species within the genus *Manganonema* in combination with a high turnover of species between different regions suggests a high degree of local speciation in the deep sea.

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