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Predatory nematodes from the deep-sea : description of species from the Norwegian Sea, diversity of feeding types and geographical distribution.

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Résumé : Douze des 114 espèces de nématodes, recensées à ce jour dans les sédiments du plateau Vöring et dans ceux des plaines abyssales de la mer de Norvège, sont classées parmi les prédateurs, d'après la structure de leur capsule buccale et leur contenu intestinal. La diversité des types et des tailles des cavités buccales indique une sélection des espèces dépendante de la dimension des proies. La plupart des études en milieu profond, comportant la signalisation de nématodes prédateurs, ont été réalisées surtout dans l'Est Atlantique. 27 espèces de nématodes prédateurs ont ainsi été identifiées, parmi lesquelles 17 appartiennent aux Sphaerolaimidae. La dispersion provoquée par des courants de fond dans la couche néphéloide peut expliquer la large répartition de 4 espèces rencontrées de la mer de Norvège à l'Atlantique Est profond.

Cinq espèces nouvelles sont décrites : *Subsphaerolaimus brevicauda* n.sp., *Sphaerolaimus kleini* n.sp. *Parasphaerolaimus antiai* n.sp., *Metasphaerolaimus gerlachi* n. sp. et *Pomponema koesteri* n.sp. et deux redécrites : *M. crassicauda* et *M. hamatus*. *Ceratosphaerolaimus* Fadeeva, 1983 est mis en synonymie avec *Metasphaerolaimus* Gourbault et Boucher, 1981.

Abstract : Among one hundred and fourteen nematode species found from sediments of Vöring plateau and adjacent deep sea plains in the Norwegian Sea, twelve are regarded as predatory as deduced from the structure of their buccal cavities and gut contents. Five new species are described, i.e. *Subsphaerolaimus brevicauda* sp. n., *Sphaerolaimus kleini* sp.n., *Parasphaerolaimus antiae* sp.n., *Metasphaerolaimus gerlachi* sp. n. and *Pomponema koesterae* sp. n. The male of *M. crassicauda* (Freudenhammer, 1975) and *M. hamatus* Gourbault and Boucher, 1981 is for the first described. *Ceratosphaerolaimus* Fadeeva, 1983 is synonymized with *Metasphaerolaimus* Gourbault and Boucher, 1981. The twelve species represent four feeding-types, and size differences of buccal cavities indicate a prey-size selection between species of the feeding types. Most studies reporting predatory nematodes from the deep-sea benthos are from the Atlantic Ocean : twenty-seven species have been identified of which seventeen belong to the Sphaerolaimidae, mainly from the East Atlantic. Dispersal mediated by near bottom currents in the nepheloid bottom layer may explain the wide occurrence of four Norwegian Sea species in the East Atlantic deep-sea ; i.e. *M. crassicauda* in the Iberian Deep Sea, and *M. hamatus*, *Halichoanolaimus minor* Ssaweljev, 1912 and *Syringolaimus renaudae* Gourbault and Vincx, 1985 off South Africa.

INTRODUCTION

Studies dealing with the trophic composition of the nematode fauna in the deep-sea have shown that 90 % or more of all nematodes are microbial feeders (Tietjen, 1984 ; Rutgers van der Loeff & Lavaleye, 1986 ; Jensen, 1988) and the remaining nematodes are mainly predators. This study is primarily based on benthic samples obtained from the Norwegian Sea at 970-3 062 m depth and is the first attempt to have a detailed specific investigation of

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the diversity (species, feeding types and geographical distribution) of deep-sea nematodes with predatory feeding habits (*sensu* Jensen, 1987).

MATERIAL AND METHODS

Benthic samples were collected with a modified USNEL box corer (50 cm x 50 cm x 50 cm) from R/V *Meteor* during two cruises to the Norwegian Sea (Table I). Sediments were also sampled with a multicorer, i.e. a sample-equipment with 10 cylindrical tubes each 10 cm in diameter, penetrating down to about 40 cm depth, and allowing the very flocculent surface material to be sampled. Salinity of the bottom water is 35 ‰ and the temperature below 1 000 m is - 0.7 °C. Sediments are silty clay ; a detailed sedimentological information is given in Jensen (1988) and Jensen *et al.* (1991). Subsamples from the uppermost 3 cm layer (1986-samples) and uppermost 10 cm layer (1988-samples) were sliced in 1 cm horizontal intervals and immediately fixed in 4 % formalin and stained with Bengal Rose. The meiofauna was extracted and concentrated on a sieve with a mesh size of 45 µm. The nematodes were mounted in glycerol on glass slides and examined using a Leitz Orthoplan microscope with a camera lucida. For abbreviations and formula used, see Jensen (1978).

TABLE I

Station data from the deep-sea benthos of the the Norwegian Sea (R/V *Meteor* cruises 2/1 and 7/4).

Sta.	Date	Coordinates Lat. (°N)	Long.	Depth (m)
59	22 June 1986	65° 31, 0'	00° 07, 1' W	3 062
61	23 June 1986	67° 43, 1'	05° 55, 4' E	1 245
66	24 June 1986	67° 39, 1'	05° 47, 7' E	1 426
70	25 June 1986	66° 59, 9'	07° 45, 7' E	970
80	28 June 1986	70° 15, 6'	03° 21, 8' W	2 133
84	30 June 1986	67° 41, 9'	03° 43, 0' E	1 255
468	19 August 1988	67° 44, 1'	05° 55, 0' E	1 245
476	21 August 1988	67° 39, 2'	05° 47, 1' E	1 424
489	23 August 1988	67° 46, 5'	06° 00, 1' E	1 286
504	25 August 1988	67° 48, 3'	06° 01, 2' E	1 310
519	27 August 1988	67° 41, 4'	05° 51, 8' E	1 325
532	30 August 1988	67° 40, 4'	05° 49, 9' E	1 400

Specimens belonging to each of the twelve species are deposited in the nematode collection of the Alfred-Wegener-Institut für Polar-und Meeresforschung, Bremerhaven, Federal Republic of Germany (NSIMB). The following five species not described herein have the subsequent catalogue numbers : *Halichoanolaimus minor* (NSIMB 562.23-27), *Enoplus* sp. (NSIMB 562.28), *Enoploides* sp. (NSIMB 562.29), *Enoplolaimus* sp. (NSIMB 562.30), *Syringolaimus renaudae* (NSIMB 562.31) (=*Syringolaimus* sp. in Jensen, 1988).

DESCRIPTION

Subsphaerolaimus brevicauda sp.n. (Fig. 1)

Material examined : one male from 3-4 cm depth in the deep-sea benthos of the Norwegian Sea.
Type locality : station 489.

Measurements :

Holotype

♂1	6	-	504	M	2 591	2 821 µm	(NSIMB 562.1)
	22	-	125	134	104		
	a = 21		b = 22.6		c = 12.6		

Description

Male. Body stout with short and narrow tail tip. Cuticle smooth. Cuticle on tail up to 13 µm thick. One crown of ten cephalic setae 1-3 µm long ; subcephalic setae in eight groups of five setae, 1-3 µm long. Somatic setae 3-5 µm long in eight longitudinal rows. Amphids circular, 8 µm in diameter or 12 % of corresponding body diameter, anterior border 40 µm behind head end. Anterior portion of buccal cavity with weakly sclerotized walls and a subcuticular longitudinal striation ; base of buccal cavity surrounded by a strongly sclerotized ring, about 20 µm wide and 90 µm in diameter, which is attached to the body cuticle. Pharyngeal lumen not distinctly sclerotized. Pharynx cylindrical and attached to base of buccal cavity. Cardia small. Ventral gland cell 140 µm behind pharyngeal-intestinal junction. Two caudal gland cells. Spicules curved, 115 µm along the arc, 100 µm from tip to tip, gubernaculum as a weakly sclerotized cap around distal portion of spicules; four copulatory gland cells in tandem in front of the cloaca. One testis, anterior directed, outstretched and right of intestine.

Differential diagnosis

Subsphaerolaimus brevicauda sp. n. differs from the four other known species of the genus [*S. gerlachi* (Wieser, 1959), *S. lamatus* (Gerlach, 1956), *S. litoralis* (Lorenzen, 1978), *S. seticaudatus* (Gourbault & Boucher, 1981)] by its very short and narrow tail and short cephalic sense organs.

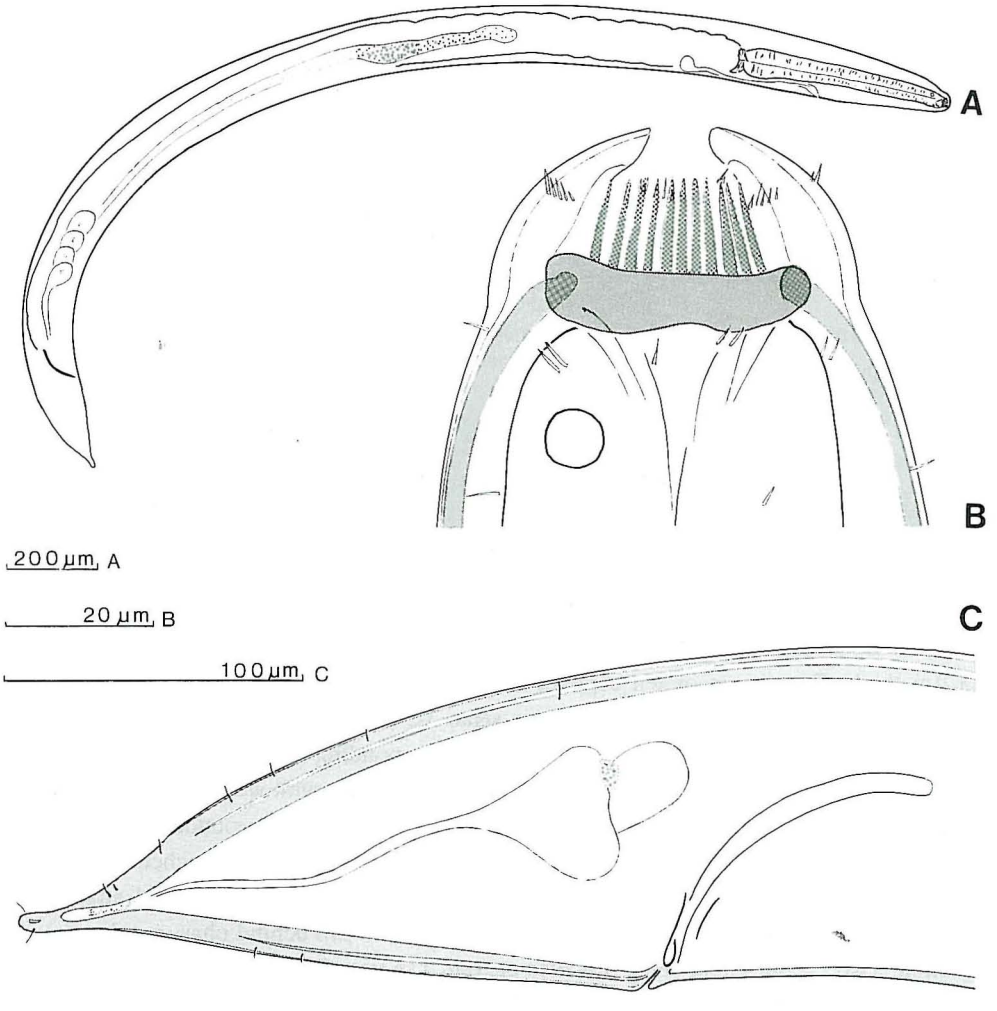

Fig. 1 : *Subsphaerolaimus brevicauda* sp.n. $_1$; A : Total view ; B : Head ; C : Posterior end.

Sphaerolaimus kleini sp.n. (Fig. 2)

Material examined : Two males and two females from the uppermost cm of sediments in the deep-sea benthos of the Norwegian Sea.

Type locality : station 468.

Other localities : stations 59 and 476.

Measurements :

Holotype

1 $\frac{4 \quad - \quad 292 \quad M \quad 1\,108}{17 \quad - \quad 37 \quad 39 \quad 33}$ 1 278 µm (NSIMB 562.2)

a = 33 b = 4.4 c = 7.6

Paratypes

2 $\frac{4 \quad - \quad 308 \quad M \quad 981}{16 \quad - \quad 43 \quad 47 \quad 40}$ 1 142 µm

a = 24 b = 43.7 c = 72

1 $\frac{4 \quad - \quad 350 \quad 932 \quad 1\,150}{14 \quad - \quad 40 \quad 42 \quad 35}$ 1 300 µm (NSIMB 562.3)

a = 23 b = 2.6 c = 6.6 V = 62 %

2 L = 1 270 µm (NSIMB 562.4)

a = 30 b = 3.9 c = 8.3 V = 71 %

Description

Males. Body slender with conical tail terminating in a narrow cylindrical portion. Cuticle annulated. One circle of ten cephalic setae : six 1 µm long setae and four 4 µm long setae ; subcephalic setae in eight groups of five setae, 4-13 µm long. Somatic setae up to 13 µm long. Amphids circular, 12 µm in diameter or 45 % of corresponding body diameter, anteriormost border 15 µm behind head end. Head capsule with dots. Buccal cavity voluminous, 16-18 µm wide and 29-33 µm deep consisting of strongly sclerotized plates and rods, posteriorly stronger developed in the ventral sector than in dorsal sector. Pharynx surrounding basal plate in ventral sector and reaching basal plate in dorsal sector indicating an asymetrical attachment. Pharynx cylindrical with strongly sclerotized lumen. Cardia small. Spicules curved and slender, 73-80 µm along the arc, 64 µm from tip to tip ; gubernaculum 10-15 µm long with a small caudal apophysis. One testis, anteriorly directed, outstretched and right of intestine.

Females. Similar to males in most respects. Amphids smaller, 6 µm in diameter or 22 % of corresponding body diameter. One ovary, anteriorly directed, outstretched and right of intestine ; postvulvar gland cell present.

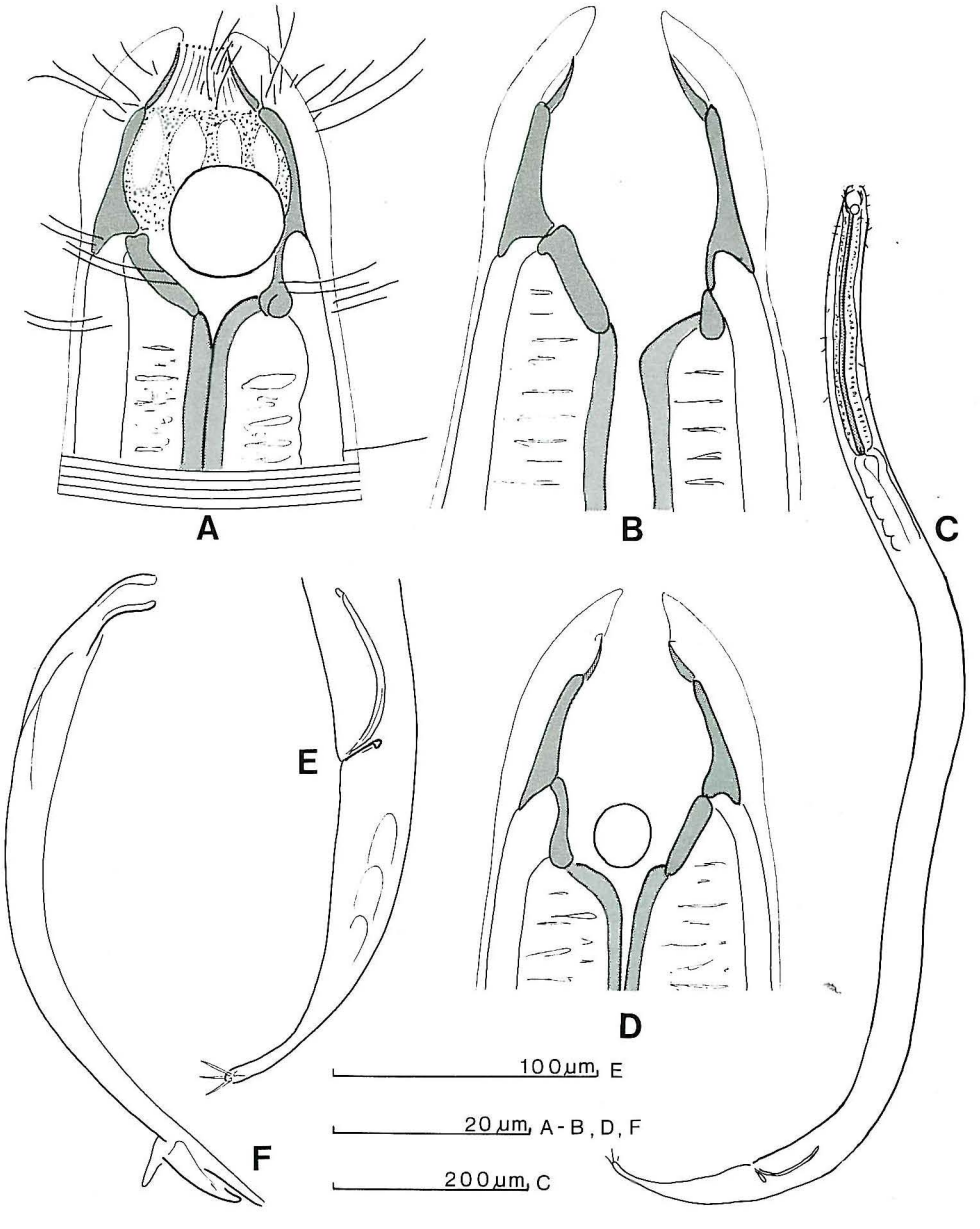

Fig. 2 : *Sphaerolaimus kleini* sp.n.
A : Head of $_1$; B : Buccal cavity of $_2$; C : Total view of $_1$; D : Buccal avity of $_1$; E : Posterior end of $_1$; F : Copulatory apparatus of $_2$.

Differential diagnosis

Sphaerolaimus kleini sp.n. (named for Dr B. Klein, co-worker in the SFB 313 team of scientists at the University of Kiel) shares the long and slender spicules, and conical tail with posteriormost portion cylindrical with *S. cuneatus* Paramonov, 1929, *S. macrocirculoides* Wieser, 1954, *S. macrocirculus* Filipjev, 1918 and *S. penicillus* Gerlach, 1956. Spicule lenght of *S. kleini* sp.n. is, however, much shorter than in above three species, ca. 70 µm vs. up to 270 µm. Moreover, *S. penicillus* has very long subcephalic setae, *S. macrocirculus* has preanal supplements, and the gubernaculum of *S. cuneatus* and *S. macrocirculoides* is much different from that present in *S. kleini* sp.n. Shape of buccal cavity and tail of *S. kleini* sp.n. is rather similar with *S. abyssorum* Allgen, 1933 from Trondhjem Fjord (Norway), however, the description is based on a single juvenile specimen. Other characteristics of *S. abyssorum* are not very clear, hence *S. abyssorum* is herein regarded a dubious species.

Parasphaerolaimus antiae sp.n. (Fig. 3)

Material examined : one female and eight juveniles from 3-5 cm depth in the deep-sea benthos of the Norwegian Sea.

Type locality : station 468.

Measurements :

Holotype

1	8	-	868	2020	2647	2982 µm	(NSIMB 562.5)
	62	-	132	145	100		
	a = 20		b = 3.3	c = 11.4		V = 69 %	

Description

Female. Body stout, attenuating towards posterior end with outermost half of tail slender. Cuticle annulated. Internal labial papillae terminating in small stout setae, external labial setae and cephalic setae in one circle of 2-8 µm long setae ; subcephalic setae up to 15 µm long and in eight groups of 1-3 setae. Somatic setae up to 30 µm long and in eight longitudinal rows. Amphids circular, 8 µm in diameter or 7 % of corresponding body diameter ; anterior border 70 µm behind head end. Anterior portion of buccal cavity weakly sclerotized and with subcuticular longitudinal striations ; posterior portion strongly sclerotized consisting of articulating plates. Pharynx cylindrical and surrounding posterior portion of buccal cavity ; dorsal pharyngeal gland cell opening into posterior portion of buccal cavity. Cardia small. Ventral gland cell not observed. Three caudal gland cells present. Vagina with strongly developed muscles ; postvulvar gland cell present; one ovary, anteriorly directed, outstretched and right of intestine.

Juveniles. Have the same stout body shape and type of buccal cavity as the female.

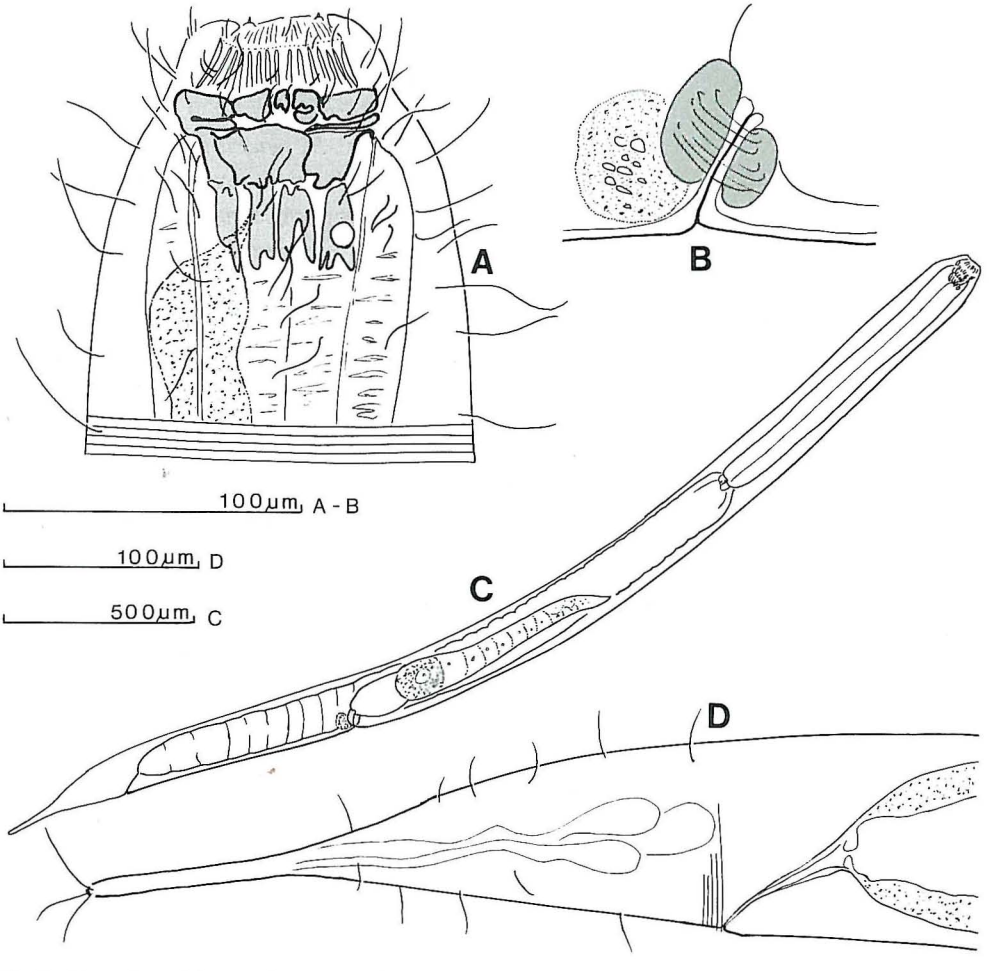

Fig. 3 : *Parasphaerolaimus antiae* sp.n.
$_1$; A : Head ; B : Vaginal region ; C : Total view ; D : Posterior end.

Differential diagnosis

Parasphaerolaimus antiae sp.n. (named for Dr A. Antia, co-worker in the SFB 313 team of scientists at the University of Kiel) differs from the only other species of the genus *P. paradoxus* Ditlevsen, 1918 (cf. redescription by Lorenzen, 1978) by shorter somatic setae and irregularly shaped plates in the buccal cavity.

Metasphaerolaimus Gourbault and Boucher, 1981
syn. *Ceratosphaerolaimus* Fadeeva, 1983 syn.n.

Metasphaerolaimus Gourbault and Boucher, 1981 is characterized by six bifurcated mandibles in the buccal cavity. They described three new *Metasphaerolaimus* species ; i.e.

M. cancellatus (type species), *M. hamatus* and *M. inglisi*, and found a similar buccal cavity in three *Sphaerolaimus* species ; i.e. *S. campbelli* Allgen, 1927, *S. crassicauda* and *S. hadalis*. Consequently, these three species were transferred to *Metasphaerolaimus*. This type of buccal cavity was also recognized by Fadeeva (1983) in a new species for which a new genus *Ceratosphaerolaimus* Fadeeva, 1983 was erected with *C. japonicus* as the type species, and *S. horrendus* was transferred to *Ceratosphaerolaimus*, too. There are, however, no doubt that *Ceratosphaerolaimus* is identical with *Metasphaerolaimus*, hence *Ceratosphaerolaimus* is regarded synonymous with *Metasphaerolaimus* and *C. horrendus* and *C. japonicus* are transferred to *Metasphaerolaimus. Metasphaerolaimus* contains above eight species and present *M. gerlachi* sp.n. (see below).

Six *Metasphaerolaimus* species are known from the deep-sea benthos (Table II). The other three species are from shallow waters : the South-West Atlantic (*M. campbelli*), the Black Sea (*M. horrendus*) and the Sea of Japan (*M. japonicus*).

Metasphaerolaimus crassicauda (Freudenhammer, 1975)
(Fig. 4)

Material examined : fifteen males, sixty-three females and thirty-seven juveniles from the uppermost 2 cm sediments in the deep-sea benthos of the Norwegian Sea.

Localities : stations 61, 66, 70, 468, 489, 504, 519, 532 ; i.e. all stations sampled so far on Vöring Plateau.

Measurements :

1	6	-	166	M	630	691 µm	(NSIMB 562.6)
	12	-	19	23	20		
	a = 30		b = 4.2		c = 11.5		
1	4	-	167	482	648	710 µm	(NSIMB 562.7)
	12	-	23	28	23		
	a = 25		b = 4.2		c = 11.8	V = 68 %	
10	L = 721-810 µm (NSIMB 562.8-11)						
	a = 27-30		b = 4.1-4.8		c = 10.7-12.4		
10	L = 704-782 µm (NSIMB 562.7, 10-15)						
	a = 34-31		b = 4.1-5.3		c = 10.1-15.9	V = 63-69 %	
5 juv.	L = 383-481 µm (NSIMB 562.16)						
	a = 22-28		b = 3.5-3.9		c = 10.1-10.9		

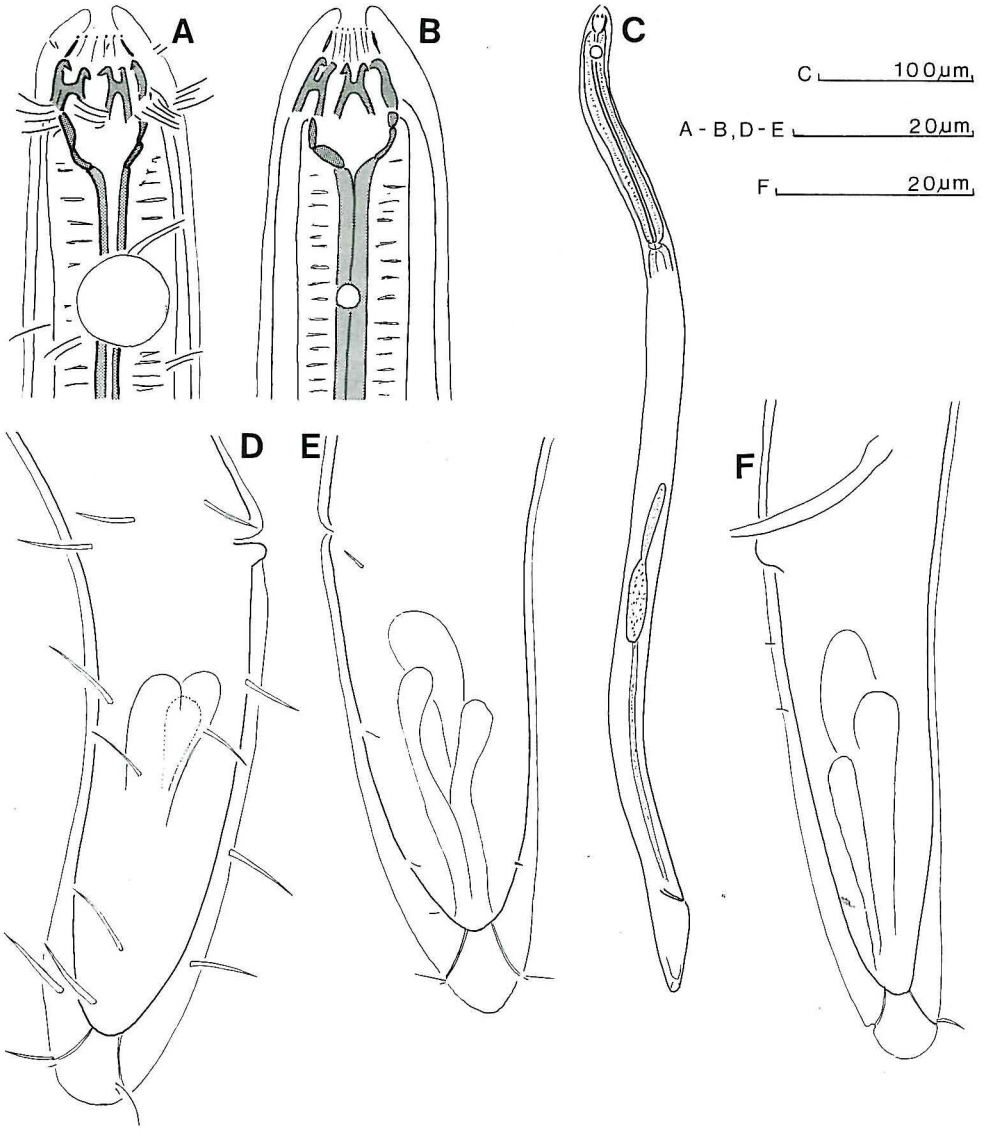

Fig. 4 : *Metasphaerolaimus crassicauda* (Freudenhammer, 1975)
A : Head of $_1$; B : Buccal cavity of $_1$; C : Total view of $_1$; D : Posterior end of $_7$; E : Posterior end of $_5$; F : Posterior end of $_1$.

Description

Males. Body slender and slightly attenuating towards the ends. Cuticle faintly striated. Head with one circle of six minute setae and four 2 µm long cephalic setae, and more posteriorly eight groups of four setae 3-5 µm long, and in some specimens a fifth very small seta is present. Somatic setae present in pharyngeal region and on tail, 3-5 µm long ; three 3-5 µm long subterminal setae present close to openings of caudal gland cells. Amphids circular, 10-12 µm in diameter or 47-50 % of corresponding body diameter ; anterior border 26-28 µm behind head end. Buccal cavity voluminous, 10 µm wide and 17 µm deep with six bifurcated mandibles in the mid-portion. Pharynx cylindrical surrounding posterior portion of buccal cavity at a ring around the buccal cavity ; pharyngeal lumen strongly sclerotized. Cardia small. Ventral gland cell posterior to cardia and opening 100-110 µm in front of cardia. Three caudal gland cells present, each opening through separate subterminal outlets. Spicules slightly curved and proximally slightly cephalated, 20-26 µm along the arc, 18-22 µm from tip to tip. Testes opposite and outstretched ; location of branches compared to intestine variable : out of ten males anterior branch was to the left of intestine and posterior branch to the right in eight specimens, both branches were to the left in one specimen, and another specimen had both branches to the right of intestine.

Females. Females are in most respects similar to males. Amphids are smaller, 3-4 µm in diameter or 12-15 % of corresponding body diameter, anterior border 30-32 µm behind head end. Setation on tail is in most females similar to males, however, in three females (♀3, ♀7 and ♀8) the tail bears more and stronger developed setae, up to 10 µm long, and most of them are directed forwards. Ovary outstretched, anterior directed and left of intestine in six out of ten females, ovary to the right of intestine in four specimens.

Juveniles. Are similar to females.

Remarks

Metasphaerolaimus crassicauda is distinguished from other *Metasphaerolaimus* species by its conical tail with subterminal outlets of caudal gland cells. Females in present large collection of adults and juveniles are in accord with the detailed original description. New information is the male characters and the presence of anteriorly directed large and strongly developed setae on tail of some females ; the latter feature is much more powerfully developed in males and females of *M. hamatus* (see below) and in *Sphaerolaimus uncinatus*.

Metasphaerolaimus gerlachi sp.n. (Fig. 5)

Material examined : two males from 1-2 cm depth in the deep-sea benthos of the Norwegian Sea.
Type locality : station 468.
Other locality : station 476.

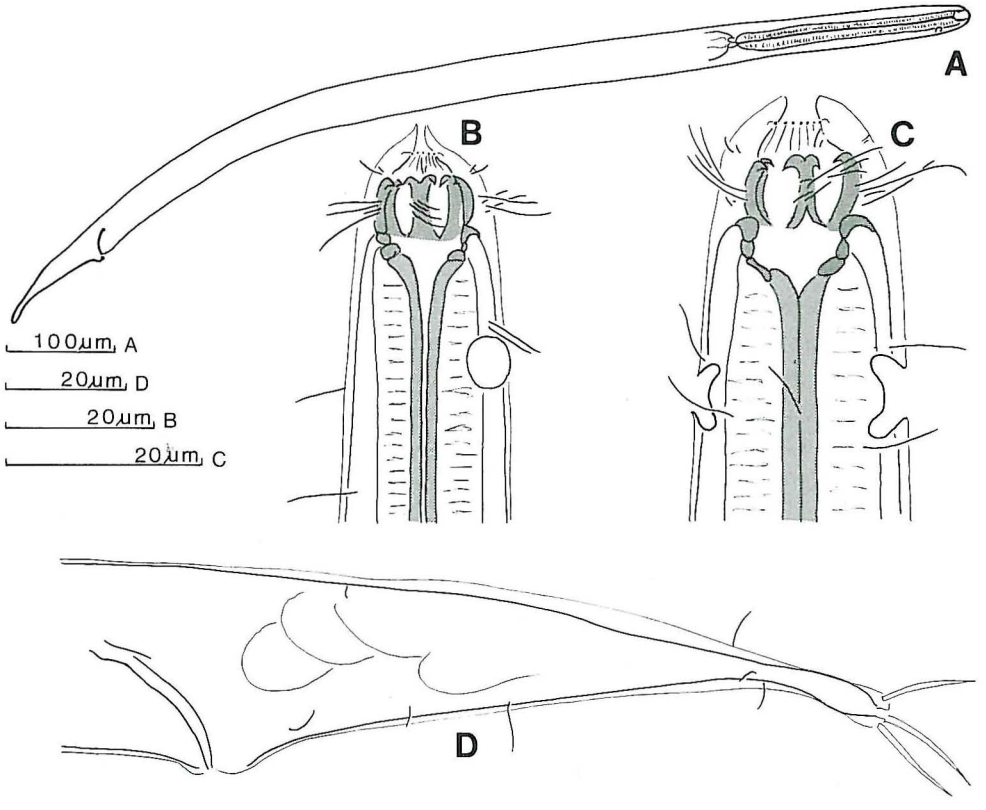

Fig. 5 : *Metasphaerolaimus gerlachi* sp.n.
A : Total view of δ_1; B : Head of δ_1 ; C : Head of δ_2 ; D : Posterior end of δ_1.

Measurements :

Holotype

δ_1 7 - 227 M 858 / 17 - 33 35 33 — 971 µm (NSIMB 562.17)

a = 28 b = 4.3 c = 8.5

Paratype

δ_2 7 - 238 M 784 / 14 - 27 28 25 — 893 µm (NSIMB 562.18)

a = 32 b = 3.7 c = 8.2

Description

Males. Body slender and attenuating towards the ends. Cuticle faintly striated. Head with one circle of six small setae and four cephalic setae 2 µm long ; subcephalic setae in eight groups with each a short seta 8 µm long and three setae 12-18 µm long. Somatic setae 8-12 µm long with shorter setae on tail. Amphids circular, 8-9 µm in diameter or 32-40 % of corresponding body diameter, anterior border 28-30 µm behind front end. Buccal cavity voluminous with six bifurcated mandibles in the mid-portion and a strongly sclerotized ring around the base. Pharynx cylindrical and surrounding the basis of the buccal cavity ; lumen strongly sclerotized. Ventral gland cell not observed. Spicules slender and slightly curved, proximally slightly cephalated, 30 µm around the arc, 29 µm from tip to tip ; gubernaculum not observed. Testes opposite and outstretched, anterior testis to the left of intestine, posterior branch to the right of intestine. Tail tip with three 17 µm long setae.

Differential diagnosis

Head end and spicules of *M. gerlachi* sp.n. (named for Professor emeritus Dr S.A. Gerlach, deputy manager of the SFB 313 at the University of Kiel) are rather similar to *M. hadalis*. *M. gerlachi* differs from *M. hadalis* by smaller amphids and spicules, longer cylindrical portion of tail, and longer terminal setae of tail.

Metasphaerolaimus hamatus Gourbault and Boucher, 1981
(Fig. 6)

Material examined : one male from 1-2 cm depth in the deep-sea benthos of the Norwegian Sea.
Locality : Station 489.

Measurements :

1	5	-	225	M	863	951 µm	(NSIMB 562.19)
	14	-	30	31	24		
	a = 31		b = 4.2		c = 11.4		

Description

Male. Body slender with conical tail and zwollen tail tip. Cuticle annulated. Head with one circle of six small setae about 1 µm long and four cephalic setae 5 µm long ; subcephalic setae in eight groups, however, number and length of setae are difficult to observe due to detritus adhering to head. Somatic setae 5-8 µm long, but setation on tail is characterized by additional strongly developed and anteriorly directed setae 11-21 µm long, most powerful developed setae at subterminal outlets of caudal gland cells. Amphids circular, 12 µm in diameter or 50 % of corresponding body diameter, anterior border 32 µm behind head end. Buccal cavity voluminous, and with six biburcated mandibles in the mid-portion, although details can not be observed because buccal cavity is filled with detritus. Pharynx cylindrical

Fig. 6 : *Metasphaerolaimus hamatus* Gourbault & Boucher, 1981.
$_1$; A-B : Posterior end ; A : Subventral view ; B : Subdorsal view.

and surrounding basis of buccal cavity. Ventral gland cell not observed. Three caudal gland cells within tail each with a separate subterminal outlet. Copulatory apparatus observed from subdorsal and subventral views; spicules slender and slightly-curved, 30 µm along the arc, 25 µm from tip to tip, distally with a weakly sclerotized gubernaculum. Testes opposite and outstretched, their exact location compared to the intestine cannot be observed.

Remarks

Although details of head end cannot be observed precisely in the specimen, I have no hesitation in identifying it as *M. hamatus*. The powerful, long and anteriorly directed setae on tail is a characteristic feature of *M. hamatus*. Other body dimensions are also in accord. Present description is the first of a male. *Sphaerolaimus uncinatus* also has powerful, long and anteriorly directed setae on tail, but structures of the buccal cavity clearly separate it from present species.

Pomponema koesterae sp.n. (Fig. 7)

Material examined : five males, seven females and eight juveniles from the uppermost 2 cm of sediments in the deep-sea benthos of the Norwegian Sea.
Type locality : station 468.
Other localities : stations 59, 61, 70, 489.

Measurements ;

Holotype

1 $\frac{4 - 210 \quad M \; 1\,074}{24 - 45 \quad 51 \quad 29}$ 1 238 µm (NSIMB 562.20)

a = 24 b = 5.9 c = 7.6

Paratypes

2 $\frac{2 - 223 \quad M \; 1\,169}{17 - 55 \quad 56 \quad 33}$ 1 467 µm (NSIMB 562.21)

a = 24 b = 6.1 c = 7.3

1 L = 1 562 µm (NSIMB 562.22)
a = 21 b = 6.1 c = 5.7 ; V = 58 %

2 L = 1 250-1 503 µm
a =18-20 b = 4.2-6.1 c = 7.6-7.9 V = 59-64 %

Description

Males. Body slender with strongly attenuating tail. Cuticle with coarse punctuations in anteriormost 74-84 µm body region, elsewhere finer dots in twice as many rows as anteriormost portion. Lateral field present from amphids to conical portion of tail, wide in pharyngeal region (ca. 10 µm), and gradually more narrow (6 µm) and raised above the body surface. Cuticular pores present along the lateral field together with 3-5 µm long somatic setae. Cephalic sense organs in two circles : one with six small and stout internal labial setae, and

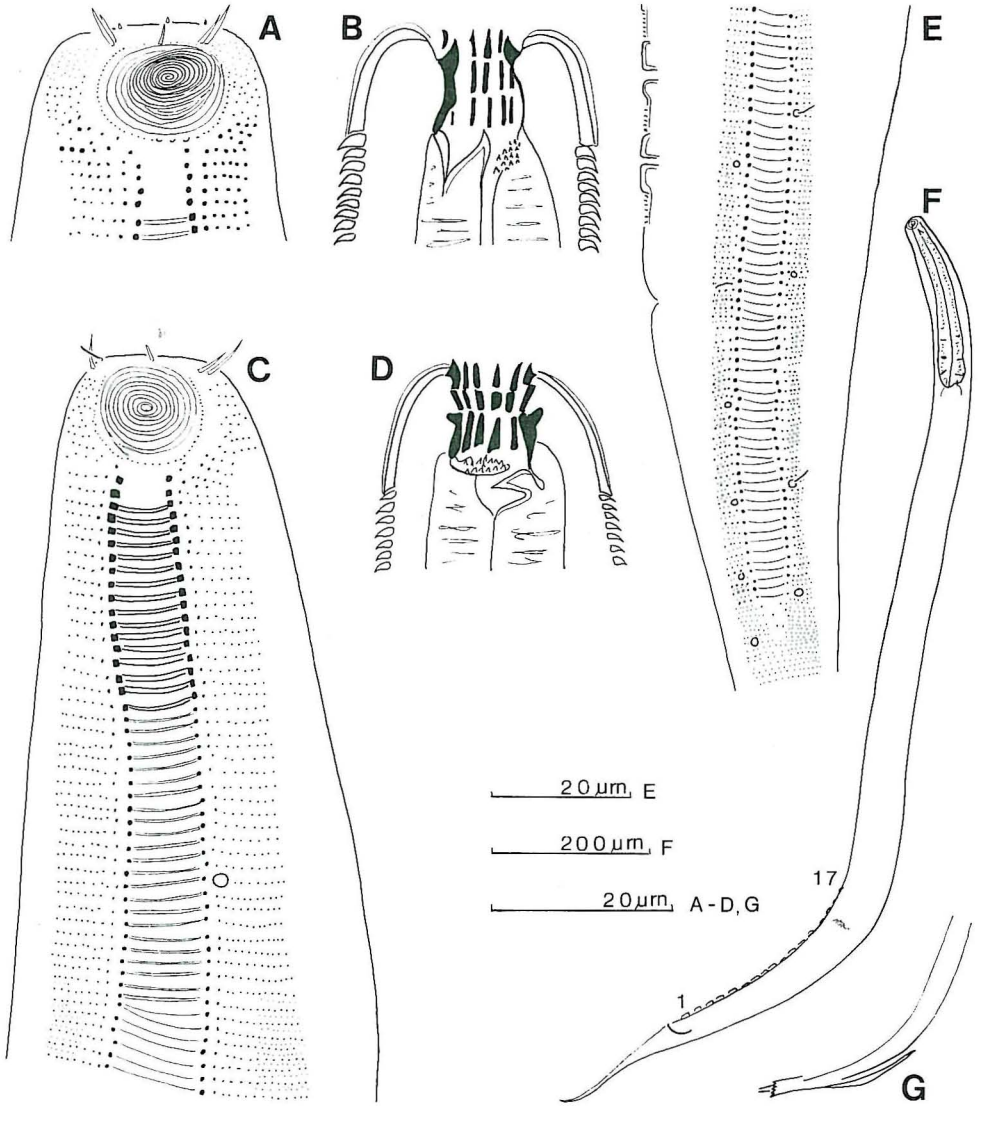

Fig. 7 : *Pomponema koesterae* sp.n.
A : Head in surface view of $_1$; B : Head in longitudinal view of $_1$; C : Anterior end in surface view of $_2$; D : Head in longitudinal view of $_2$; E : Cloacal region in surface view of $_2$; F : Total view of $_1$; G : Copulatory apparatus of $_2$.

the second with six external labial setae 3-4 µm long and four cephalic setae 6-7 µm long. Amphids circular, spiralized with about 10 narrow turns, 13-16 µm in diameter or 55 % of corresponding body diameter, anterior border situated at head end close to second circle of cephalic sense organs. Mouth opening surrounded by strongly sclerotized rugae in the shape of teeth, further posteriorly articulating rods and terminating with a strongly sclerotized dorsal tooth opposed to a large area of denticles. Pharynx surrounding posterior portion of buccal cavity and posteriorly slightly enlarged. Ventral gland cell opening about 120 µm behind head end. Spicules curved and slender, 37-41 µm along the arc, 32-33 µm from tip to tip ; gubernaculum as a slender rod, distally enlarged and dentated, 19-21 µm long. 15-17 cup-shaped preanal supplements present. Testis anteriorly directed, outstretched and left of intestine.

Females. Females are in most respects similar to males. Single ovary anteriorly directed, reflexed and left of intestine. Flagelli-formed sperm cells present.

Juveniles. Similar to adults.

Differential diagnosis

Pomponema koesterae sp.n. (named for Dr M. Köster, co-worker in the SFB 313 team of scientists at the University of Kiel) is closely related to *P. papillatum* (Filipjev, 1922) ; similar characters are head end, shape of tail, cuticular ornamentation, and a single ovary. They differ in the structures of the copulatory apparatus : slender spicules and dentated gubernaculum in *P. koesterae* vs. cephalated spicules and not dentated gubernaculum in *P. multipapillatum*.

DIVERSITY OF FEEDING TYPES

The twelve predatory nematode species from the deep-sea benthos of the Norwegian Sea belong to six families and ten genera of which Sphaerolaimidae is represented with six species belonging to four genera (Table II). The buccal cavity of one representative of each of the ten genera is illustrated in Fig. 8.

One feeding type is composed of six species which are provided with mandibles to hold prey; i.e. *Enoplus* sp., *Enoploides* sp., *Enoplolaimus* sp., and the three *Metasphaerolaimus* species (*M. crassicauda*, *M. gerlachi* and *M. hamatus*). The *Metasphaerolaimus* species do not have teeth in contrast to the other three species. *Subsphaerolaimus brevicauda, Sphaerolaimus kleini, Parasphaerolaimus antiae* form a second feeding type with voluminous buccal cavities constructed of articulating walls without teeth. *Halichoanolaimus minor* and *Pomponema koesterae* share many elements of a buccal cavity provided with articulating stiffening ribs, teeth and denticles. *Syringolaimus renaudae* is separated from all other species by its protrudable teeth at the outermost end of a long, narrow buccal cavity (cf. Van Der Heiden, 1975).

The illustrations of the head of ten representatives of predatory nematode species show at first glance a large size difference between species (Fig. 8). The widest buccal cavity is present in *Parasphaerolaimus antiae* (65 µm) and most narrow in *Syringolaimus renaudae*

TABLE II

Records of predatory nematode families, genera and species from the deep-sea benthos.

Species	Region	Water depth (m)	Reference
Cyatholaimidae			
Pomponema corniculata Gourbault, 1980	SE Atlantic ; Angola Bassin	2 063-3 615	Gourbault (1980)
Pomponema koesterae sp.n.	Norwegian Sea	970-3 062	Present study
Pomponema segregatum Wieser, 1959	NW Atlantic off N. Carolina	100-750	Tietjen (1976)
Selachinematidae			
Choniolaimus sp.	NW Atlantic ; off N. Carolina	50-2 000	Tietjen (1976)
	Venezuela Bassin	3 858	Tietjen (1984)
Halichoanolaimus macramphis Gourbault & Vincx, 1985	SE Atlantic Cap Bassin	4 180	Gourbault & Vincx (1985 a)
Halichoanolaimus macrocephallus Gourbault & Vincx, 1985	SE Atlantic ; Cap Bassin	4 180	Gourbault & Vincx (1985 a)
Halichoanolaimus minor Ssaweljev, 1912	Norwegian Sea	970-1 426	Present study
	SE Atlantic ; Angola and Cap Bassins	2 063-4 308	Gourbault & Vincx (1985 a)
Halichoanolaimus quattuordecimpapillata Chitwood, 1951	NW Atlantic off N. Carolina	50-600	Tietjen (1976)
Halichoanolaimus sp.	NW Atlantic off N. Carolina	750-2 500	Tietjen (1976)
	Puerto Rico Trench	2 217	Tietjen (1989)
	W Atlantic ; Hatteras Plain	5 411	Tietjen (1989)
Sphaerolaimidae			
Subsphaerolaimus brevicauda sp.n.	Norwegian Sea	1 286	Present study
Subsphaerolaimus seticaudatus Gourbault & Boucher, 1981	SE Atlantic ; Cap Bassin	3 694	Gourbault & Boucher (1981)
Sphaerolaimus crenellatus Warwick, 1973	Arabian Sea	660	Warwick (1973)
Sphaerolaimus ferulaceus Gourbault & Boucher, 1981	SE Atlantic ; Cap Bassin	2 992	Gourbault & Boucher (1981)
Sphaerolaimus ibericus Freudenhammer, 1975	Iberian Deep-Sea	1 174	Freudenhammer (1975)
Sphaerolaimus kleini sp.n.	Norwegian Sea	1 245-3 062	Present study
Sphaerolaimus lutarius Gourbault & Boucher, 1981	SE Atlantic ; Angola Bassin	3 615-4 308	Gourbault & Boucher (1981)
Sphaerolaimus paragracilis Vitiello, 1971	Puerto Rico Trench	7 460	Tietjen (1989)
Sphaerolaimus peruanus Freudenhammer, 1975	Shelf of Peru Trench	520	Freudenhammer (1975)
Sphaerolaimus uncinatus Freudenhammer, 1970	Iberian Deep Sea	1050	Freudenhammer (1970)
	Bay of Biscay	1 920-4 725	Dinet & Vivier (1979)
Sphaerolaimus sp.	Venezuela Bassin	3 517-5 054	Tietjen (1984)
	Puerto Rico Trench	7 460-8 380	Tietjen (1989)

	W. Atlantic ; Hatteras Plain	5 411	Tietjen (1989)
	NW Atlantic off Scotian Rice	4 626	Thistle & Sherman (1985)
Sphaerolaimus 2 spp.	NW Atlantic off N. Carolina	600-2 500	Tietjen (1976)
Sphaerolaimus 4 spp.	Bay of Biscay	1 920-4 725	Dinet & Vivier (1979)
Parasphaerolaimus antiae sp. n.	Norwegian Sea	1 245	Present study
Metasphaerolaimus cancellatus Gourbault & Boucher, 1981	SE Atlantic ; Angola Bassin	4 308	Gourbault & Boucher (1981)
Metasphaerolaimus crassicauda (Freudenhammer, 1975)	Iberian Deep Sea	1 311-1 944	Freudenhammer (1975)
	Bay of Biscay	1 920-4 725	Dinet & Vivier (1979)
	Norwegian Sea	970-1 426	Present study
Metasphaerolaimus gerlachi sp.n.	Norwegian Sea	1 245-1 426	Present study
Metasphaerolaimus hadalis (Freudenhammer, 1975)	Peru Trench	6 313	Freudenhammer (1975)
	Bay of Biscay	1 920-4 725	Dinet & Vivier (1979)
Metasphaerolaimus hamatus Gourbault & Boucher, 1981	SE Atlantic ; Cap Bassin	2 944	Gourbault & Boucher (1981)
	Norwegian Sea	1 286	Present study
Metasphaerolaimus inglisi Gourbault & Boucher, 1981	SE Atlantic ; Angola and Cap Bassins	2 944 2 063	Gourbault & Boucher (1981)
Enoplidae			
Enoplus sp.	NW Atlantic off N. Carolina	50-600	Tietjen (1976)
	Norwegian Sea	1 400	Present study
Thoracostomopsidae			
Enoploides sp.	NW Atlantic off N. Carolina	50-600	Tietjen (1976)
	Norwegian Sea	1 245	Present study
Enoplolaimus sp.	Norwegian Sea	1 286-3 062	Present study
Mesacanthion sp.	NW Atlantic off N. Carolina	50-800	Tietjen (1976)
	Puerto Rico Trench	2 217-8 189	Tietjen (1989)
Synonchus alisonae Warwick, 1972	Arabian Sea	2 480	Warwick (1973)
Ironidae			
Syringolaimus renaudae Gourbault & Vincx, 1985	SE Atlantic ; Angola and Cap Bassins	3 694-4 180	Gourbault & Vincx (1985 b)
	Norwegian Sea	1 245-1 426	Jensen (1988)
Syringolaimus filicaudatus Vitiello, 1970	Venezuela Bassin	3 517-3 858	Tietjen (1976)
Syringolaimus sp.	NW Atlantic ; Scotian Rice	4 626	Thistle & Sherman (1985)
Syringolaimus 2 spp.	Bay of Biscay	1 920-4 725	Dinet & Vivier (1979)
	W. Atlantic ; Hatteras Plain	5 411	Tietjen (1989)
	Puerto Rico Trench	8 189	Tietjen (1989)

and *Enoploides* sp. (ca. 6 µm). A prey-size selection is likely to take place by species within each feeding type ; i.e. among species with mandibles *Enoplus* sp. (juvenile) has a 30 µm wide buccal cavity opposed to *Enoploides* sp. (6 µm, juvenile) and *Metasphaerolaimus* spp. with a ca. 9 µm wide buccal cavity. Observations from shallow water have shown that predatory nematodes swallow their prey whole ; i.e. a size-range from small-sized nematodes up to oligochaetes. Results from this study suggest that such a size-range of prey organisms is likely also included in the diet of deep-sea predatory nematodes (cf. also Freudenhammer, 1975). Gut contents of *H. minor* studied herein included a large accumulation of undigested sclerotized elements of nematode copulatory apparatus different from the species itself substantiating its predatory nature (cf. also Gourbault & Vincx, 1985 a). Some juveniles of *M. crassicauda* had sclerotized elements of a buccal cavity similar to their own in their gut which at first glance suggests cannibalism. Since I only found such examples among juveniles I am more inclined to suggest that the buccal cavity in the gut in fact is their own moult from the former juvenile stage ; i.e. *M. crassicauda* displays a moulting mechanism comparable with that found in Chromadoridae species where it is known that the juveniles eat the sclerotized linings of their own feeding apparatus at each moult (Jensen, 1983).

GEOGRAPHICAL DISTRIBUTION AND DISPERSAL MECHANISM

Fourteen studies have described or listed predatory nematodes from the deep-sea benthos (Table II). Most are from the Atlantic Ocean but one is from the Arabin Sea (Indian Ocean) and one is from the Peru Trench (Pacific Ocean). Twenty seven predatory nematode species and 6 families have been identified. Sphaerolaimidae contains seventeen identified species. The studies from the East Atlantic (Freudenhammer, 1970, 1975 ; Dinet & Vivier, 1979 ; Gourbault & Boucher, 1981 ; present study) have each dealt with 5-7 Sphaerolaimidae species in their samples in contrast to records of 1-2 sphaerolaimid species in each of the studies from the West Atlantic (Tietjen, 1976, 1984, 1989 ; Thistle & Sherman, 1985).

Four of the twelve predatory nematodes from the deep-sea benthos of the Norwegian Sea were found elsewhere in the East Atlantic ; i.e. *M. crassicauda* in the Iberian Deep Sea, and *M. hamatus, H. minor* and *S. renaudae* were found in silty-clay deep-sea bottoms off South Africa (Table II). These records from the East Atlantic deep-sea do not exclude their occurrence in the West Atlantic deep-sea because at least two predatory nematode species from the Mediterranean : *Syringolaimus filicaudatus* and *Sphaerolaimus paragracilis* have been recorded from the West Atlantic deep-sea benthos (Tietjen, 1976, 1989). The occurrence of the four nematode species over such a long latitudinal distance in the deep-sea of the East Atlantic (20 °S to 70 °N) suggest that they are dispersed by nearbottom currents in the nepheloid bottom layer (cf. Jensen *et al.*, 1991). Such a dispersal mechanism in the deep-sea is likely to be widespread among small-sized organisms in the range of µg WW (see also Tietjen, 1989), although it has been suggested (Thistle & Sherman, 1985) that for example some groups of deep-sea nematodes by their tail shapes are adapted to avoid being

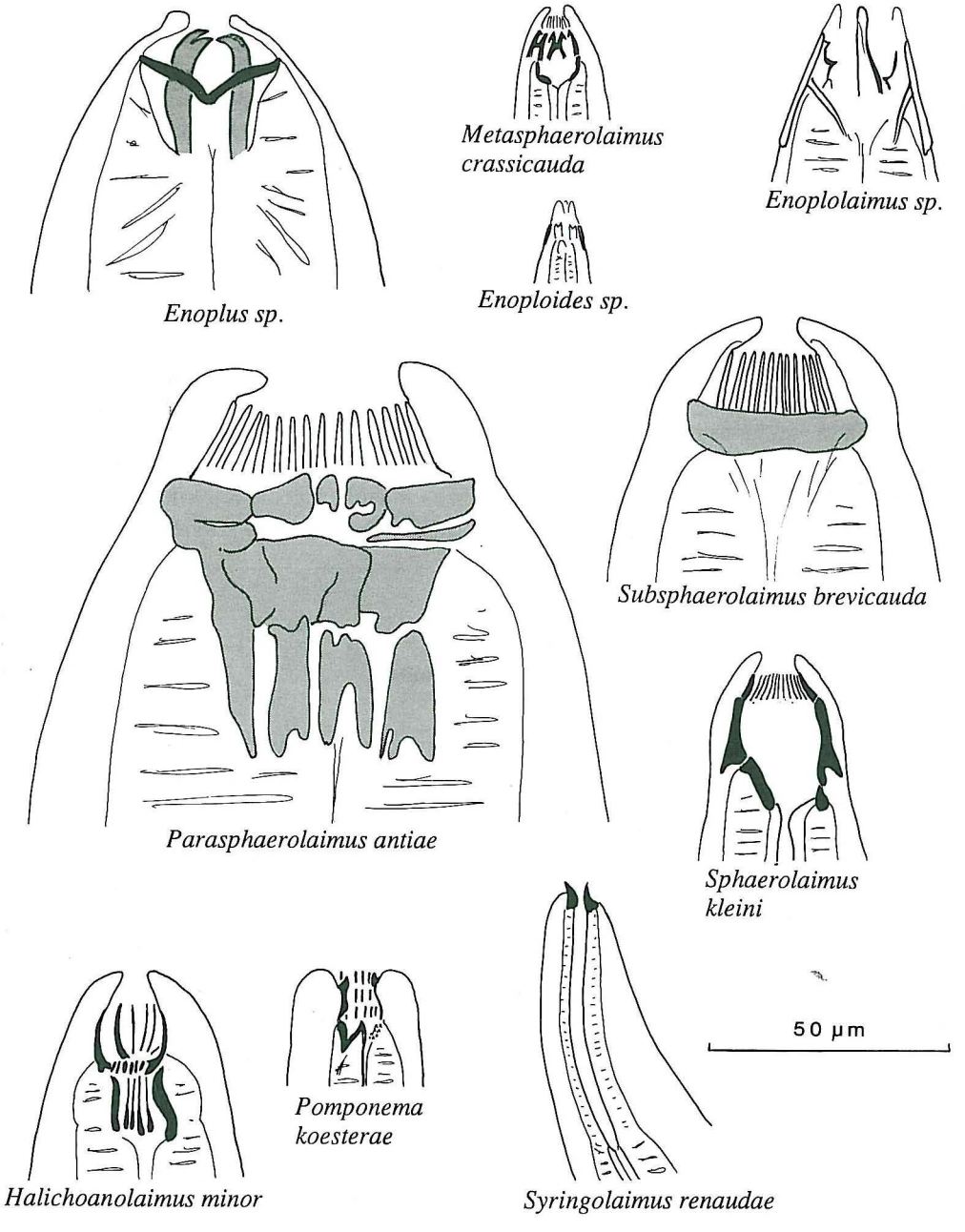

Fig. 8 : Predatory nematodes from the deep-sea benthos of the Norwegian Sea.
Diversity of feeding types as deduced from the structure of the buccal cavities. *Enoplus* sp., *Enoploides* sp. and *Enoplolaimus* sp. are juveniles. All drawings to same scale.

dispersed through suspended material. Deep-sea animals do not demand the physiological adaptations with regard to the chemical barriers (e.g. oxygen and salinity) and temperature differences which generally exlude long-distance dispersal of species in shallow waters. One of the species *H. minor*, however, has been reported from shallow waters in the harbour of Kola Bight, White Sea (Ssaweljev, 1912), and among seegrasses and mud along the coast of Chile (Wieser, 1954). Tietjen (1976) also observed predatory nematodes (and other nematodes as well, see also Decraemer, 1985) in the sediments of the North Carolina shelf : *Pomponema segregatum, Choniolaimus* sp., *Halichoanolaimus* sp. and *Mesacanthion* sp. (Table II) indicating a dispersal mechanism by vertical transport of sediments down the continental shelf after which horizontal dispersal by means of near-bottom currents in the nepheloid bottom layer may have taken place. Romero-Wetzel & Gerlach (1991) made a similar observation with some macrofauna species from the deep-sea benthos of the Norwegian Sea which were reported from shallow waters, too, including the Baltic Sea. Moreover, onboard R/V *Meteor* cruise 7/4 we observed benthic meiofaunal organisms (foraminifera and nematodes) from Vöring Plateau (1 000-1 600 m depth, Norwegian Sea) that adapted themselves within a few hours to a pressure difference from more than 100 bars to shipboard conditions where they behaved as shallow water species do ; these observations were substantiated with tube-building activity performed by deep-sea polychaetes after a few days acclimatization onboard the ship.

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