

Taxonomy and biogeography of *Molgolaimus* Ditlevsen, 1921 (Nematoda: Chromadoria) with reference to the origins of deep sea nematodes

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Abstract: *Molgolaimus* is a genus of free-living marine nematodes which is found in high densities (10–35% of the total community) up to 2000 m depth. Its occurrence is often associated with organically enriched and recently disturbed areas. Currently, only 16 species have been described, mainly from shallow waters. The present study contributes 17 new species mainly from the Weddell Sea but also from the Pacific Ocean, and provides an illustrated polytomous identification key to species level. The 33 *Molgolaimus* species described can be identified based on just a few morphometric features: spicule length, body length, anal body diameter, tail length and pharynx length. A first insight into the biogeography of this deep sea genus at species level is presented. A comparison of morphometric characteristics between species suggests that the most similar species co-occur in the same geographical region, rather than within the same bathymetric zones or similar ecosystems separated over long distances. These observations suggest that deep sea nematodes may not have a common origin but might have derived “recently” from shallow water taxa. Therefore, global distribution of nematodes could be explained by means of palaeogeographical events.

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Key words: Desmodoridae, Molgolaiminae, polytomous key, Southern Ocean

Introduction

Since the beginning of the last century many scientific expeditions have explored the Southern Ocean. Up to now, the Antarctic mega- and macrobenthic fauna has been regarded as very diverse and endemic (Dayton 1990, Arntz *et al.* 1994). Nematoda, the most abundant taxon of the meiofauna (80–90%; Vanreusel *et al.* 1995, Vanaverbeke *et al.* 1998, Vanhove *et al.* 1999, Netto *et al.* 2005) is also characterized by a high number of species, of which only very few are as yet described (Vermeeren *et al.* 2004).

Ecological studies on marine nematodes in the Weddell Sea and adjacent areas have shown that the genus *Molgolaimus* Ditlevsen, 1921 is one of the most abundant genera (Vanhove *et al.* 1999, 2004, Lee *et al.* 2001). Moreover, this genus is present in all oceans from shallow waters to the deep sea in relatively high abundances (10–35% of the total community) (Muthumbi & Vincx 1996, Vanreusel *et al.* 1997, Danovaro *et al.* 1999, Vanhove *et al.* 1999, Lamshead *et al.* 2000, Gambi *et al.* 2003). The genus often appears to be more abundant in recently colonized sediments, such as sediments near hydrothermal vents (Vanreusel *et al.* 1997) or on the continental slope of the Weddell Sea, where physical disturbance occurs by the constant shifting of large amounts of sediment due to iceberg scour (Vanhove *et al.* 1999, Lee *et al.* 2001). In an

experimental study on the colonization of sediments, Schratzberger *et al.* (2003) also found that a species of *Molgolaimus* is an opportunistic colonizer in shallow sandy sediments.

In general, the biogeographical distribution of small deep sea endobenthic species is poorly known (Gage 1996, Rex 1997). Nematodes, the most abundant and probably most speciose endobenthic metazoan group, have not yet been investigated. Nevertheless, speculations on the total number of deep sea nematodes species are ongoing since the discussion on the conservation of the marine ecosystem has gained more attention in recent decades (Lamshead 1993, Snelgrove & Smith 2002, Lamshead *et al.* 2003).

At present, the genus *Molgolaimus* contains 16 species. The present work describes 17 new species and provides an illustrated polytomous identification key to the species level. Polytomous or lattice identification keys were first introduced for the plant parasitic nematodes (Luc & Dalmaso 1974) and more recently for marine taxa (Decraemer & Gourbault 2000). The addition of scatter-plot graphs for morphometric data and illustrations of the different *Molgolaimus* species reduces the numbers of steps in the identification process and allows new species to be easily added.

Table I. Coordinates of the sampling stations with the respective sediment layer and water depth.

Locations	Coordinates		Slice (cm)	Depth (m)
Fiji	16°57.50'S	173°55.75'E	0–1	2000
Kapp Norvegia	70°52.1'S	10°29.4'W	0–1	244
			1–3	
			3–5	
	71°32.3'S	13°31.7'W	0–1	255
			1–3	
			3–5	
	70°49.4'S	10°38.7'W	0–1	332
			1–3	
			3–5	
Vest Kapp	71°06.2'S	13°02.0'W	0–1	1200
			1–3	
			3–5	
	73°34.2'S	22°38.0'W	0–1	994
			1–3	
			3–5	
Bransfield Strait	73°23.7'S	22°09.1'W	0–1	1985
			1–3	
			3–5	
	62°15.8'S	58°42.7'W	0–1	207
			1–3	
			3–5	
	70°49.8'S	10°38.9'W	0–1	298
			1–3	
			3–5	
	62°16.8'S	58°42.1'W	0–1	423
			1–3	
			3–5	
Drake Passage	61°34.5'S	58°07.0'W	0–1	429
			1–3	
			3–5	
	61°26.7'S	58°06.6'W	0–1	1028
			1–3	
			3–5	
Epos Cruise	73°28.0'S	20°38.0'W	0–1	217
			1–3	
			3–5	
Halley Bay	74°32.2'S	29°17.7'W	0–1	1200
South Sandwich Trench	57°35.28'–58°50.85'S	23°58.26'–26°27.57'W	0–1	747
			0–1	1100
			0–1	2000
			0–1	4000

Methodology

The present study is based on the material collected at seven sites in the Atlantic part of the Southern Ocean and in one site in the Pacific Ocean near Fiji Island. The Southern Ocean samples were taken at four sites on the continental slope of the Weddell Sea (i.e. Kapp Norvegia, Vestkapp, Halley Bay and Epos), one site in the Drake Passage, one site at the South Sandwich Trench and one site in the Bransfield Strait near King George Island (Table I). Details on the southern stations are given by EPOS (Vanhove *et al.* 1997), EASIZ (Dahms *et al.* 1990), LAMPOS (Bohlman *et al.* 2003) and ANDEEP (Vanreusel & De Mesel 2003) reports. The ecological data on the meiofauna and nematodes, especially nematode genera composition of

these sites, are described in Vanhove *et al.* (1999), and Vanhove *et al.* (2004), while data from the Pacific are given in Vanreusel *et al.* (1997).

All samples were taken by sediment coring and fixed and maintained in formalin 4% until specimens were transferred to anhydrous glycerol following the method of De Grisse (1969). All specimens were mounted on Cobb slides.

Drawings were made with a Leica DMLS microscope. All measurements (in μm) were performed by video capture and Leica Q500+MC software. The curved structures were measured along the arch. The abbreviations of the measurements used are: De Man (1884) 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, c' = tail length divided by the anal body diameter, V = distance of the vulva from the anterior end, V% = distance from the vulva from the anterior end divided by the total body length, L = total body length, W = maximum body width, spic = spicules length, sup = supplement, ph = pharynx length, nr = distance of nerve ring from anterior end, hd = head width at the level of the cephalic setae, amph = diameter of amphidial fovea, amph ant = position of the amphidial fovea from the anterior end, anus = distance of the anus from the anterior end, cbd = corresponding body diameter, F = female, M = male, H = holotype, P = paratype, A = allotype.

Type material has been deposited in the nematode collections of the Ghent University.

Classification of the genus *Molgolaimus*

In agreement with Lorenzen (1981, 1994) the genus *Molgolaimus* belonging to the monogeneric subfamily Molgolaiminae, is classified within the family Desmodoridae based on the presence of a single anterior testis (synapomorphy of the order Desmodorida) and antidromously reflexed ovaries. *Molgolaimus* differs from the other taxa of this family mainly by the possession of round amphidial fovea.

Diagnosis of the genus *Molgolaimus* (adapted)

Desmodoridae: Molgolaiminae. Cuticle finely striated to apparently smooth. Amphidial fovea round and posterior to the cephalic constriction. Inner labial and outer labial sensilla small and in many species difficult to distinguish by light microscopy. Cephalic setae (C. setae in Tables II–V) close to the cephalic constriction (anterior or posterior). Buccal cavity small, weakly sclerotized, narrow and with small teeth. Pharynx corpus narrow cylindrical, ending in a pronounced mainly spherical muscular bulb; pharyngeal lumen weakly sclerotized throughout the corpus but heavily sclerotized at the bulb. Cardia of variable length. Excretory-secretory pore anterior to the nerve ring, seldom posterior to it (may be obscure). Female reproductive system didelphic-

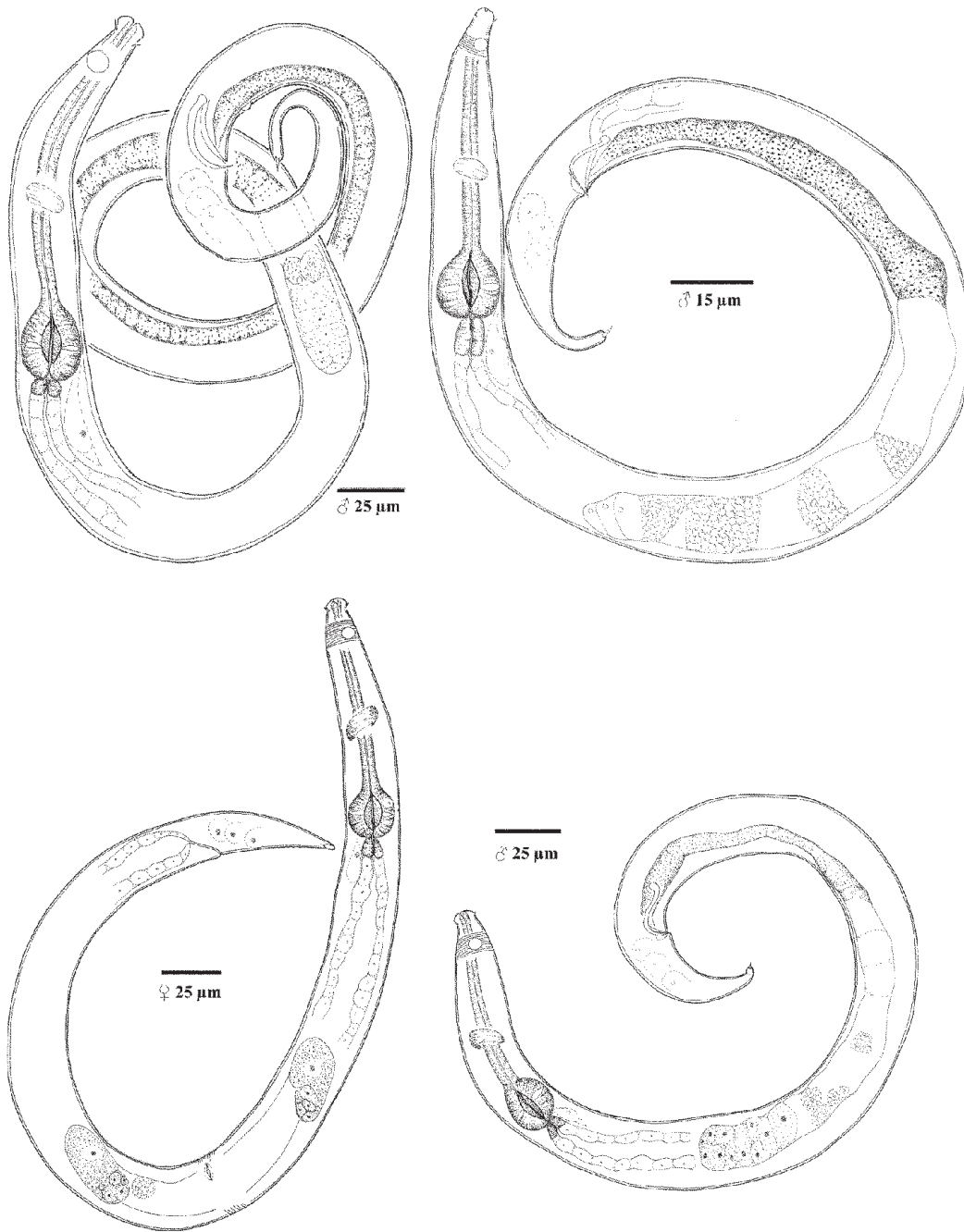


Fig. 1. Total body view:
a. *M. drakus* sp. nov.,
b. *M. carpediem* sp. nov.,
c. *M. sapiens* - female sp.
 nov., **d.** *M. sapiens* sp.
 nov. - male.

amphidelphic, with ovaries reflexed; position of genital branches variable: anterior branch left and posterior branch right of the intestine or reversed, or both branches on the same side of the intestine, either left or right. Spermatheca sometimes present. Male reproductive system monorchic, with a single anterior outstretched testis left or right of the intestine. Vas deferens long and thin. Spicules of variable length and shape from short and bent to long and sinusoidal or straight. Gubernaculum with or without apophysis. Pre-cloacal supplements often present. Tail of varying shape and length, from short conical to elongate slender with the posterior portion cylindrical (digitate).

Descriptions of new species

Molgolaimus drakus sp. nov.
 (Fig. 1)

Etymology: Named after the Drake Passage

Material studied: Three males: 1 holotype male, 2 paratype specimens (slide no. 104070)

Locality: Drake Passage

Measurements: Table II.

Description: Body cylindrical and short. Anterior end

tapering gradually towards an offset head marked by a depression or a faint constriction. Cephalic setae posterior to the cephalic depression. Amphidial fovea 3.5–4.5 μm in diameter at 3 hd from the anterior end. Cardia rather small. Ventral gland cell of the excretory-secretory system relatively large, displacing the intestine towards the dorsal side. Tail long, narrowing gradually posteriorly.

Male testis left of the intestine. Testis relatively small with round sperm cells. Spicules short with a distinct capitulum. Gubernaculum not distinct by light microscopy. One pre-cloacal supplement at 13 μm .

Females unknown.

Diagnosis: *Molgolaimus drakus* sp. nov. is characterized by the short and relatively slim body ($a = 35.5\text{--}42.7$), the small spicules (19–20 μm), the presence of one pre-cloacal supplement and the posterior position of the amphidial fovea from the anterior end (= 3 hd).

Relationships: *M. drakus* is morphologically closely related to the species in group 1b of the identification key, characterized by short spicules (< 35 μm) and a ratio of the spicule divided by the anal body diameter ranging from 1 to 3. Among the species of the group 1b, *M. drakus* has the longest body with the shortest spicules. In addition this species can be differentiated by the presence of one pre-cloacal supplement and the slim body.

Molgolaimus carpediem sp. nov.

(Fig. 1)

Material studied: Three males: 1 holotype male, 2 paratype specimens (slide no. 104071)

Locality: Vest Kapp and Drake Passage

Measurements: Table II.

Description: Body largely cylindrical and short, anterior and posterior end tapered evenly. Head relatively small. Cephalic sensilla short. Amphidial fovea relatively small and 1–1.5 hd from anterior end. Cardia relatively long. Ventral gland cell small. Tail conical relatively short.

Male testis right of the intestine. Testis relatively long with a small germinal zone. Sperm cells round arranged in rhomboid to squared shaped groups. Vas deferens wide at the proximal part and narrower distally near the spicules. Spicules small with a clear capitulum and a curved blade. Gubernaculum small, flanking the distal tip of the spicules. No pre-cloacal supplements observed.

No females collected.

Diagnosis: *Molgolaimus carpediem* sp. nov. is characterized by the short body length (450–505 μm), short spicules (23–26 μm), absence of pre-cloacal supplements, small head diameter (4–5 μm), and a short tail (61–64 μm).

Table II. Morphometric data of *Molgolaimus carpediem* sp. nov., *M. drakus* sp. nov., *M. mareprofundus* sp. nov., *M. sapiens* sp. nov., *M. nettoensis* sp. nov., *M. sabakii*, *M. australis* sp. nov. and *M. unicus* sp. nov. (measurements in μm).

	L	W	hd	amph cbd	amph ant	nr cbd	nr	ph cbd	abd	spic	anus	sup	C. setae	a	b	c	c'	V%	nr/ ph	spic/ abd
<i>M. carpediem</i> sp. nov.																				
H	460	23	5	2	7	6	19	50	21	16	26	395	27	3	20.1	5.2	7.5	3.7	0.6	1.6
P1	510	19	4	4	7	5	15	41	20	16	23	445	-	-	27.1	5.6	8.3	3.8	-	1.4
P2	450	20	4	3	8	6	18	48	19	16	23	390	17	-	22.7	5.7	7.0	4.1	0.6	1.4
<i>M. drakus</i> sp. nov.																				
H	495	12	5	3	8	12	11	41	14	13	20	425	-	2	42.7	6.6	7.1	5.4	0.5	1.6
P1	525	15	5	4	9	13	12	37	14	13	20	460	-	-	35.5	6.1	7.9	5.3	0.4	1.6
P2	575	14	5	4	9	13	12	36	14	13	19	490	13	2	42.4	7.0	7.0	6.2	0.4	1.4
<i>M. mareprofundus</i> sp. nov.																				
H	630	20	5	3	10	10	-	-	20	17	32	540	-	-	30.7	6.7	7.3	5.1	0.0	1.9
P1	610	25	6	4	10	10	18	46	21	18	29	525	-	1	24.1	5.8	7.2	4.6	0.4	1.6
A	630	22	5	3	9	8	18	38	20	17		545	-	2	28.3	6.5	7.6	4.9	0.5	0.4
<i>M. sapiens</i> sp. nov.																				
H	500	24	7	5	11	11	19	48	21	19	35	455		-	21.0	5.9	10.2	2.6	0.6	1.9
A	435	22	6	5	12	10	18	43	18	15		385		-	19.5	5.4	8.8	3.3	0.5	0.5
P1	620	25	7	5	13	15	21	49	21	17		560		2	24.5	6.8	10.5	3.5	0.5	0.5
<i>M. nettoensis</i> sp. nov.																				
H	515	19	6	4	10	9	16	48	20	15	50	430			27.6	5.9	6.0	5.7	0.6	3.3
A	500	23	5	3	8	10	14	41	16	13		415		1	22.0	6.7	6.2	6.4	0.5	0.6
<i>M. sabakii</i>																				
-	590	16	5	5	10	15	13	42	15	13	39	485	12		35.8	6.5	5.5	8.2	0.5	3.0
<i>M. australis</i> sp. nov.																				
H	525	25	5	4	9	6	20	47	21	16	36	465	-	2	20.6	6.1	8.6	3.8	0.6	2.2
P ₁	490	24	5	4	8	6	-	-	22	15		440	-	1	20.3	5.7	9.3	3.6	0.5	-
A	525	26	6	5	10	8	16	35	20	14		460	-	-	20.2	6.1	8.2	4.6	0.5	0.4
P ₂	510	24	6	3	11	10	20	48	21	16		455	-	2	21.1	6.3	9.2	3.4	0.5	0.6
<i>M. unicus</i> sp. nov.																				
H	1060	24	7	4	11	13	21	70	21	19	56	985	20		44.1	8.9	14.6	3.9	0.6	3.0

Relationships: This species is similar to group 1b₂ of the identification key, characterized by short spicules (18–27 μm), ratio spicules divided by the anal body diameter ranging from 1 to 3, and short body length (up to 550 μm). *Molgolaimus carpEDIEM* resembles *M. galluccii* sp. nov. in the general aspects but possesses a lower spic/abd value and head continuous with rest of body. The new species is unique within the species group in having shorter spicules and a very thin L-shaped spicule blade.

Molgolaimus sapiens sp. nov.
(Fig. 1)

Etymology: wisdom

Material studied: One male and two females: 1 holotype male, 1 paratype female, 1 paratype specimens (slide no. 104072)

Locality: South Sandwich Trench

Measurements: Table II.

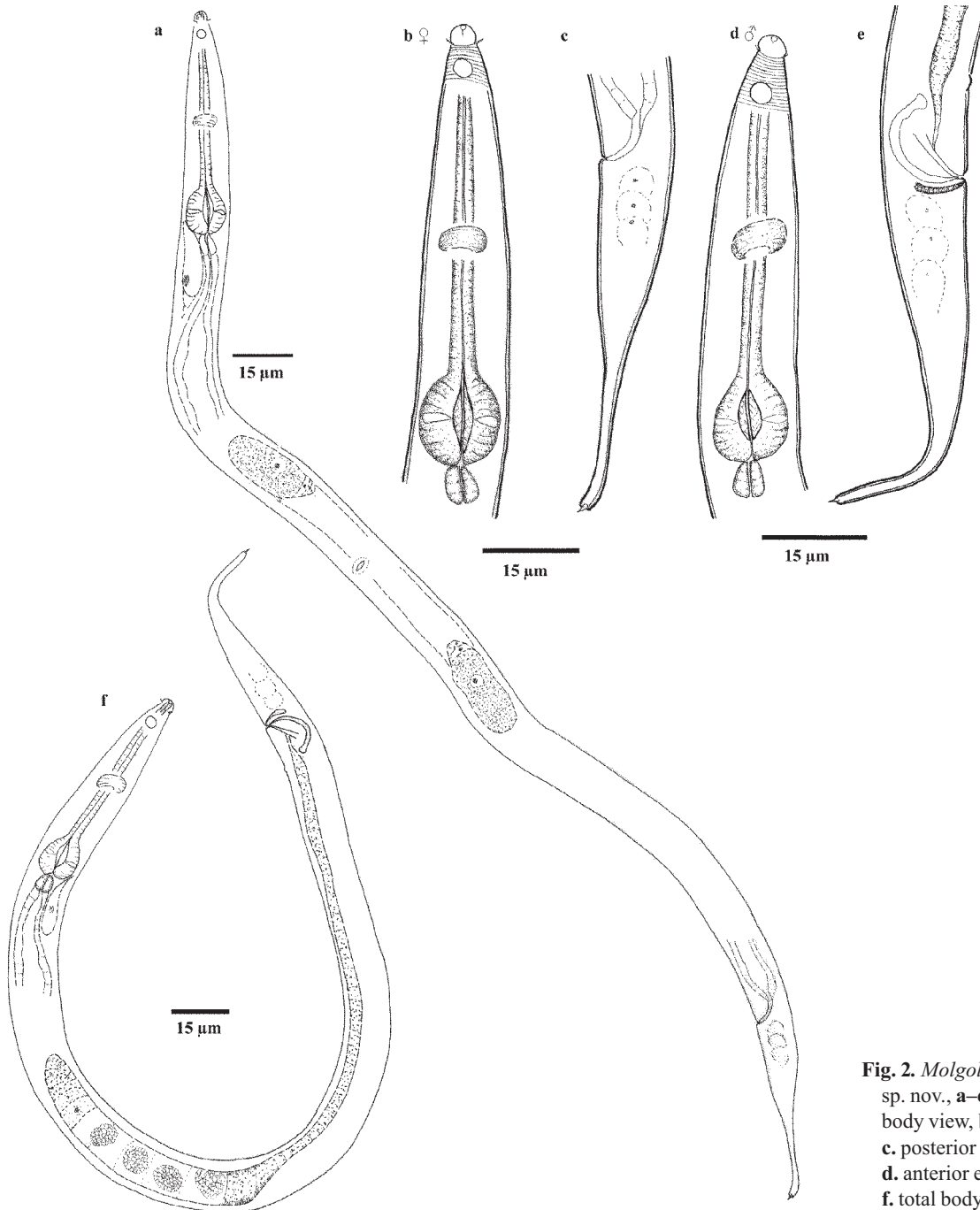


Fig. 2. *Molgolaimus mareprofundus* sp. nov., **a–c**: female, **a**. total body view, **b**. anterior end, **c**. posterior end, **d–f**: male, **d**. anterior end, **e**. posterior end, **f**. total body view.

Description: Body short and cylindrical tapering at both ends. Cephalic setae short at the level of the cephalic constriction. Head relatively wide (see Table V). Amphidial fovea small at 2 hd from the anterior end. Ventral gland small. Cardia small, as long as wide. Tail short and conical.

Male with testis left of the intestine. Spicules slightly curved ventrally with a distinct capitulum. Gubernaculum short, restricted to the distal region of the spicules. No pre-cloacal supplements observed. Spermatozoa round and clustered.

Female reproductive system with the anterior branch left of the intestine and posterior branch to the right. Anterior branch relatively longer than the posterior. Germinal zone relatively short.

Diagnosis: *Molgolaimus sapiens* sp. nov. is characterized by ventrally curved spicules, 1 anal body diameter long, a short body (415–620 μm), a wide head diameter (6–7 μm), relative small amphidial fovea (5 μm in diameter), a short conical tail (49–59 μm) and absence of pre-cloacal supplements.

Relationships: *M. sapiens* is morphologically close to *M. exceptionregulum*, *M. drakus*., *M. gazii* (Muthumbi & Vincx 1996), but differs from them by a longer body length (> 700 μm). *Molgolaimus sapiens* is comparable to *M. drakus* and *M. exceptionregulum* in spicule length but

differs in spicule shape, S-shaped blade and a round capitulum, and by the smaller amphidial fovea, 50% of the cbd vs more than half the cbd in the other species.

Molgolaimus mareprofundus sp. nov.
(Fig. 2)

Etymology: deep sea

Material studied: Two males and one female: 1 holotype male, 1 allotype female, 1 paratype specimens (slide no. 104073)

Locality: Kapp Norvegia

Measurements: Table II.

Description: Body relatively short and slim, tapered gradually towards both ends. Head offset by a clear constriction. Cephalic setae inserted at level of cephalic constriction. Amphidial fovea 2 hd from the anterior end corresponding to 35–40% of the cbd. Cardia relatively short, 5 μm long. Ventral gland cell relatively large, displacing the intestine dorsally, and with two additional cells posterior to it. Tail long and conical.

Male with testis left of the intestine. Testis characterized by a small germinal zone. Sperm cells round clustered in spheres. Spicules ventrally curved with a pronounced capitulum and a very thin blade. Gubernaculum simple and

Table III. Morphometric data of *Molgolaimus exceptionregulum* sp. nov., *M. galluccii* sp. nov. and *M. macilenti* sp. nov. (measurements in μm , average (av), minimum (min) and maximum (max)).

		L	W	hd	amph	amph	amph	nr	nr	ph	abd	spic	anus	sup	C.	a	b	c	c'	V%	nr/	spic/
					cbd	ant	cbd	cbd	cbd	cbd	cbd				setae						ph	abd
<i>M. exceptionregulum</i> sp. nov.																						
H.	M	585	19	5	4	9	9	17	44	20	17	28	520	16	1	28.4	5.7	7.5	3.6		0.4	1.6
P ₁₋₉	av	500	15	5	4	7	42	14	31	16	15	29	430	15	1	33.9	5.8	7.1	4.7		0.4	1.9
P ₁₋₉	min	595	20	5	4	10	10	17	47	20	18	30	520	23	1	29.7	5.9	8.0	4.3		0.5	1.7
P ₁₋₉	max	600	21	5	4	10	11	18	50	21	18	31	520	29	2	31.5	6.1	8.9	4.6		0.5	1.8
A.	F	520	20	5	4	8	8	15	49	17	13		445		2	26.0	5.8	7.0	5.7	0.5	0.5	
P ₁₋₂	av	585	21	4	4	9	9	17	46	19	14		515		2	28.5	6.3	8.3	5.0	0.5	0.5	
P ₁₋₂	min	565	18	4	4	8	9	16	45	17	13		495		2	26.1	6.0	7.9	4.6	0.5	0.5	
P ₁₋₂	max	605	23	5	4	9	9	19	46	21	15		535		2	30.9	6.7	8.8	5.5	0.5	0.5	
<i>M. galluccii</i> sp. nov.																						
H.	M	405	15	4	4	10	7	13	32	15	13	22	350	24	1	26.4	6.3	7.4	4.1		0.5	1.7
P ₁₋₁₁	av	410	15	4	4	9	8	14	39	16	14	25	350	24	1	26.7	5.5	6.7	4.4		0.5	1.8
P ₁₋₁₁	min	355	14	4	3	8	7	13	32	14	13	22	300	21	1	22.1	5.2	6.1	3.9		0.4	1.6
P ₁₋₁₁	max	450	18	5	4	10	9	16	47	17	15	27	380	28	2	31.1	6.3	7.4	4.8		0.6	2.1
A.	F	410	15	4	3	8	9	13	36	16	11		350		1	26.4	5.6	6.9	5.4	0.53	0.5	
P ₁₋₅	av	415	18	5	3	9	8	14	42	16	12		350		1	23.3	5.4	6.8	5.3	0.4	0.6	
P ₁₋₅	min	380	15	4	3	8	7	12	36	13	10		325		1	20.5	5.3	6.5	4.4	0.0	0.5	
P ₁₋₅	max	440	20	5	4	9	10	15	48	17	13		375		1	26.4	5.6	7.1	5.9	0.5	0.6	
<i>M. macilenti</i> sp. nov.																						
H.	M	515	17	5	4	8	12	14	45	16	13	44	440	19	1	30.7	6.0	7.1	5.5		0.5	3.3
P ₁₋₇	av	475	17	5	4	8	11	13	44	16	13	43	410	17	1	28.1	5.8	7.3	5.1		0.6	3.3
P ₁₋₇	min	415	15	5	3	7	9	11	36	13	11	37	360	14	1	24.4	5.0	6.3	4.5		0.4	3.1
P ₁₋₇	max	550	22	5	4	10	14	18	51	19	16	52	475	16	1	30.4	6.4	7.7	6.2		0.6	3.5
A.	F	540	18	5	3	6	6	13	35	16	13		465		1	30.1	6.3	7.1	5.8	0.5	0.4	
P ₁₋₁₅	av	505	19	5	4	9	11	15	43	18	12		430		1	26.6	5.9	6.9	6.2	0.5	0.5	
P ₁₋₁₅	min	420	14	5	2	7	6	13	31	15	10		355		1	21.3	5.0	5.7	5.2	0.4	0.4	
P ₁₋₁₅	max	580	26	6	5	11	14	17	51	33	15		490		2	30.8	7.5	8.0	7.1	0.5	0.6	

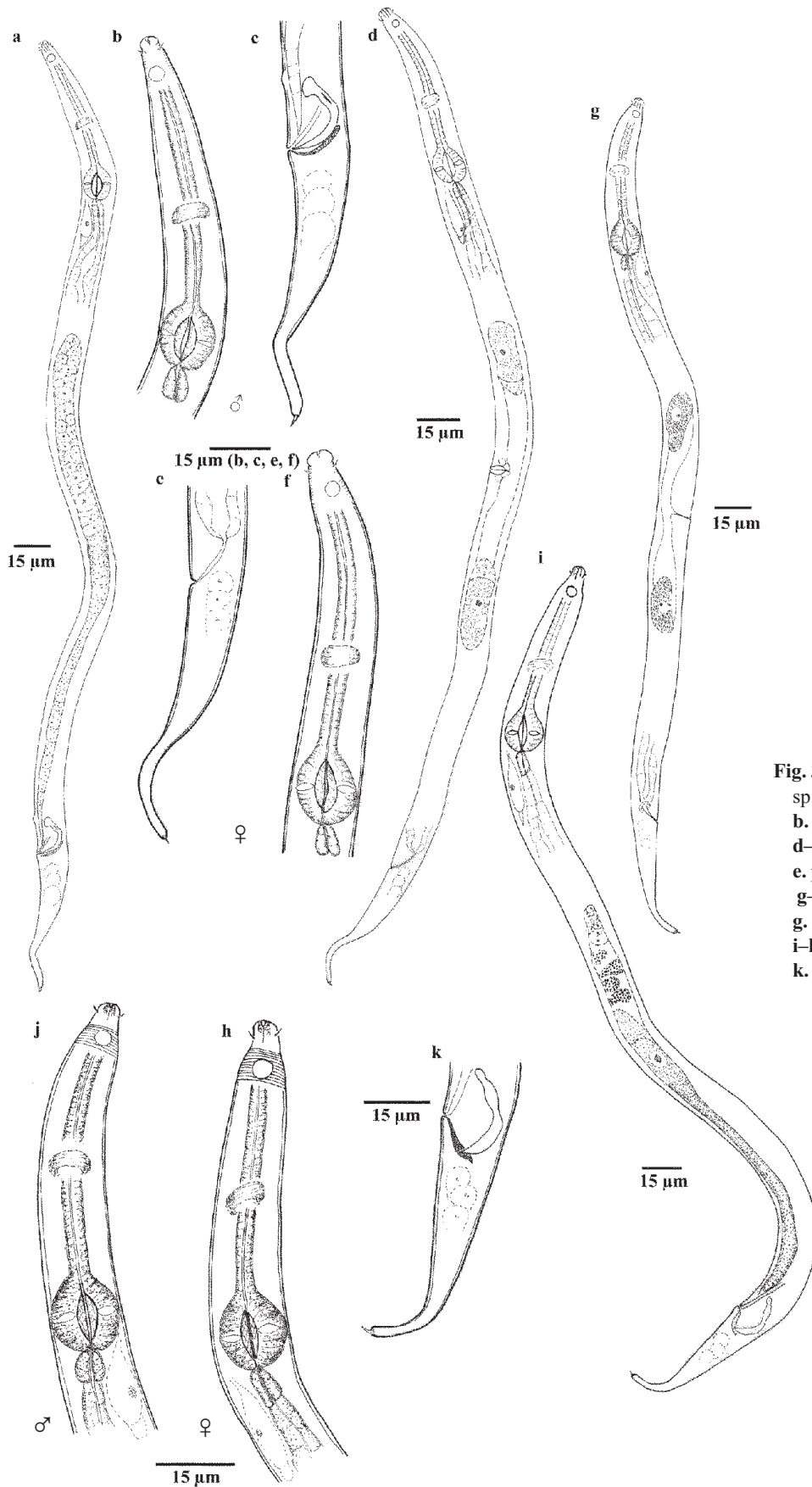


Fig. 3. a–f. *Molgolaimus exceptioregulum* sp. nov., a–c. male, a. total body view, b. anterior end, c. posterior end, d–f: female, d. total body view, e. posterior end, f. anterior end. g–k. *M. galluccii* sp. nov., g–h. female, g. total body view, h. anterior end, i–k: male, i. total body, j. anterior end, k. posterior end.

straight, its length corresponding to one third of the spicule length. One pre-cloacal supplement present.

Female reproductive system with the anterior genital branch left of the intestine and posterior one on the right. Germinal zone short, restricted to 2–3 rows of cells.

Diagnosis: *Molgolaimus mareprofundus* sp. nov. is characterized by the short ventrally curved spicules (29–32 μm), the short body length (610–630 μm), the presence of one pre-cloacal supplement, and a large ventral gland cell.

Relationships: Among the species of group 1b of the identification key, the new species most resembles *M. exceptionregulum* but differs from it by the smaller body length, more slender spicules, the shorter gubernaculum, a testis with a longer germinal zone, and sperm cells clustered in a round shape.

Molgolaimus exceptionregulum sp. nov.

(Fig. 3)

Etymology: “Rule exception”

Material studied: Ten males and three females: 1 holotype male, 1 allotype female, 11 paratype specimens (slide no. 104074)

Locality: Vest Kapp

Measurements: Table III.

Description: Body largely cylindrical and short; anterior end narrowing gradually towards an offset head, separated from the rest of the body by a conspicuous constriction. Cephalic setae relative short, posterior to head constriction. Amphidial fovea representing 40–50% of cbd at 2 hd from the anterior end. Cardia cylindrical, 6–7 μm long. Ventral

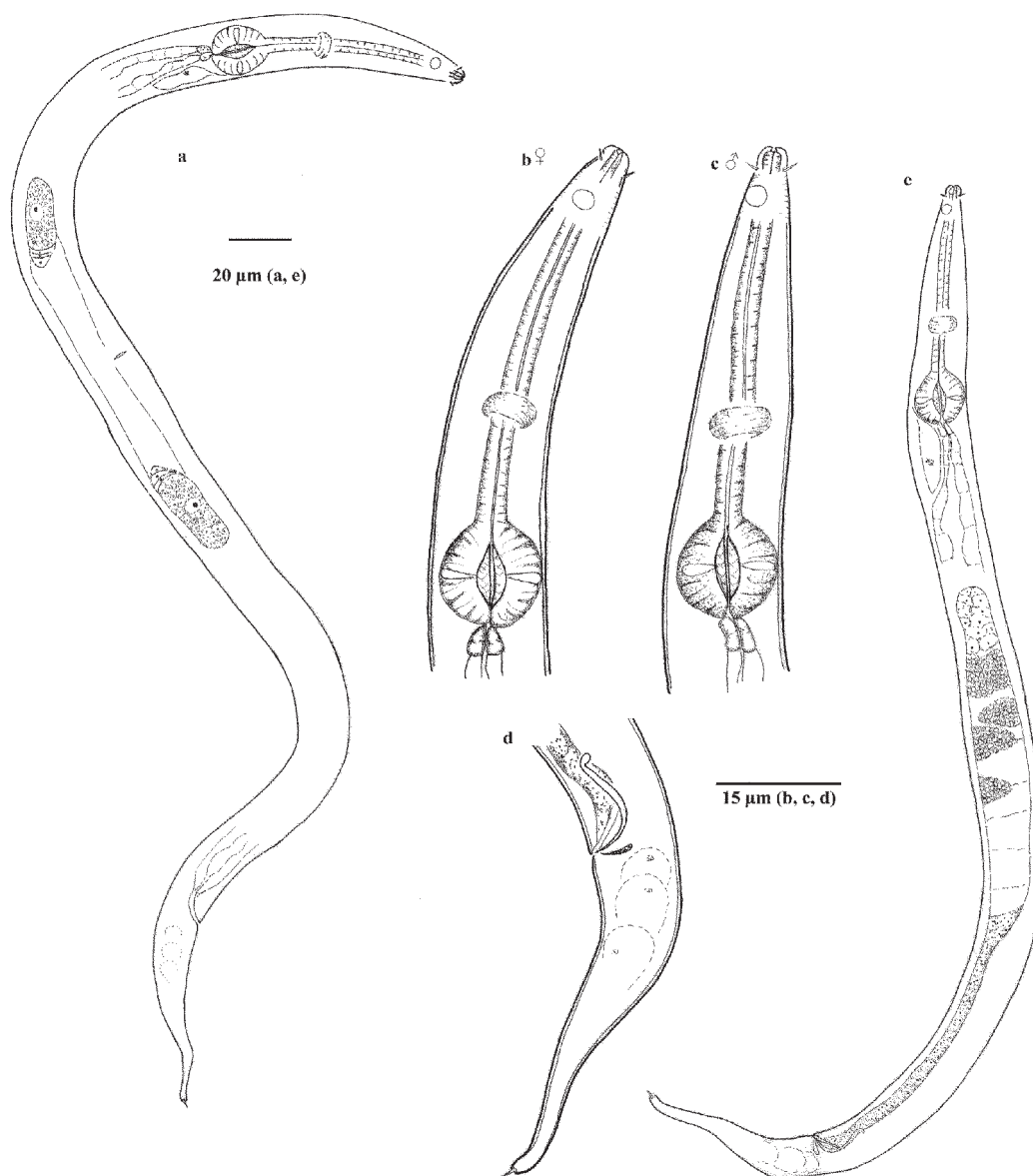


Fig. 4. *Molgolaimus falliturvisus* sp. nov., **a–b**: female, **a**. total body, **b**. anterior end, **c–e**: male, **c**. anterior end, **d**. posterior end, **e**. total body.

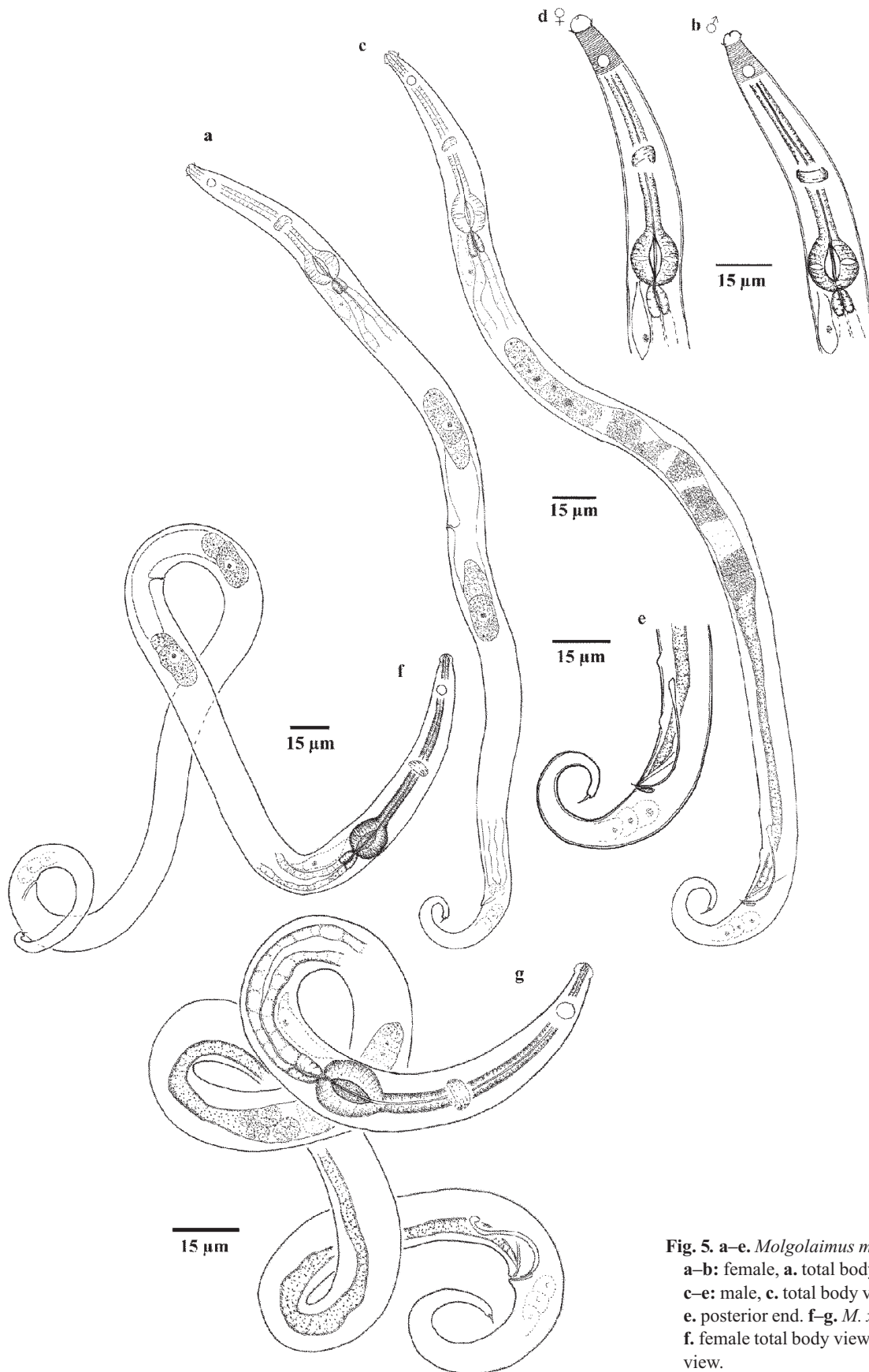


Fig. 5. a–e. *Molgolaimus macilenti* sp. nov., a–b: female, a. total body view, b. anterior end, c–e: male, c. total body view, d. anterior end, e. posterior end. f–g. *M. xuxunaraensis* sp. nov., f. female total body view, g. male total body view.

Table IV. Morphometric data of *Molgolaimus liberalis* sp. nov., *M. walbethi* sp. nov., *M. xuxunaraensis* sp. n and *M. falliturvisus* sp. nov. (measurements in μm , average (av), minimum (min) and maximum (max)).

		L	W	hd	amph cbd	amph ant	nr cbd	nr	ph cbd	abd	Spic	Sup	Tail tip	C. setae	Anus	a	b	c	c'	V%	nr/ ph	spic/ abd	
<i>M. liberalis</i> sp. nov.																							
H.	M	530	15	5	5	10	12	15	49	16	14	59	15		1	440	35.6	6.0	6.1	6.4		0.6	4.3
P ₁₋₁₄	av	545	19	5	4	10	12	16	46	18	15	57	18		1	460	28.0	6.2	6.4	5.8		0.5	3.9
P ₁₋₁₄	min	445	16	5	4	8	10	14	37	16	13	53	15		1	370	25.2	5.4	5.6	4.8		0.5	3.4
P ₁₋₁₄	max	640	23	6	4	11	13	18	53	20	16	64	24		1	535	32.4	6.9	7.5	7.3		0.6	4.2
A	F	580	19	5	5	10	10	15	45	17	13				1	485	30.3	6.9	6.3	7.1	0.5	0.5	
P ₁₋₁₃	av	565	20	5	4	10	12	16	46	18	13				1	475	29.1	6.2	6.2	6.9	0.4	0.5	
P ₁₋₁₃	min	450	15	5	4	8	11	13	38	15	11				1	385	23.5	5.4	5.5	5.4	0.4	0.4	
P ₁₋₁₃	max	660	22	6	5	11	14	19	55	20	15				1	550	35.2	7.3	7.7	8.3	0.5	0.6	
<i>M. walbethi</i> sp. nov.																							
H.	M	540	17	5	3	10	10	15	40	17	12	71	20		1	465	32.5	5.6	7.2	6.2	0.0	0.4	5.8
P ₁	M	560	18	6	4	9	12	15	54	18	13	65	26			475	31.1	5.8	6.7	6.6	0.0	0.6	5.1
A	F	575	19	4	3	9	10	16	44	19	15				1	495	29.6	5.8	7.5	5.2	0.5	0.4	0.0
P ₁₋₃	av	575	20	5	4	9	11	15	40	18	13				1	505	28.6	6.0	8.1	5.6	0.5	0.4	0.0
P ₁₋₃	min	540	18	4	3	8	9	14	30	18	12				1	475	26.8	5.9	7.2	4.1	0.4	0.3	0.0
P ₁₋₃	max	610	23	5	4	9	12	15	49	19	15				1	530	32.1	6.3	9.8	6.6	0.5	0.5	0.0
<i>M. xuxunaraensis</i> sp. nov.																							
H.	M	670	16	5	6	9	12	16	64	18	15	39				585	42.3	6.9	7.7	5.7		0.7	2.6
P ₁	M	700	19	6	4	10	13	17	56	17	15	31				605	37.4	6.9	7.3	6.2		0.6	2.0
A	F	685	16	5	4	9	12	15	52	16	11					595	42.0	6.8	7.7	7.8	0.5	0.5	
P ₁₋₄	av	650	19	5	4	9	13	15	46	16	12					560	34.7	6.6	7.6	6.8	0.5	0.5	
P ₁₋₄	min	600	18	5	4	9	11	13	36	15	12					530	31.5	5.8	7.2	5.9	0.4	0.4	
P ₁₋₄	max	705	20	5	5	10	13	17	53	17	13					610	37.6	7.6	8.3	7.4	0.5	0.5	
<i>M. falliturvisus</i> sp. nov.																							
H.	M	495	22	5	3	8	7	17	47	20	15	26		28	2	425	23.0	5.7	6.9	4.8		0.5	1.7
A	F	520	20	5	4	10	10	17	40	20	14			30	1	450	25.9	5.6	7.4	5.2	0.5	0.4	
P ₁₋₃	av	580	22	5	4	10	10	18	46	20	15			31	1	500	25.9	5.9	7.6	5.1	0.5	0.5	
P ₁₋₃	min	520	20	5	3	9	9	17	40	20	14			27	1	450	24.9	5.6	6.8	4.8	0.5	0.4	
P ₁₋₃	max	615	24	5	5	10	11	19	50	21	16			34	2	520	26.5	6.3	8.3	5.7	0.5	0.5	

gland cell large, with two additional cells posterior to it. Tail conical ending with a digitate prolongation which corresponds to one-quarter of the tail.

Male testis left of the intestine and relatively long, representing 40% of the reproductive system. Spicules short with a pronounced capitulum and a ventrally curved blade; near capitulum, blade provided with an extra lateral structure. Gubernaculum long, i.e. half as long as spicules, and narrow. One pre-cloacal supplement at 16–20 μm .

Female with the anterior genital branch left of the intestine and the posterior branch to the right. Germinal zone relatively short. Vagina differentiated into a more or less oval, refractive pars distalis vaginae and a less marked pars proximalis vaginae.

Diagnosis: *Molgolaimus exceptionregulum* sp. nov. is characterized by small body length, presence of one pre-cloacal supplement, stout spicules with a pronounced capitulum, a blade characterized by a lateral differentiation and a tail with a digitate prolongation.

Relationships: This species is morphologically closely related to *M. drakus*, *M. sapiens*, *M. gazii* (Muthumbi & Vincx 1996), which belong to group 1b of the identification key but differs from them in the longer spicules (28 μm) and

body length ranging from 500 to 600 μm , spicules with a conspicuous L-shape and lateral differentiation, and the presence of a single pre-cloacal supplement.

Molgolaimus galluccii sp. nov.
(Fig. 3)

Etymology: Named after Fabiane Gallucci

Material studied: Twelve males and six females: 1 holotype male, 1 allotype female, 16 paratypes specimens (slide no. 104075)

Locality: Kapp Norvegia, Bransfield Strait (near King George Island) and Epos (near Halley Bay).

Measurements: Table III.

Description: Body short and slender attenuating towards the extremities; head offset by a constriction. Head width narrower than the amphidial body diameter. Cephalic setae relatively short posterior to the cephalic constriction. Amphidial fovea at 2 hd from anterior end. Cardia small, twice as long as wide. Ventral gland cell large displacing the intestine dorsally. Tail conical with a digitate prolongation.

Male testis left of the intestine. Germinal zone relatively

short. Sperm cells clustered, forming a round mass. Spicules ventrally curved with a pronounced capitulum. Gubernaculum weakly sclerotized, straight and small, with posteriorly curved apophysis. One inconspicuous pre-cloacal supplement.

Female reproductive system with the anterior and posterior ovaries left of the intestine.

Diagnosis: *Molgolaimus galluccii* sp. nov. is characterized by a short body (355–450 µm), a narrowing anterior end, ventrally curved spicules with an offset capitulum, gubernaculum with apophysis and one pre-cloacal supplement.

Relationships: *M. galluccii* resembles *M. kiwayui* (Muthumbi & Vincx 1996), *M. carpediem*, *M. falliturvisus*, *M. abyssorum* (Muthumbi & Vincx 1996), *M. minutus* (Jensen, 1988: wrong date in Muthumbi & Vincx 1996), but differs in a very narrow anterior body end, the shape of the spicules with proximal part wider than the distal part, the tail length (52–70 µm) and ratio of spicules divided by cloacal body diameter (1.6–2.1).

Molgolaimus falliturvisus sp. nov.
(Fig. 4)

Etymology: “Appearances are deceptive”

Material studied: One male and four females: 1 holotype male, 1 allotype female, 3 paratype specimens (slide no. 104076)

Locality: Vest Kapp

Measurements: Table IV.

Description: Body largely cylindrical, tapering towards both ends. Head offset by a constriction. Cephalic setae short, inserted close to head constriction. Amphidial fovea at 1.5–2 hd from anterior end, and corresponding to 40–45% cbd. Cardia 7–8 µm long. Ventral gland cell twice as long as cardia. Tail conical proximally, tapering sharply distally towards a cylindrical portion.

Male reproductive system left of the intestine. Germinal zone short; vesicula seminalis relatively large, representing 50% of the reproductive system. Sperm cells round clustered, in a rhomboid shape. Spicules 2 abd long. Capitulum bent dorsally, blade thin and L-shaped. Gubernaculum thin and weakly sclerotized. No pre-cloacal supplements observed.

Female with the anterior genital branch left to the intestine and slightly longer than the posterior branch which is right of the intestine. Germinal zone formed by three rows of cells.

Diagnosis: *Molgolaimus falliturvisus* sp. nov. is characterized by small L-shaped spicules (26 µm), absence of pre-cloacal supplements, long tail tapering sharply near the tip (70–90 µm), large ventral gland cell, and cephalic

setae posterior to head constriction.

Relationships: This new species belongs to group 1b₂ of the identification key, characterized by short spicules ranging from 18 to 26 µm long and a body length between 290 and 500 µm. Among the species of the group (*M. carpediem*, *M. galluccii*, *M. abyssorum*, *M. kiwayui*, *M. minutus*) *M. falliturvisus* has the longest tail and different spic/abd ratio (1.7). The species is closest related to *M. galluccii* and *M. minutus*, but differs from the first species by the continuous head shape and the thin spicules, and from the second species by a gubernaculum without apophysis and by the small body length.

Molgolaimus macilenti sp. nov.
(Fig. 5)

Etymology: thin

Material studied: Eight males and fifteen females: 1 holotype male, 1 allotype female, 21 paratype specimens (slide no. 104077)

Locality: Drake Passage, Kapp Norvegia and Bransfield Strait (near King George Island)

Measurements: Table III.

Description: Body cylindrical with the pharyngeal region very slender. Head offset from the rest of the body by a constriction. Cephalic sensilla small at the level of the constriction. Amphidial fovea circular and small (3.5–4 µm) i.e. 50% of the correspondent body diameter at 10–12 µm from the anterior end. Cardia twice as long as wide. Tail conical cylindrical.

Male reproductive system left of the intestine. Sperm cells clustered. Spicules medium-sized, 3.2–3.5 abd long; capitulum poorly developed. Gubernaculum small and straight. Two equidistant pre-cloacal supplements.

Female with the anterior and posterior ovaries at the right side of the intestine.

Diagnosis: *Molgolaimus macilenti* sp. nov. is characterized by the narrow anterior body region, the medium-sized spicules (43–52 µm), presence of two pre-cloacal supplements and the relatively short tail (54–75 µm).

Relationships: *M. macilenti* is morphologically similar to representatives of group 2 (*M. nettoensis*, *M. australis*, *M. xuxunaranesis*, *M. allgeni* (Allgen 1935), *M. sabakii* (Muthumbi & Vincx 1996)). It is differentiated from these species mainly by the short tail (< 72 µm) and the slender anterior end, but also by the straight spicules, two pre-cloacal supplements and small amphidial fovea (3–4 µm).

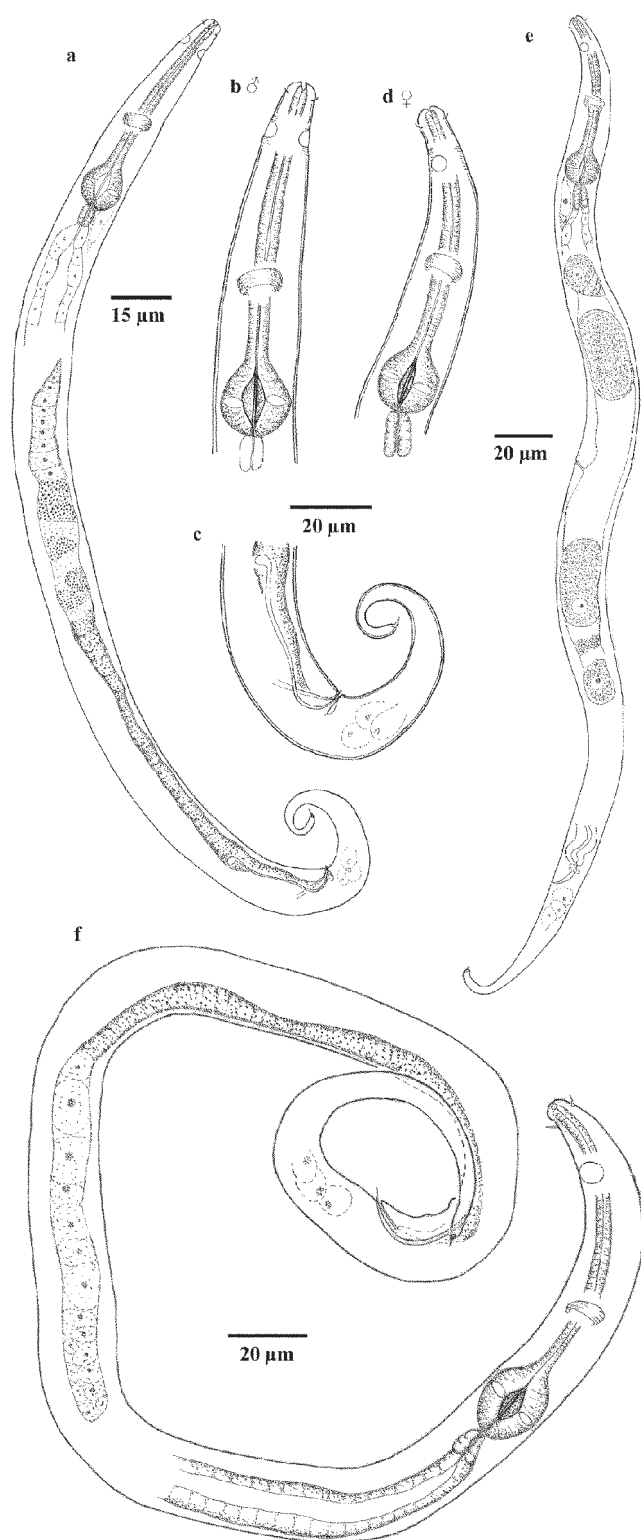


Fig. 6. *Molgolaimus nettoensis* sp. nov., **a–c:** male, **a.** total body view, **b.** anterior end, **c.** posterior end, **d–e:** female, **d.** anterior end, **e.** total body view. **f.** *M. sabakii* total body view.

Molgolaimus xuxunaraensis sp. nov.
(Fig. 5)

Etymology: Named after Maria (Xuxu) Franco and Tania Nara

Material studied: Two males and five females: 1 holotype male, 1 allotype female, 5 paratype specimens (slide no. 104078)

Locality: Kapp Norvegia

Measurements: Table IV.

Description: Body shape slender tapering gradually at both ends. Head offset from the body by a constriction. Cephalic setae not observed by light microscopy. Amphidial fovea 2–2.5 hd posterior to the anterior end. Ventral gland cell relatively large pushing the intestine dorsally. Tail cylindrical.

Male reproductive system left of the intestine. Sperm cells round. Spicules medium-sized (2–2.6 abd), ventrally curved (S-shaped) and with distinct capitulum. Gubernaculum weakly sclerotized and relatively thin. Pre-cloacal supplements lacking.

Female with the anterior ovary located on the left side of the intestine and the posterior one on the right side.

Diagnosis: *Molgolaimus xuxunaraensis* sp. nov. is characterized by an offset head, a slender body shape, absence of pre-cloacal supplements, medium-sized ventrally curved spicules (35–39 µm long) with pronounced capitulum.

Relationships: *M. xuxunaraensis* belongs to species group 2 of the identification key with spicule length ranging from 35 to 53 µm. This new species is close to *M. australis*, *M. allgeni* and *M. macilenti*, but differs by the S-shapes spicules, a tail length ranging from 80 to 90 µm and a c-ratio of 7.5.

Molgolaimus nettoensis sp. nov.
(Fig. 6)

Etymology: Named after Sérgio Antonio Netto

Material studied: One male and one female: 1 holotype male, 1 allotype specimens (slide no. 104079)

Locality: Bransfield Strait (near King George Island)

Measurements: Table II.

Description: Body long and cylindrical, tapering gradually at both ends. Head offset from the rest of the body by a depression. Cephalic setae short and close to head depression. Amphidial fovea 2 hd from anterior end corresponding to 40% cbd. Cardia twice as long as wide. Ventral gland cell small. Tail conical.

Male reproductive system right to the intestine. Testis relatively long with the germinal zone extending to halfway

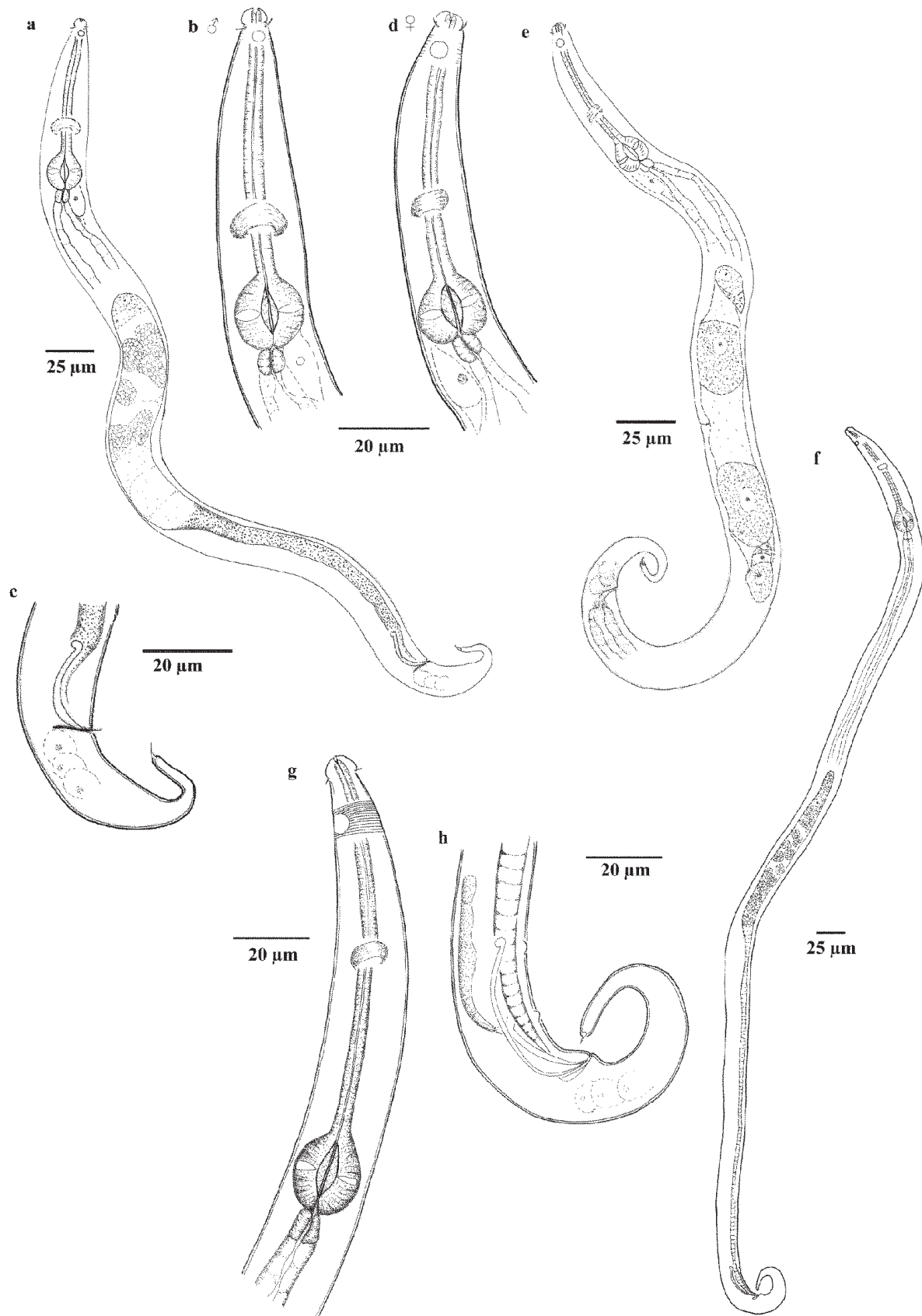


Fig. 7. a–e. *Molgolaimus australis* sp. nov., a–c: male, a. total body view, b. anterior end, c. posterior end, d–e: female, d. anterior end, e. total body view. f–h. *M. unicus* sp. nov., f. total body view, g. anterior end, h. posterior end.

the gonad. Spicules medium-sized (3.3 spic/abd) with a pronounced capitulum and a thin blade. Pre-cloacal supplements absent. Gubernaculum thin and weakly sclerotized.

Female with the anterior and posterior genital branches lying to the right side of the intestine. Germinal zone relatively short. Both uteri with an oval egg.

Diagnosis: *Molgolaimus nettoensis* sp. nov. is characterized by a short body length (500–515 µm), medium-sized spicules (50 µm) with a pronounced capitulum and absence of pre-cloacal supplements.

Relationships: *M. nettoensis* belongs to the group 2 of the identification key, where the spicule length ranges from 35 to 53 µm long. Within the group, the new species can be distinguished by the low *c* values and the length of the spicules as well as by the sinusoidal spicule shape and pronounced capitulum

Molgolaimus sabakii (Muthumbi & Vincx, 1996)
(Fig. 6)

Material studied: One male and one juvenile (slide no. 104080)

Locality: South Sandwich Trench

Measurements: Table II.

Description: Body short, cylindrical and thin. Anterior end tapering gradually towards an offset head, marked by a constriction. Short cephalic setae posterior to the constriction. Amphidial fovea 3–4 hd the anterior end corresponding to 50–60% cbd. Ventral gland cell small. Tail conical and long.

Male reproductive system located on the left side of the intestine. Vesicula seminalis relatively long corresponding to 40% of the total reproductive system. Spicules medium sized (3 abd), with a flat capitulum and a thin blade. Spicules slightly curved ventrally. Two supplements equidistant anterior to the cloacal aperture.

Diagnosis: *Molgolaimus sabakii* (Muthumbi & Vincx, 1996) is characterized by a short body (590 µm), a long tail (108 µm), presence of two pre-cloacal supplements and medium-sized spicules (39 µm).

Relationships: Specimens for the South Sandwich Trench largely agree with the original species description by Muthumbi & Vincx (1996). The species belongs to group 2 of the identification key (*M. sapiens*, *M. macilenti*, *M. nettoensis*, *M. australis*, *M. xuxunaraensis*, *M. allgeni*). It is easily distinguished from the other species of this group by the longer tail, the lower *c*-ratio value and the more posterior position of the amphidial fovea.

Molgolaimus australis sp. nov.
(Fig. 7)

Etymology: referring to geographic region

Material studied: One male and three females: 1 holotype male, 1 allotype female, 2 paratype specimens (slide no. 104081)

Locality: South Sandwich Trench

Measurements: Table II.

Description: Body cylindrical, tapering towards both ends. Head offset by a constriction. Cephalic setae relatively short located posterior to the constriction. Amphidial fovea 1–1.5 hd from anterior end. Ventral gland cell relatively large, displacing the intestine towards the dorsal side; one small additional cell at its base. Tail short conical

Male reproductive system left of the intestine. Testis large, germinal zone relatively short restricted from three to four rows of cells. Sperm cells round and clustered in a rhomboid shape. Vesicula seminalis relatively wide, occupying about the entire body cavity. Spicules characterized by a round capitulum and a thin sinusoidal blade. Gubernaculum thin and weakly sclerotized. No pre-cloacal supplements.

Female with the anterior branch located left of the intestine, the posterior branch right of the intestine.

Diagnosis: *Molgolaimus australis* sp. nov. is characterized by a medium-sized ventrally curved spicules (36 µm long), absence of pre-cloacal supplements, a short conical tail (53–64 µm) and a large testis.

Relationships: In the identification key *M. australis* is included within the second species group (*M. sapiens*, *M. macilenti*, *M. nettoensis*, *M. xuxunaraensis*, *M. allgeni*, *M. sabakii*), with spicule length ranging from 35 to 53 µm. Among the species of this group, *M. australis* can be distinguished by the short tail and high *c* value. *Molgolaimus australis* is morphologically close to *M. allgeni* and *M. xuxunaraensis* but differs in the absence of pre-cloacal supplements, short spicules and position of the amphidial fovea close to the head.

Molgolaimus unicus sp. nov.
(Fig. 7)

Etymology: unique

Material studied: One male: 1 holotype male (slide no. 104082)

Locality: Bransfield Strait (near King George Island)

Measurements: Table II.

Description: Body long and slender. Anterior end evenly tapered towards the head an offset by a constriction. Cephalic sensilla relatively short, inserted at the level of the

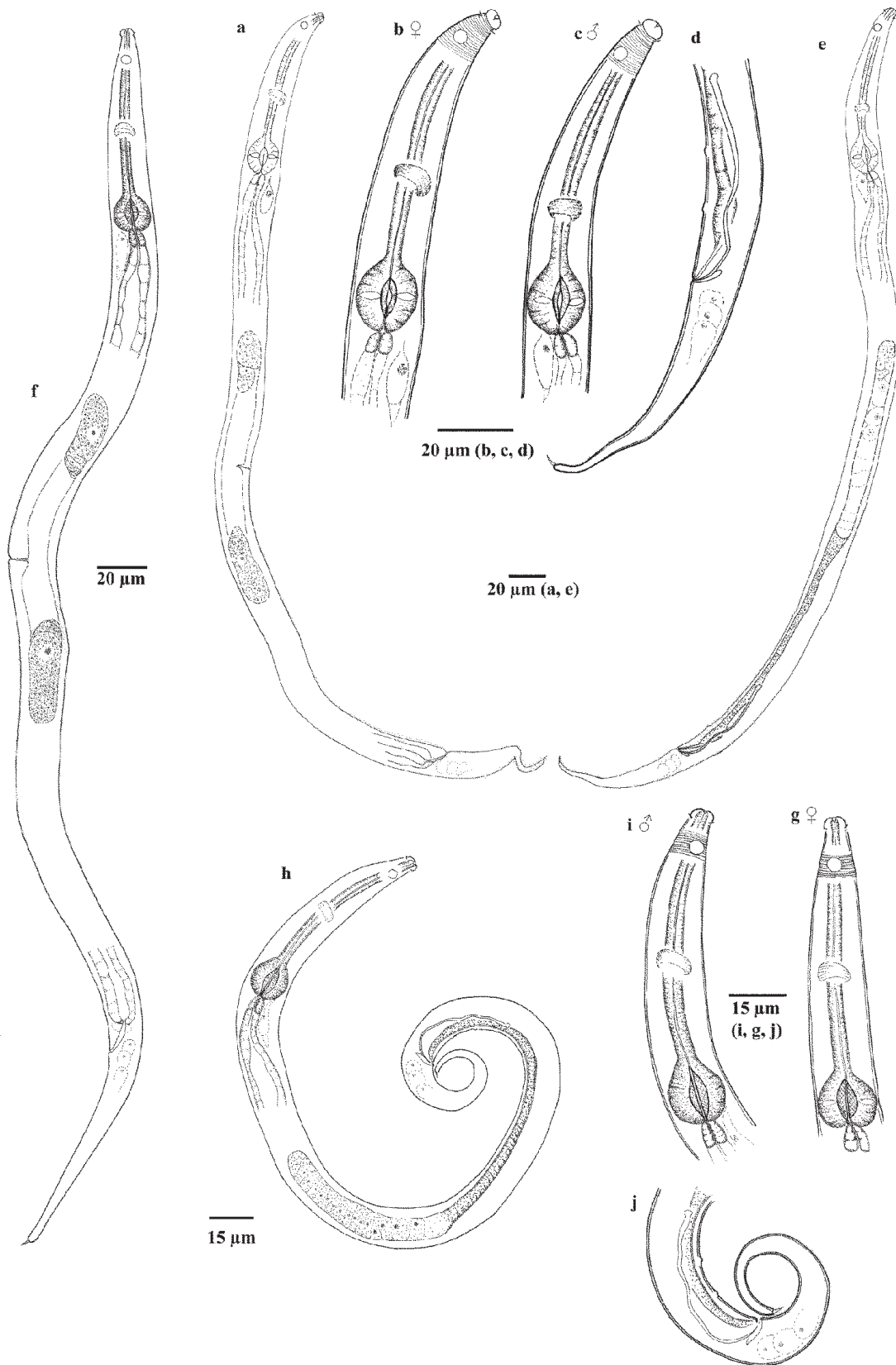


Fig. 8. a–e. *Molgolaimus walbethi* sp. nov., a–b: female, a. total body view, b. anterior end, c–e: male, c. anterior end, d. posterior end, e. total body view. f–j. *M. liberalis* sp. nov., f–g: female, f. total body view, g. anterior end, h–j: male, h. anterior end, i. total body view, j. posterior end.

constriction. Amphids at 1.7 hd from anterior end, the diameter 35% of cbd. Ventral gland cell obscure. Tail short and conical.

Male testis left of the intestine and characterized by a relative small germinal zone. Sperm cells clustered together in a rhomboid to a round shape. Vas deferens relatively long and narrow. Two equidistant pre-cloacal supplements. Spicules medium-sized (56 μm) with a thin blade and a round capitulum. Gubernaculum small and thin.

No females observed.

Diagnosis: *Molgolaimus unicus* sp. nov. is characterized by a long body, an offset head, medium-sized spicules (3 abd), presence of two pre-cloacal supplements, and a relatively short conical tail.

Relationships: *M. unicus* is grouped with *M. liberalis* and *M. walbethi* forming group 3, characterized by spicules ranging from 53 to 80 μm in length. Among the sub-group, the new species can be distinguished by its larger size.

Molgolaimus liberalis sp. nov.
(Fig. 8)

Etymology: named after its wide occurrence

Material studied: Fifteen males and fourteen females: 1 holotype male, 1 allotype female (slide no. 104083), 17 paratype specimens.

Locality: Halley Bay, Kapp Norvegia, South Sandwich Trench and Drake Passage

Measurements: Table IV.

Description: Body cylindrical tapering gradually at both ends. Head offset from the rest of the body by a constriction. Cephalic setae relatively short at level of cephalic constriction. Amphidial fovea 1.5–2 hd from the anterior end and its diameter 40% of the cbd. Cardia relatively long, i.e. about one-third of the bulb diameter. Ventral gland cell small, displacing the intestine dorsally. Tail relatively long, conical and thin.

Male reproductive system left of the intestine. Testis characterized by a long germinal zone. Spicules medium-sized (3.5–4.5 abd) with a round capitulum and a thin sinusoidal blade. Gubernaculum small and surrounding the tip of the spicules. Two equidistant supplements anterior to the cloacal aperture.

Female with the anterior and posterior genital branches located left of the intestine. Anterior branch slightly longer than the posterior one.

Diagnosis: *Molgolaimus liberalis* sp. nov. is characterized by a short body (450–650 μm), presence of two pre-cloacal supplements, medium sized spicules (3.5–4.5 abd), an offset head and a long tail.

Relationships: *M. liberalis* is closely related to *M. unicus*

and *M. walbethi*, species belonging to group 3 of the identification key (spicules ranging between 53 and 80 μm). *Molgolaimus liberalis* is more similar to *M. walbethi* in body and spicules length than to *M. unicus*. However, *M. liberalis* differs from *M. walbethi* sp. nov. by a lower c-ratio, a larger anal body diameter and tail shape (i.e. tail tapering continuously vs tail tapering sharply in the end).

Molgolaimus walbethi sp. nov.
(Fig. 8)

Etymology: Named after Walter Fonseca and Elizabeth Fonseca

Material studied: Two males and four females: 1 holotype male, 1 allotype female, 4 paratype specimens (slide no. 104084)

Locality: Vest Kapp

Measurements: Table IV.

Description: Body long and slender. Anterior end evenly narrowed. Head separated from the rest of the body by a constriction. Cephalic setae short and just posterior to the constriction. Amphidial fovea at 2–2.5 hd from anterior end, its diameter corresponding to 35–45% of cbd. Tail conical proximally, tapering abruptly in the posterior most third towards a digitate prolongation.

Male testis left of the intestine. Vesicula seminalis relatively long, representing 50% of the reproductive system. Sperm cells round. Spicules medium-sized (5–6 abd long), with a round capitulum and a sinusoidal thin blade. Gubernaculum small and weakly sclerotized. Two pre-cloacal supplements equidistant.

Female reproductive system with the anterior branch located left of the intestine and the posterior branch right of the intestine.

Diagnosis: *Molgolaimus walbethi* sp. nov. is characterized by a slender body, posterior position of the amphidial fovea, insertion of the cephalic setae posterior to the cephalic constriction, medium-sized spicules (65–71 μm), presence of two pre-cloacal supplements, and a tail with a digitate prolongation.

Relationships: In the identification key *M. walbethi* is grouped within group 3 together with *M. liberalis* and *M. unicus*., all possessing spicules with a length ranging between 53 and 80 μm . *Molgolaimus walbethi* resembles *M. liberalis* in body length but differs in a low anal body diameter value and a different tail shape.

Molgolaimus pacificus sp. nov.
(Fig. 9)

Etymology: referring to geographic region

Material studied: Five males and five females: 1 holotype

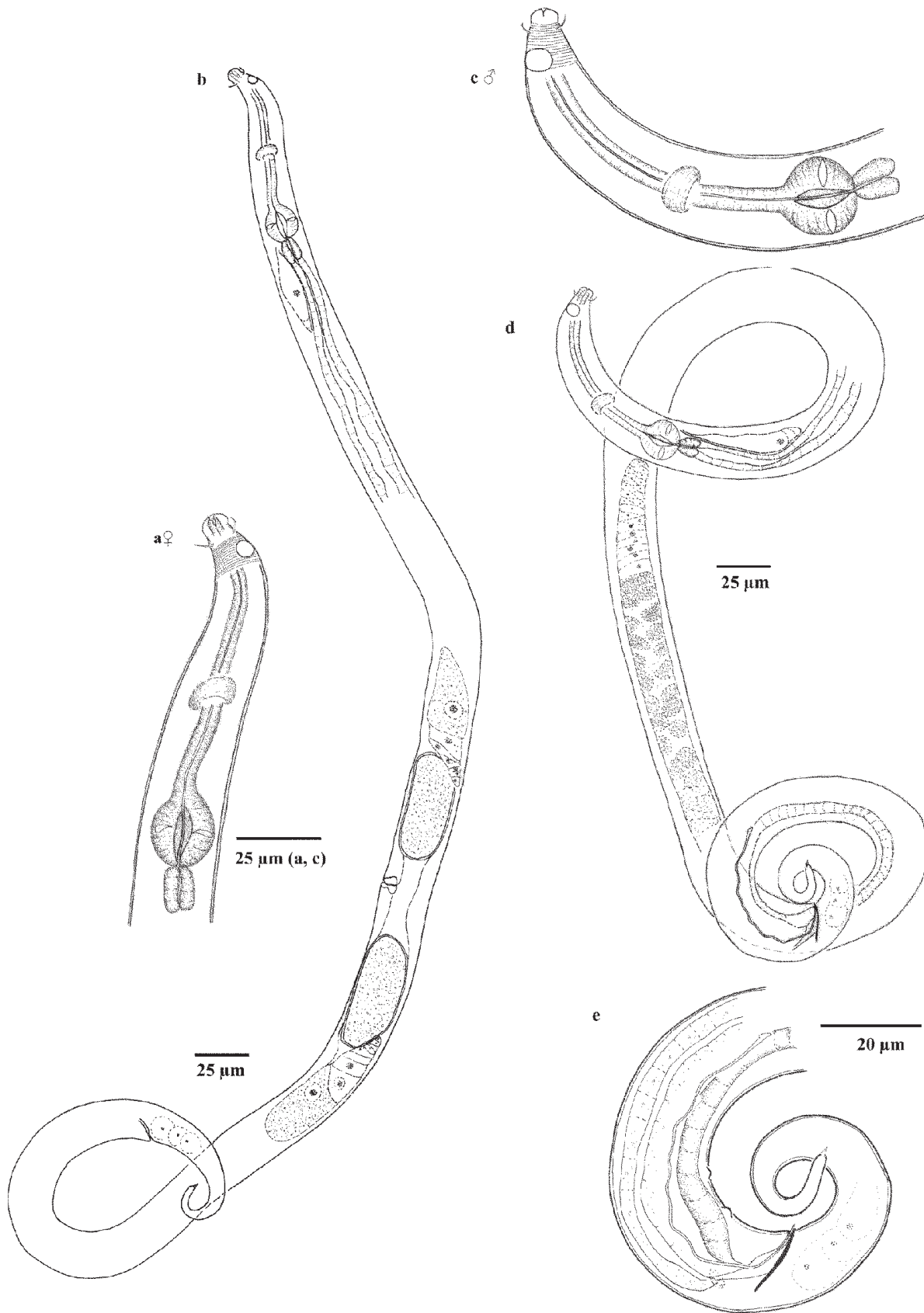


Fig. 9. *Molgolaimus pacificus* sp. nov., **a–b**: female, **a**. anterior end, **b**. total body view, **c–e**: male, **c**. anterior end, **d**. total body view, **e**. posterior end.

Table V. Morphometric data of *Molgolaimus gigasproximus* sp. nov., *M. gigaslongincus* sp. nov. and *M. pacificus* sp. nov. (measurements in μm , average (av), minimum (min) and maximum (max)).

		L	W	hd	amph	amph	amph	nr	nr	ph	abd	Spic	Anus	Tail	Sup	C.	a	b	c	c'	V%	nr/ph	spic
							cbd	ant	cbd		cbd			tip		setae							/abd
<i>M. gigasproximus</i> sp. nov.																							
H	M	1080	36	7	4	11	7	29	64	33	30	101	980	36	27	2	30.1	9.1	10.8	3.3		0.5	3.3
P ₁₋₁₁	av	1030	36	7	4	10	8	29	61	31	30	103	925	43	27	2	28.8	9.0	10.2	3.4		0.5	3.5
P ₁₋₁₁	min	845	29	5	4	9	6	25	55	28	26	91	755	35	27	2	26.8	7.7	8.8	2.9		0.5	3.2
P ₁₋₁₁	max	1190	41	7	6	13	10	31	66	34	32	115	1075	50	27	3	31.7	10.4	11.4	3.7		0.6	3.8
A	F	1090	37	7	4	10	5	29	64	32	28		985	59		2	29.3	9.1	10.4	3.8	0.5	0.5	
P ₁₋₄	av	1040	38	6	4	10	7	28	56	31	28		945	59		2	27.4	9.6	11.1	3.3	0.5	0.5	
P ₁₋₄	min	810	31	6	3	9	6	19	45	22	21		735	59		2	26.3	9.2	10.3	2.8	0.5	0.4	
P ₁₋₄	max	1260	45	7	4	12	8	31	64	37	31		1145	59		2	28.5	10.4	12.1	3.7	0.5	0.6	
<i>M. gigaslongincus</i> sp. nov.																							
H	M	1110	30	6	5	9	9	24	62	26	25	108	1025	29	38	3	37.7	9.7	12.8	3.4		0.5	4.3
P ₁₋₁₃	av	1095	31	6	5	10	9	23	59	26	24	120	1010	31	20	3	35.9	9.8	13.5	3.4		0.5	5.1
P ₁₋₁₃	min	850	23	5	4	7	8	19	50	21	19	106	780	25	15	2	31.7	8.5	10.6	2.8		0.5	4.2
P ₁₋₁₃	max	1240	35	7	5	11	11	27	67	30	26	148	1145	37	25	3	42.2	10.8	15.7	4.2		0.6	6.0
A	F	980	32	6	4	9		21	58	25	23		905	35		2	31.0	8.5	13.2	3.3	0.5	0.5	
P ₁₋₁₃	av	1095	35	6	4	10	9	23	59	26	24		1015	34		2	31.7	9.9	13.6	3.4	0.4	0.5	
P ₁₋₁₃	min	945	31	5	3	7	7	19	50	23	19		890	29		2	24.8	9.1	11.1	2.6	0.5	0.5	
P ₁₋₁₃	max	1350	46	7	6	13	13	29	72	32	31		1255	40		3	38.5	11.4	19.1	4.3	0.5	0.6	
<i>M. pacificus</i> sp. nov.																							
H	M	935	24	6	5	10	10	19	46	21	18	95	855		15	4	39	9.9	11.6	4.5		0.5	5.3
P ₁₋₄	av	915	23	6	5	10	10	17	46	20	19	91	835		15	3	40.0	9.8	11.2	4.4		0.5	4.9
P ₁₋₄	min	780	19	6	5	9	8	14	39	17	17	88	705		14	3	36.4	9.6	10.4	4.1		0.4	4.5
P ₁₋₄	max	1055	26	6	6	10	11	19	60	25	21	95	965		16	3	43.8	10.3	12.2	4.7		0.5	5.3
A	F	895	23	6	5	11	9	17	47	18	16		810			2	38.7	10.4	10.8	5.3	0.5	0.5	
P ₁₋₄	av	955	25	6	5	10	9	17	47	20	17		875			3	38.1	10.5	11.7	4.9	0.5	0.5	
P ₁₋₄	min	865	22	6	4	9	8	15	41	17	16		795			2	35.9	9.8	10.8	4.6	0.5	0.5	
P ₁₋₄	max	1060	29	6	5	11	11	20	54	23	19		965			3	43.3	11.2	12.6	5.3	0.5	0.5	

male, 1 allotype female, 8 paratype specimens (slide no. 104085)

Locality: Fiji Island, Pacific Coast

Measurements: Table V.

Description: Body long and cylindrical, tapering gradually towards both ends. Head separated from the body by a depression. Cephalic setae relatively short and located posterior to the head. Amphidial fovea at 1.5 hd from anterior end. Cardia relatively long (6–8 μm). Ventral gland cell large, pushing the intestine dorsally. Tail long and conical.

Male testis left of the intestine with a short germinal zone. Vesicula seminalis relatively long. Sperm cells clustered in a round shape. Spicules relatively long with a flat capitulum and a thin sinusoidal blade, 4.6–5.4 abd long. Gubernaculum weakly sclerotized and straight. Two to six mammilliform pre-cloacal supplements.

Female with the anterior and posterior genital branches left of the intestine. Oogonia relatively long. Vagina differentiated into a more or less oval, refractive pars distalis vaginae and a less obvious pars proximalis vaginae.

Diagnosis: *Molgolaimus pacificus* sp. nov. is characterized by a long wide body (780–1055 μm), with a relatively low a-ratio value (36.5–43.8), long spicules (> 4.5 spic/abd),

presence of 2–6 pre-cloacal supplements, a long testis, a large ventral gland cell, and a cylindrical tail tapering evenly towards the tip.

Relationships: *M. pacificus* belongs to group 4 of the identification key (spicules > 80 μm). The new species is morphologically closely related to *M. tenuispiculum* (Lorenzen 1976), *M. gigasproximus*, *M. gigaslongincus*, *M. tanai* (Muthumbi & Vincx 1996), *M. longispiculum* (Timm 1961). It differs from the last two species by a shorter pharynx and higher b-ratio. *Molgolaimus pacificus* can be differentiated from the other species by the higher value of the ratio spic/abd although they possess the shortest spicules, and by the tail shape without digitate prolongation, present in the other species.

Molgolaimus gigasproximus sp. nov.
(Fig. 10)

Etymology: Referring to the large body and the position of the amphidial fovea

Material studied: Twelve males and five females: 1 holotype male, 1 allotype female (slide no 104086), 15 paratype specimens

Locality: Drake Passage and Bransfield Strait (near King George Island)

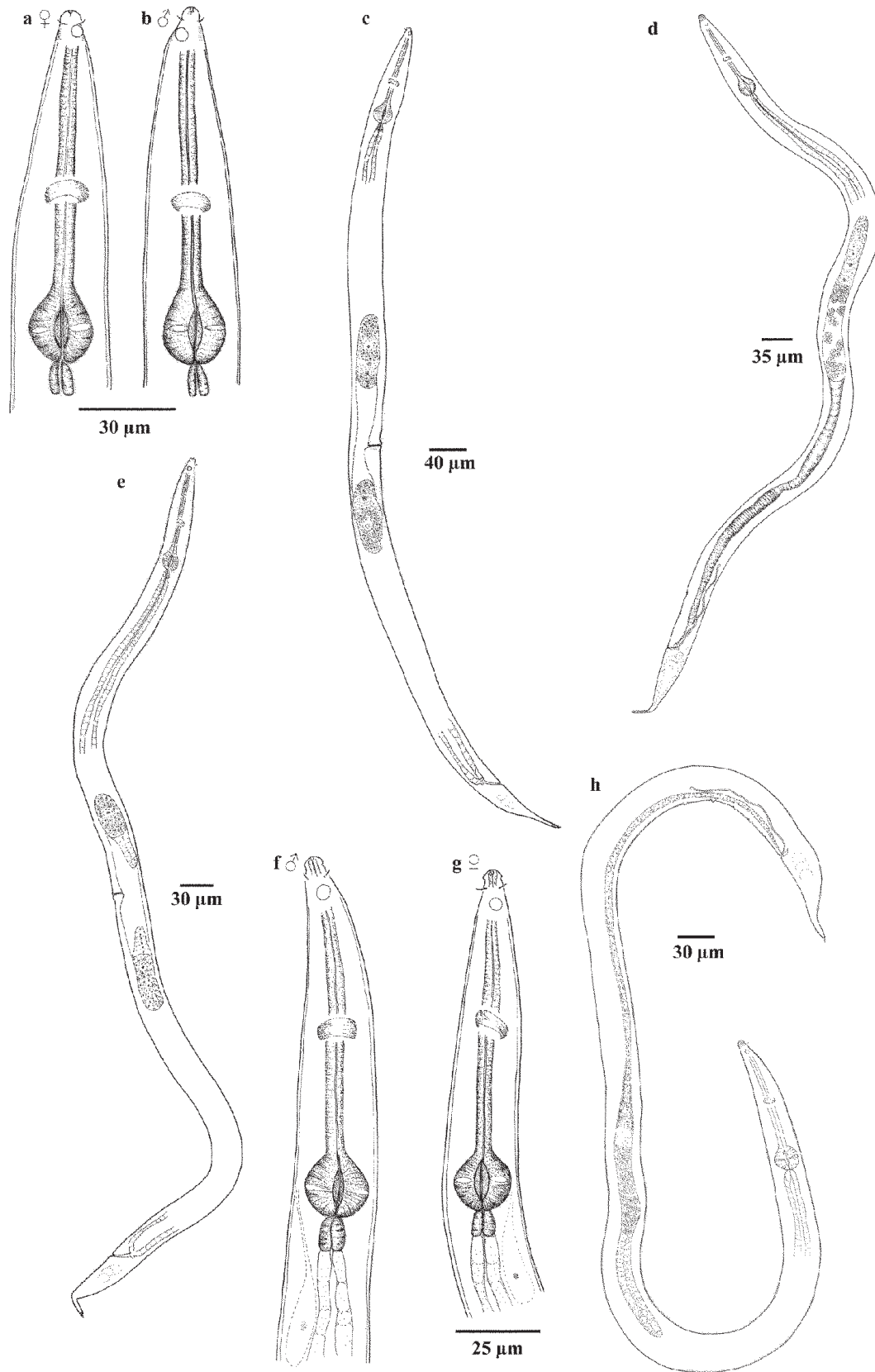


Fig. 10. a–d. *Molgolaimus gigasproximus* sp. nov., a, d: male, a. anterior end, d. total body view, b–c: female, b. anterior end, c. total body view. e–h. *M. gigaslongincus* sp. nov., e, g: female, e. total body view, g. anterior end, f, h: male, f. anterior end, h. total body view.

Measurements: Table V.

Description: Body relatively long and wide, tapering sharply near the anterior and posterior end; anterior narrowing more pronounced next to the amphidial fovea. Head marked from the body by a depression. Cephalic setae short at the level of the depression. Amphidial fovea, 4–6 µm in diameter or 40–50% of cbd, located close to the cephalic depression. Underneath the cuticle, round dense light brown structures present. Cardia relatively long. Ventral gland cell not observed. Tail conical in the proximal half and distally characterized by a digitate prolongation.

Male reproductive system located right of the intestine. Testis relatively small with a small germinal zone. Sperm cells clustered forming a trapezoid structure. Vas deferens long and wide with two distinct zones: at the proximal portion characterized by round cells and distally by thinner cylindrical cells. Spicules relatively long (100–115 µm) corresponding to 3–4 abd. Gubernaculum small, restricted to the distal half of the cloaca. Two pre-cloacal supplements equidistant.

Female with the anterior and posterior genital branches right of the intestine. Ovaries relatively short, with five rows of long oögonia.

Diagnosis: *Molgolaimus gigasproximus* sp. nov. is characterized by a long body (> 845 µm), long spicules (100–115 µm), presence of two pre-cloacal supplements, a testis with a short germinal zone and a differentiated vas deferens and a tail with a digitate prolongation.

Relationships: *M. gigasproximus* belongs to group 4 of the identification key together with *M. gigaslongincus*, *M. tanai*, *M. longispiculum*, *M. gigasproximus*, *M. pacificus* and *M. tenuispiculum*. The species differs from *M. tanai* and *M. longispiculum* by the higher b-ratio. *Molgolaimus gigasproximus*, when compared to the other species in group 4a, possesses the lowest value of the ratio spic/abd and a testis with the shortest germinal zone.

Molgolaimus gigaslongincus sp. nov.
(Fig. 10)

Etymology: Referring to the large body and the position of the amphidial fovea

Material studied: Fourteen males and fourteen females: 1 holotype male, 1 allotype female (slide no. 104086), 26 paratype specimens

Locality: Kapp Norvegia, Drake Passage, Vest Kapp and Bransfield Strait (near King George Island)

Measurements: Table V.

Description: Body relatively long and cylindrical, tapering evenly near both ends. Head slightly offset by a depression. Cephalic setae short, located posterior to the cephalic depression at 1–1.5 hd from anterior end. Amphidial fovea

at 1.5–2 hd from anterior end. Cardia twice as long as wide. Ventral gland cell large, displacing the intestine dorsally. Tail conical ending on a digitate prolongation.

Male reproductive system right of the intestine. Testis characterized by a long germinal zone. Sperm cells round in shape. Spicules relatively long, with a round capitulum and a thin sinusoidal blade. Gubernaculum small and weakly sclerotized. Six equidistant pre-cloacal supplements.

Female with the anterior and posterior genital branches located at the right side of the intestine. Oögonia long, with 6–8 rows of cells.

Diagnosis: *Molgolaimus gigaslongincus* sp. nov. is characterized by a long body (850–1240 µm), long spicules (106–148 µm), presence of 6 pre-cloacal supplements, a testis with a long germinal zone and a tail with a digitate prolongation.

Relationships: *M. gigaslongincus* resembles *M. gigasproximus*, *M. pacificus* and *M. tenuispiculum* (group 4 of the identification key). When compared with *M. gigasproximus*, *M. gigaslongincus* can be distinguished by a more slender anterior end, a higher value of the ratio spic/abd, a testis with a longer germinal zone, and round sperm cells. In comparison to the others species of group 4, *M. gigaslongincus* has a shorter pharynx, longer spicules and a smaller c-ratio. So far, only *M. pacificus* and *M. gigaslongincus* possess six pre-cloacal supplements, but both species can be easily differentiated by the spicule length and tail shape.

Identification key

Based on a frequency distribution for the spicule length, four species groups were distinguished (Fig. 11a; Group 1: species with spicules smaller than 35 µm, Group 2: spicules ranging between 35 and 53 µm, Group 3: spicules ranging between 53 and 80 µm, and Group 4: spicules longer than 80 µm). At the second step different combinations of characters are used for different groups:

⇒ Group 1 (Fig. 11b)

Spicules length/anal body diameter: group 1a, 1b, 1c

° Group a (Fig. 12)

Relation of spicules length versus anal body diameter: *Molgolaimus citrus* (Gerlach 1959), *M. lazonus* (Vitiello & Boucher 1971), *M. turgofrons* (Lorenzen 1972), *M. cuanensis* (Platt 1973), *M. parallgeni* (Vitiello & Boucher 1971)

° Group 1b

• Group 1b₁ (Fig. 13a)

Relation of body length versus spicules length: *Molgolaimus drakus*, *M. sapiens*, *M. gazii* (Muthumbi & Vincx 1996), *M. exceptionregulum*, *M. mareprofundus*.

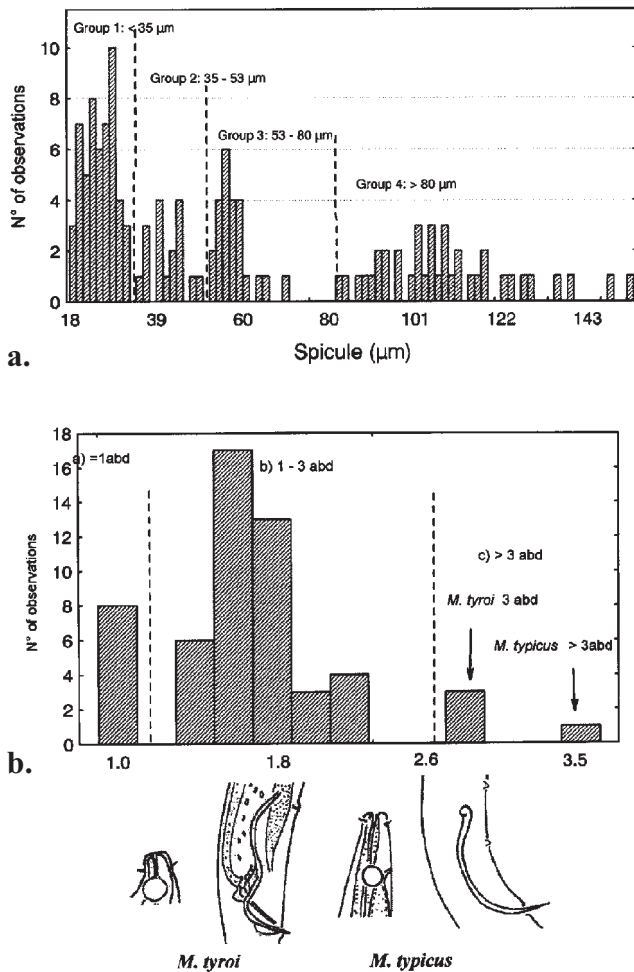


Fig. 11a. Number of observations of the spicules length of the species from the genus *Molgolaimus*, showing the different groups, **b.** Group 1: Number of observations of the spic/abd within the group.

- Group 1b₂ (Fig. 13b)
Relation of tail length versus spicules length/anal body diameter: *Molgolaimus kiwayui* (Muthumbi & Vincx 1996), *M. minutus* (Jensen 1988), *M. abyssorum* (Muthumbi & Vincx 1996), *M. carpediem*, *M. gallucci*, *M. falliturvisus*.
- Group 1c (Fig. 11b)
Frequency distribution of the spicules length divided by the anal body diameter for all species from the group 1: *Molgolaimus tyroi* (Muthumbi & Vincx 1996), *M. typicus* (Furstenberg & Vincx 1992)

⇒ Group 2 (Fig. 14a)

Relation of tail versus ratio c: *Molgolaimus macilenti*, *M. nettoensis*, *M. australis*, *M. xuxunaranesis*, *M. sabakii* (Muthumbi & Vincx 1996), *M. allgeni* (Allgen 1935)

⇒ Group 3 (Fig. 14b)

Relation of body length versus anal body diameter: *Molgolaimus liberalis*, *M. unicus*, *M. walbethi*.

⇒ Group 4 (Fig. 15a & b)

Relation of ratio b (body length/pharynx length) versus (spicules/anal body diameter): group 4a and 4b

◦ Group 4a (Fig. 15a)

M. gigasproximus, *M. tanai* (Muthumbi & Vincx 1996), *M. longispiculum* (Timm 1961)

◦ Group 4b (Fig. 15b)

Relation of the spicules length versus c' ratio (tail/anal body diameter): *Molgolaimus gigaslongincus*, *M. pacificus*, *M. tenuispiculum* (Ditlevsen 1921)

The graphical illustrated identification key presented is a simple modification of the lattice key introduced for the identification of species of the genus *Xiphinema* of the plant-parasitic nematode family Longidoridae (Luc & Dalmasso 1974) and the polytomous species identification key recently published for the free-living marine genus, *Metepsilonema* (Decraemer & Gourbault 2000).

The principles for separating the species are the same for both keys. The morphometric data of specimens are collected into a matrix and, when possible, different morphometrical ranges or groups are identified for each character in order to differentiate different species groups. In the case of the illustrated polytomous key the species groups are identified graphically in accordance with the different (frequency) peaks found in the distribution range of one character. The best character to use at each (hierarchical) step of the key has the highest number of peaks (polymodal distribution), in view of the highest variation. Thus, the morphometrical characters which present a normal distribution over all different species are not considered.

However, depending on the step in the key and on the differences between the species, it may be necessary to use combinations of two or three characters to separate species. To illustrate the combination of morphometric characters the measurements are plotted against each other in normal 2-dimensional or 3-dimensional scatter plots, depending on the number of characters included. The aim of the graphs is to separate groups of similar species and to simplify the identification. For the identification of the 33 species belonging to the genus *Molgolaimus* the combination of five morphometric features and their ratios (total body length, spicule length, tail length, pharynx length, and the anal body diameter) seems sufficient to differentiate the species.

In addition to the numerical key, the head region and the tail region with the male copulatory apparatus is shown for each species, serving as a pictorial key to morphological features. This tool has already proved to be very useful for the identification to genus level of marine nematodes (Warwick *et al.* 1998).

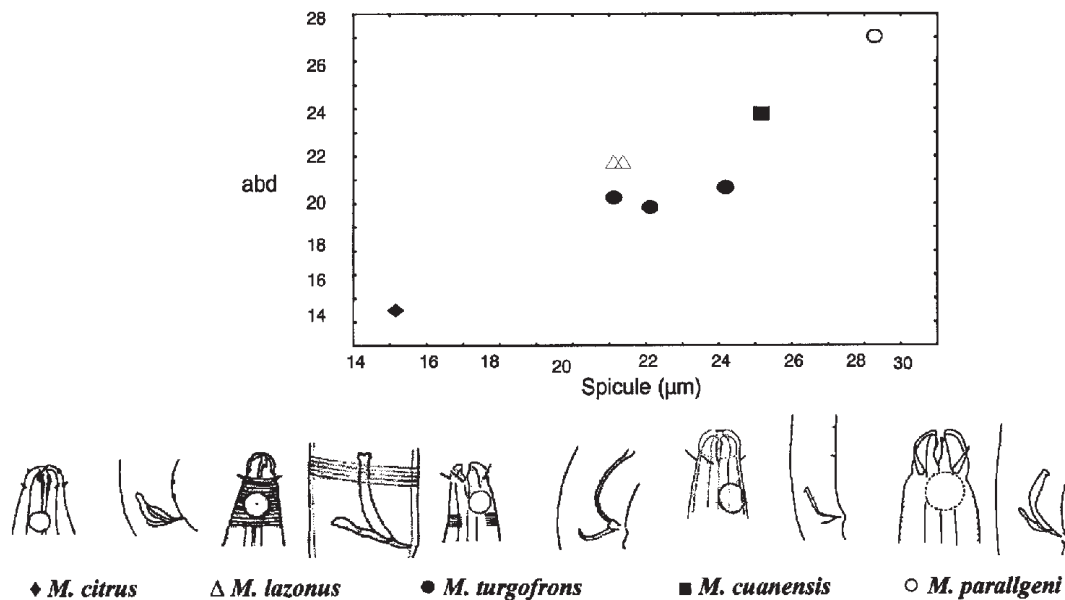


Fig. 12. Group 1a:
Relation of spic.
vs abd.

The advantage of this key over traditional polytomous identification key is the possibility to illustrate easily the variability of the measurements for each species. Another advantage is that it is simple to modify and include new species by adding new morphometric data to the graph. Descriptions of new species based on a larger number of individuals certainly make the key more accurate and representative.

At each step of this polytomous key a group of species is separated based on few morphometric characters. For example, the first step of the present key separates four major groups of species based on the spicules length (see Fig. 11a). The next step combines two characters which vary across the different groups and so on. The combination of characters can be repeated until all the species are completely distinguished.

It is also important to remember that these groups created by the polytomous key are not necessarily based on phylogenetic relationships; they were chosen to facilitate identification (Decraemer & Gourbault 2000).

Genus and species distribution

Most marine nematode genera are known to be cosmopolitan. Although many genera have a preference for particular environmental conditions, other genera do inhabit all kinds of environments in different densities. Deep sea sediments are often characterized by the dominance of similar nematode genera worldwide (Gage 1996). In addition, a deep sea sample is usually characterized by a high number of genera in low dominance, which explains to a large extent the high deep sea diversity among nematodes (Gage & Tyler 1991, Vanreusel *et al.* 1997, Lamshead *et al.* 2003).

The description of large scale patterns (latitudinal, water

depth gradient, primary production, etc.) of nematode diversity in the deep sea has been a hot topic over the last decade (Rex 1981, 1997, Rex *et al.* 1993, 2001, Lamshead 1993, Rex & Etter 1998, Danovaro *et al.* 1999, Lamshead *et al.* 2000, 2001, 2003, Lamshead & Boucher 2003). However, none of these studies investigated deep sea nematodes species composition. The present work shows that for the genus *Molgolaimus* most of the species studied in the deep sea were different from shallow water species and new to science. This fact not only illustrates the shortage of taxonomic studies but also confirms the high species diversity within particular genera in the deep sea.

In order to unravel the possible relationships between *Molgolaimus* species from shallow water and the deep sea, the distribution of species belonging to the same morpho group (as identified by the polytomous key; Fig. 11a) was analysed in relation to environment and geographical distribution. In this approach two possible patterns were expected:

1. groups of morphologically similar species are always found at similar environments independent of the geographical region, or
2. groups of similar species come from the same region regardless of the environment (Southern Ocean, Europe, Pacific, Mediterranean, etc.).

To test the environment related hypothesis, the distribution of the six different morphological groups, as identified in the polytomous key, were plotted for their presence in the different bathymetric zones (coast line, shelf and deep sea; Fig. 16a). It was expected that similar morphotypes would be present in similar environments - which was not the case. Species from each of the morpho groups appeared from coastal zones to the deep sea.

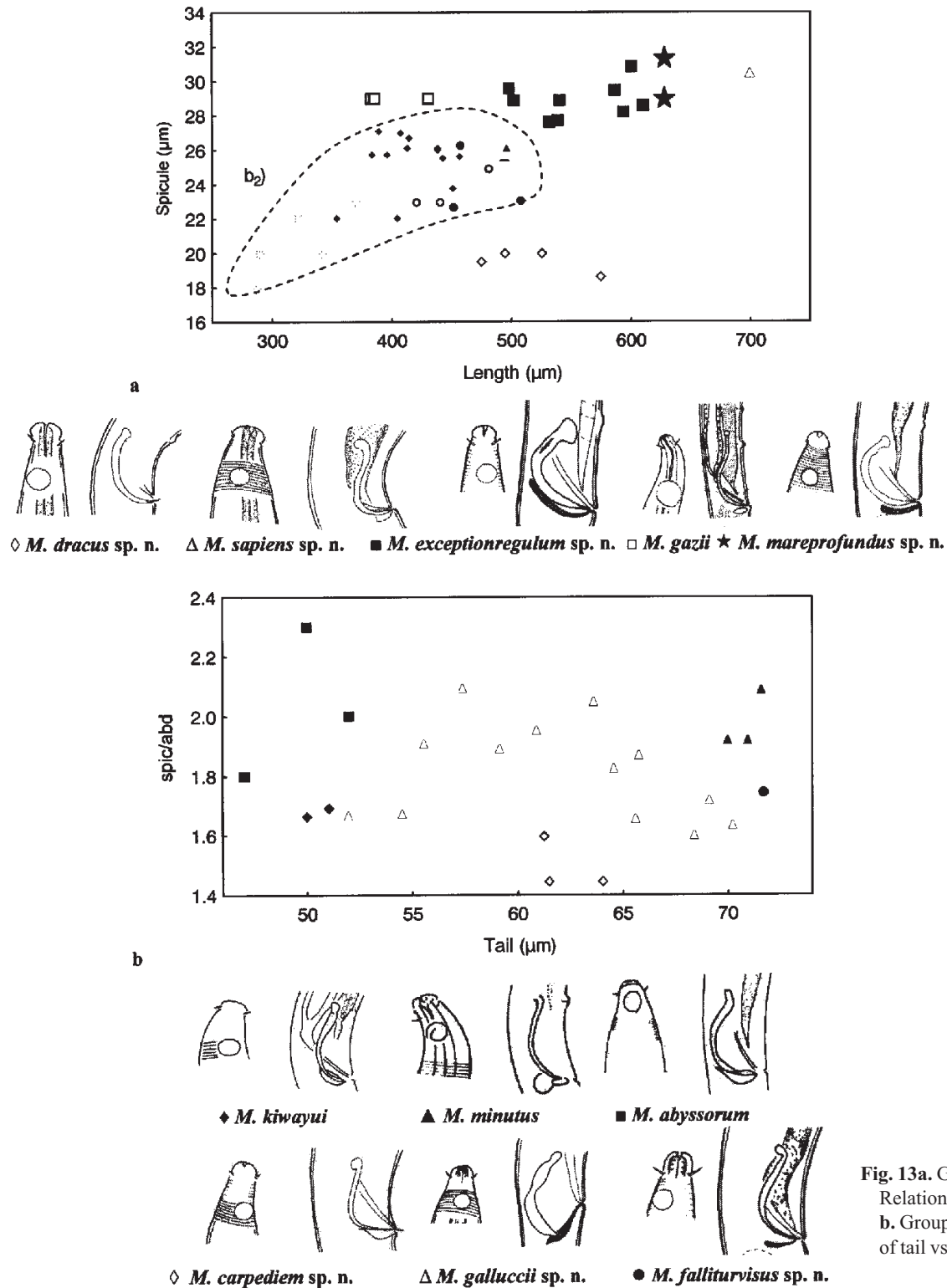


Fig. 13a. Group 1b₁:
Relation of L vs spic,
b. Group 1b₂: Relation
of tail vs spic/abd.

The second hypothesis tested whether similar species (morpho groups) share the same geographical region, independently of the environment of occurrence. Therefore, the different morpho groups were plotted on a world map (Fig. 16b). Apparently, similar species from *Molgolaimus* occur in the same or adjacent geographical areas. The first

species group (1a) includes all species occurring near Europe. Species group 1b, 1c and 2 occur in the Southern Ocean and on the African coast while group 3 is restricted to the Weddell Sea. Species from group 4 are spread from the Southern Ocean (Antarctic, Pacific) to the Indian Ocean. However, while group 4a is restricted to the Indian Ocean,

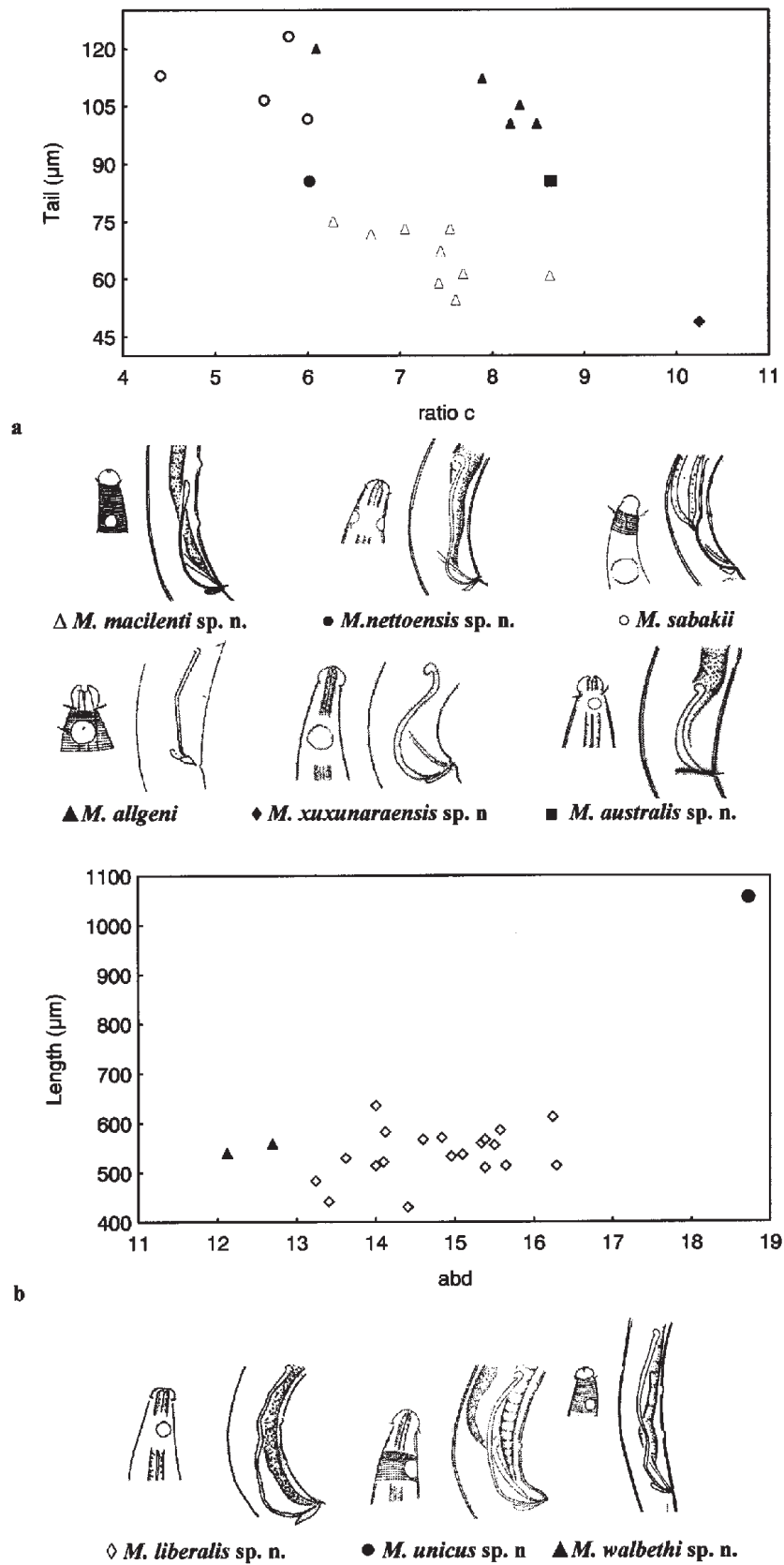


Fig. 14a. Group 2: Relation of tail vs c-ratio, **b.** Group 3: Relation of L vs abd.

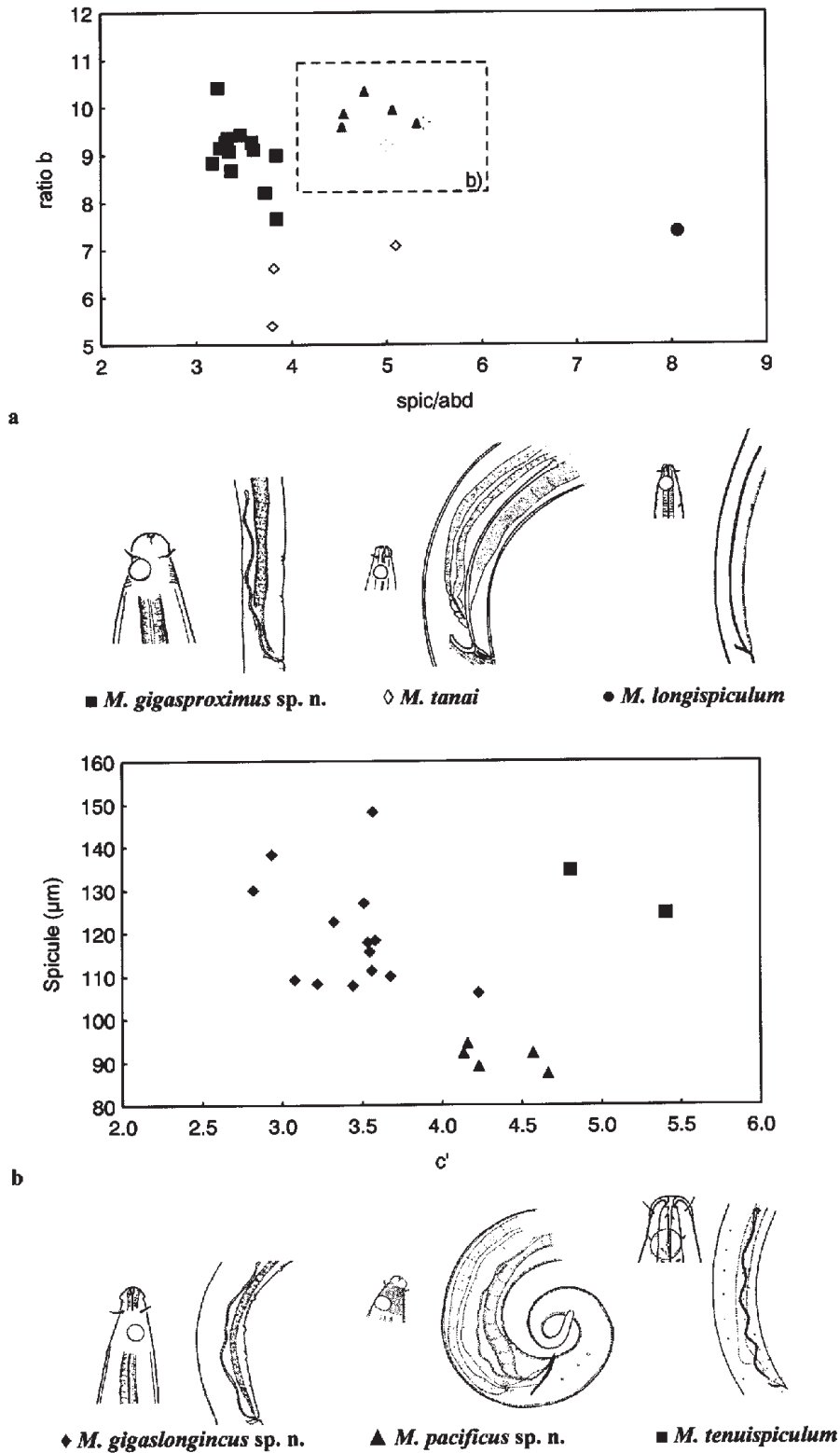


Fig. 15a. Group 4: Relation of b-ratio vs spic/abd, **b.** Group 4b: Relation of spic vs c'-ratio.

group 4b plus *M. gigaslongincus* is found mainly in the Antarctic and Pacific Ocean near New Zealand (Fig. 16b). Exceptions to the trends just described are two species assigned to group 1b and 2 which were found in the European region, *M. minutus* and *M. allgeni*. The first of

these species shares many morphological similarities with group 1a species, although it is placed within the group 1b. For example, the presence of a gubernaculum with apophysis in *M. minutus* is similar to *M. turgofrons* and *M. lazonus* which are species from the group 1a. On the

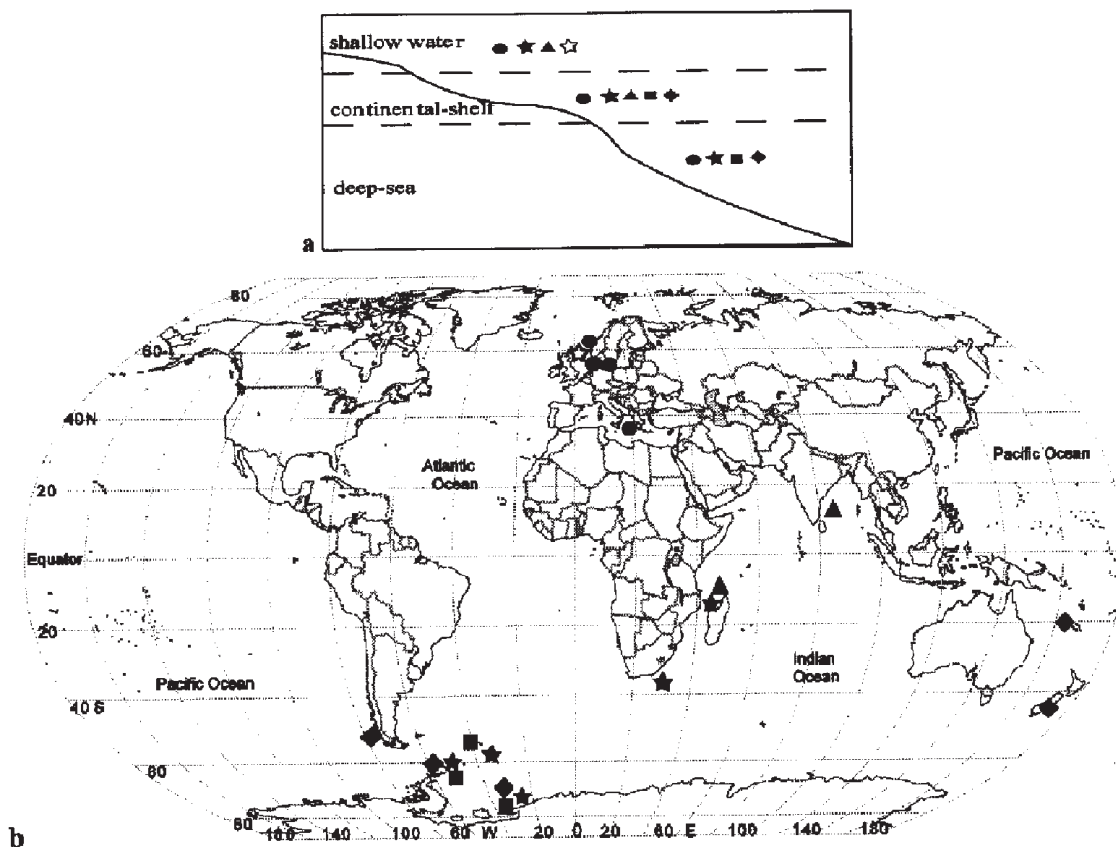


Fig. 16. a. Environmental distribution, and **b.** world spatial distribution of the different morphological groups of *Molgolaimus* species, where: ● = group 1a, ★ = group 1b, 1c & 2, ■ = group 3, ▲ = group 4a, ◆ = group 4b + *M. gigaslongincus*, ☆ = outliers species: *Molgolaimus allgeni* and *M. minutus*.

other hand, the close relationship between *M. allgeni* and the species from group 1a is not clear. This species is morphologically grouped with the second group, which mainly occur in the Southern Ocean and on the African coast (Fig. 16b).

Discussion

Proponents of a theory suggesting a recent shallow origin of the current deep sea fauna include Wolf (1960), Kussakin (1973), and Stock (1986). Data on the deep sea Foraminifera (Douglas & Woodruff 1981) and Ostracoda (Benson *et al.* 1984, 1985) support a period of great faunal change during the middle part of the Cenozoic, with many species having derived recently from shallow water taxa. Moreover, many of these works argue for an ongoing colonization of the deep sea from Antarctic shallow waters where cold conditions provide an isothermal conduit for migration to the deep sea (Wolf 1960). Nevertheless, some authors argue that temperature range may not be important in influencing deep sea fauna (Thistle & Hessler 1976, Hessler & Wilson 1983, Vacelet *et al.* 1994, Vanhove *et al.* 1999).

The present study shows that geographical rather than

environmental clustering of “morphologically” similar *Molgolaimus* species does not support the idea of a common origin of deep sea nematode species. Possibly, the distribution of nematodes can be explained on a global scale by means of paleogeographical events, like the movements of tectonic plates. It is assumed that nematodes, as well as many other moulting invertebrates, originated during the Cambrian period (Adoutte *et al.* 1999, Valentine *et al.* 1999, Conway-Morris 2003). Before this period, continents were joined for 400 million years (Ma) and only in the last 100 Ma the present oceans started to appear (Golonka & Bocharova 2000). Studies dealing with animals which have a hard shell and therefore are found in the fossil record (e.g. Foraminifera, Mollusc, Isopods and Ostracoda) have shown the link between biogeography and phylogeny (Mancenido 2002, Vannier *et al.* 2002, Rode & Lieberman 2004). However, paleogeographical events by themselves are not the only explanation for the current distribution pattern of deep sea benthic organisms, and recent migration from shallow water towards the deep sea is apparently also occurring (Douglas & Woodruff 1981, Benson *et al.* 1984, 1985).

Although based on limited samples and a small genus, this study is the first attempt to discuss global patterns for

marine nematodes. Hopefully, confirmation of this hypothesis will come in the future with the combination of morphological and molecular evidence from phylogeographic studies.

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