Journal of Nematology 29(1):65–81. 1997.
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Descriptions of *Eumonhystera borealis* n. sp. and *Sphaerolaimus occidentalis* n. sp., and a Redescription of *S. gracilis* de Man 1876 (Nemata) from Bothnian Bay, Baltic Sea

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Abstract: The free-living nematodes *Eumonhystera borealis* n. sp., *Sphaerolaimus occidentalis* n. sp., and *S. gracilis* de Man 1876 from Bothnian Bay in the northern Baltic Sea are described and illustrated. *Eumonhystera borealis* n. sp. differs from other species by its small body size (314–393 µm), narrow body (a = 37–49), and large anterior amphids. In *Sphaerolaimus occidentalis* n. sp. the amphids are posterior to the buccal cavity, and it differs from other similar species by having two sclerotized rings in the posterior part of the buccal cavity. An intersex is reported for *S. gracilis*. *Sphaerolaimus gracilis* is cannibalistic or a predator of other species, with a preference for *E. borealis* n. sp. *Sphaerolaimus occidentalis* n. sp. coexists with *S. gracilis* at depths of 80 m but not at 12 m.

Key words: Baltic Sea, ecology, *Eumonhystera borealis* n. sp., feeding behavior, intersex, *Monhystrella anophthalma*, nematode, new species, predator, race, redescription, scanning electron microscopy, *Sphaerolaimus gracilis*, *Sphaerolaimus occidentalis* n. sp., taxonomy, transmission electron microscopy.

This study is part of a research project on the systematics, anatomy, and ecology of Bothnian Bay nematodes (Turpeenniemi 1993, 1995, 1996; Turpeenniemi and Hyvärinen, 1996). Bottom samples collected from Bothnian Bay, in the northern Baltic Sea, at depths of 12, 17, and 80 m contained numerous specimens of *Sphaerolaimus gracilis* de Man, 1876 and representatives of two unknown species, herein described.

Materials and Methods

Materials and methods for light microscopy (LM) and transmission electron microscopy (TEM) were identical to those used by Turpeenniemi (1993, 1995). For scanning electron microscopy, nematodes were fixed overnight in 2% glutaraldehyde buffered with sodium cacodylate at 4 °C. Nematodes were left in buffer at 4 °C for several days, transferred into a graded ethanol series, and then transferred finally into 100% alcohol. Nematodes were critical-point dried, coated with 42 nm gold, and studied with a JEOL JSM-35CF scanning electron microscope (SEM) at 15 kV. Part of the material for SEM of *S. occidentalis* n. sp. included specimens permanently mounted in glycerin. All other specimens were collected live.

Systematics

Eumonhystera borealis n. sp.
(Monhysteridae, Monhysterinae)
(Figs. 1;8C,D;9)

Measurements of holotype male, allotype female, paratype males, and paratype females are given in Table 1.

Males (n = 4): Body elongate, tapering at both ends, tapering more gradually anteriorly. Body 1.5 times head diameter at base of esophagus. Head end swollen (Fig. 1A). Cuticle with transverse rows of small dots, visible with phase contrast (Fig. 1A,E), rows about 0.7 µm apart. Somatic setae submedian, 3.0–3.5 µm long (one-third of body diameter at midbody) (Fig. 1D). Six inner labial papillae, 0.3 µm long; outer labial setae and cephalic setae in one circle; six outer labial setae, 2.2–2.5 µm long (Fig. 1A); four cephalic setae, 1.8–2.0 µm long (40% of head diameter) (Fig. 1A). Cephalic setae more slender than outer labial setae (Fig. 1A). Cheilostom sclerotized, about 1.5 µm high, 2.0–2.5 µm wide at base (3/5 of head

Received for publication 11 August 1995.
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The author thanks Drs. R. V. Anderson and E. C. Bernard for comments on the manuscript, I. J. Holopainen for checking the English language, and J. Hulkkonen for assistance in drawings.
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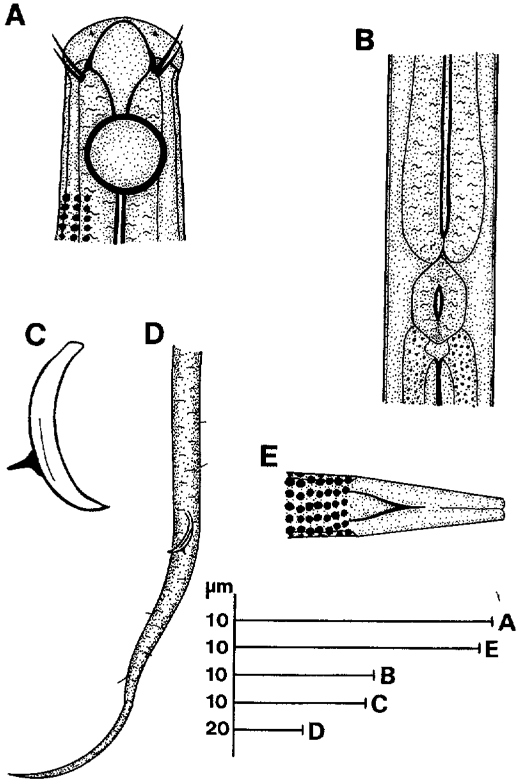

FIG. 1. Drawings of *Eumonhystera borealis* n. sp. males. A) Anterior end. B) Esophago-intestinal junction. C) Spicule. D) Posterior body. E) Tail tip.

width) (Fig. 1A). Amphid aperture circular, 3.0 µm in diameter, 60% of corresponding body diameter, anterior end 3–4 µm (0.6–0.8 head diameter) from head end (Fig. 1A). Esophagus gradually widening posterior to nerve ring (Fig. 1B); esophagus 3 µm wide anteriorly, 6–7 µm wide posteriorly (Fig. 1B). Luminal lining of esophagus slightly sclerotized (Fig. 1B). Cardia ovoid or hexagonal, 3.0–3.5 µm wide, 5–6 µm long, with central, weakly sclerotized globular or longitudinal lumen, 0.6 µm in diameter (Fig. 1B). Luminal lining of intestine 2.0–2.5 µm wide (half of esophagus width), consisting of an inner, darker, thinner layer and an outer, wider, more hyaline layer (Fig. 1B). Testis monorchic, outstretched, on right side (n = 3), anterior end 35–56 µm from esophagus base. Spicules arcuate, wide, 13–14 µm long (n = 4), distally bluntly pointed, proximally narrowing into cylindrical manubrium (Figs. 1C,D;9B,C). Gubernaculum 3–4 µm long, about 0.3 µm thick, apophysis 1.5–2.0 µm long (Figs. 1C;9B,C). Tail anteriorly conoid (Fig. 1D), posterior half conoid-filiform (Fig. 1D). Filiform part ventrally bent (n = 4); conoid part ventrally bent (n = 2) or straight (n = 2) (Fig. 1D).

Females (n = 4): Body tapering at both ends. Body width at base of esophagus 1.5 times head diameter. Body slightly constricted in vulval region. Amphid aperture circular, 2.8 µm in diameter (55% of body diameter), anterior end 2–3 µm (0.6 head diameter) from head end. Ovary antepudendal, monodelphic, outstretched, lying on right side of intestine (n = 4). Anterior end of ovary 37–51 µm from esophagus. Vagina 5 µm long. Vaginal wall 1 µm thick. Tail conoid, gradually tapering to pointed end, the last three-fourths of tail filiform. Tail tip conoid, last 5 µm without punctations.

Type locality

Collected in mud at 80-m depth and in fine clayish sand bottom at 17-m depth and 12-m depth, close to island Hailuoto in Bothnian Bay, northern Baltic Sea; water salinity 2–4%.

Type specimens

Holotype male slide BBh 8, paratype male 1 BBi 29, paratype male 2 BBi 36, paratype female 2 BBh 72, paratype female 3 BBc 11, paratype female 1 BBh 89, allotype female BBh 98; paratype male BBa 61 (in the gut of *S. gracilis* male), paratype female, BBj 19 (in the gut of *S. gracilis* male); paratypes (spicules): 10 pairs on slide BBh 60 (in the gut of *S. gracilis* female); 8 pairs on slide BBh 81 (in the gut of *S. gracilis* female). Slides BBh 8, BBj 19, BBh 60, and BBc 11 deposited in the Zoological Museum, University of Helsinki; remaining slides deposited in the Nematode Collection of Instituut voor Dierkunde, Ledeganckstraat 35, B-9000 Gent, Belgium.

Diagnosis

Eumonhystera borealis n. sp. is characterized by short (314–393 µm) and slender (a = 37–49) body, wide head, high and wide cheilos-

TABLE 1. Measurements, ratios, and percentages of holotype male, paratype males (n = 2), allotype female, and paratype females (n = 3) of *Eumonhystera borealis* n. sp.

Character	Holotype male	Paratype males 1	Paratype males 2	Allotype female	Paratype females 1	Paratype females 2	Paratype females 3
			Measurements (μm)				
Body length	389	314	380	328	288	256	393
Esophagus length	81	65	76	62	61	58	73
Tail length	83	65	86	78	62	62	75
Body width	8	7	8	8	7	7	8
Head width	4.5	4.5	4.5	4.5	4.5	4	4.5
Body width at end of esophagus	8	6.5	7	7	7	6	8
Anal width	8	7	8	5.5	6	5	6.5
Spicule length	13	13	12.5				
			Ratios				
a	48.6	44.9	47.5	41.0	48.0	36.8	49.1
b	4.8	4.8	5.0	5.3	4.7	4.4	5.4
c	4.6	4.8	4.4	4.2	4.6	4.1	5.2
			Percentages				
V				57.9	62.8	61.7	60.6

tom, large anterior amphid, and ventrally bent, conoid-filiform male tail.

Relationships

The wide V or Y-shaped, unspecialized stoma indicates that *Eumonhystera borealis* n. sp. is a member of Monhysterinae (Jacobs, 1987). The outstretched ovary, slightly posterior position of vulva, small body size, and short spicules place the species in the genus *Eumonhystera* (Andrássy, 1984). From *E. tatrica* Daday, 1896, *E. borealis* n. sp. differs in having a more slender body (body width at end of esophagus 2.7 times head diameter in *E. tatrica* vs. 1.5–1.6 times head diameter in *E. borealis* n. sp.). From *E. multisetosa* (Meyl, 1960), *E. borealis* n. sp. differs by its larger amphid (40% vs. 55% of corresponding body diameter), shorter cephalic setae (length 50% of head diameter in *E. multisetosa* [Meyl, 1960], 15% of head diameter in *E. borealis* n. sp.), and different gubernaculum shape (Lorenzen, 1969). Spicules in *E. multisetosa* are slender, with a length 1.1–1.3 times the cloacal body diameter; in *E. borealis* n. sp. they are rather thick, with a length 2 times the cloacal body diameter.

Remarks

Gut content analysis (n = 8): One female had a row of 5 spheroidal cells of 2–3 μm in diameter in the foregut, and one male had 4 similar cells in the posterior gut. In the midgut of another male there were two similar cells 25 μm apart. One male had a similar cell in the foregut and large numbers of small, irregular bodies with the appearance of broken filaments or rods about 0.1 μm in diameter. Other types of cells were also present. One female had two granular cells, 8–10 μm long and 3–4 μm wide, abutting each other. These cells were characterized by a circular, sclerotized ring in one end and a slender flagellum-like structure in the same end (Fig. 8D). One male had a similar cell in its foregut. Two females had empty guts.

Sphaerolaimus occidentalis n. sp.
(Figs. 2A–D;3A–E;5D–E;7A)

Description

Measurements of holotype male, paratype males, and paratype females are given in Table 2.

Males (n = 7): Body stout, width 65–85 μm, white in LM. Cuticle with transverse striations, 14 annules/10 μm. Somatic setae fine, tapering gradually, 6–15 μm long in cervical and midbody region, 6–9 μm on tail, arranged in eight longitudinal rows, more numerous in esophageal region and tail region

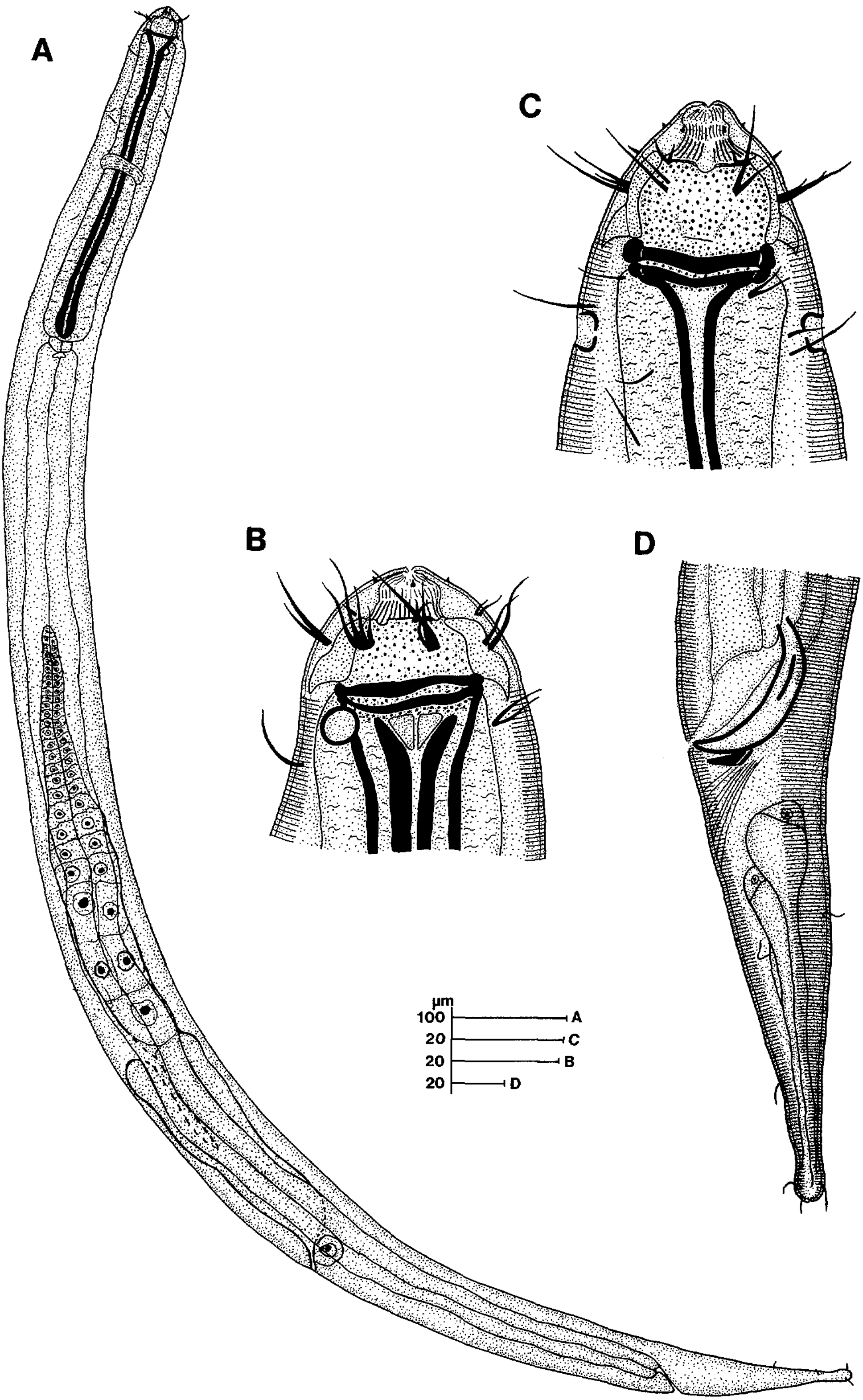

FIG. 2. Drawings of *Sphaerolaimus occidentalis* n. sp. A) Female. B) Head of female, sublateral view. C) Head of female, ventral view. D) Tail of male.

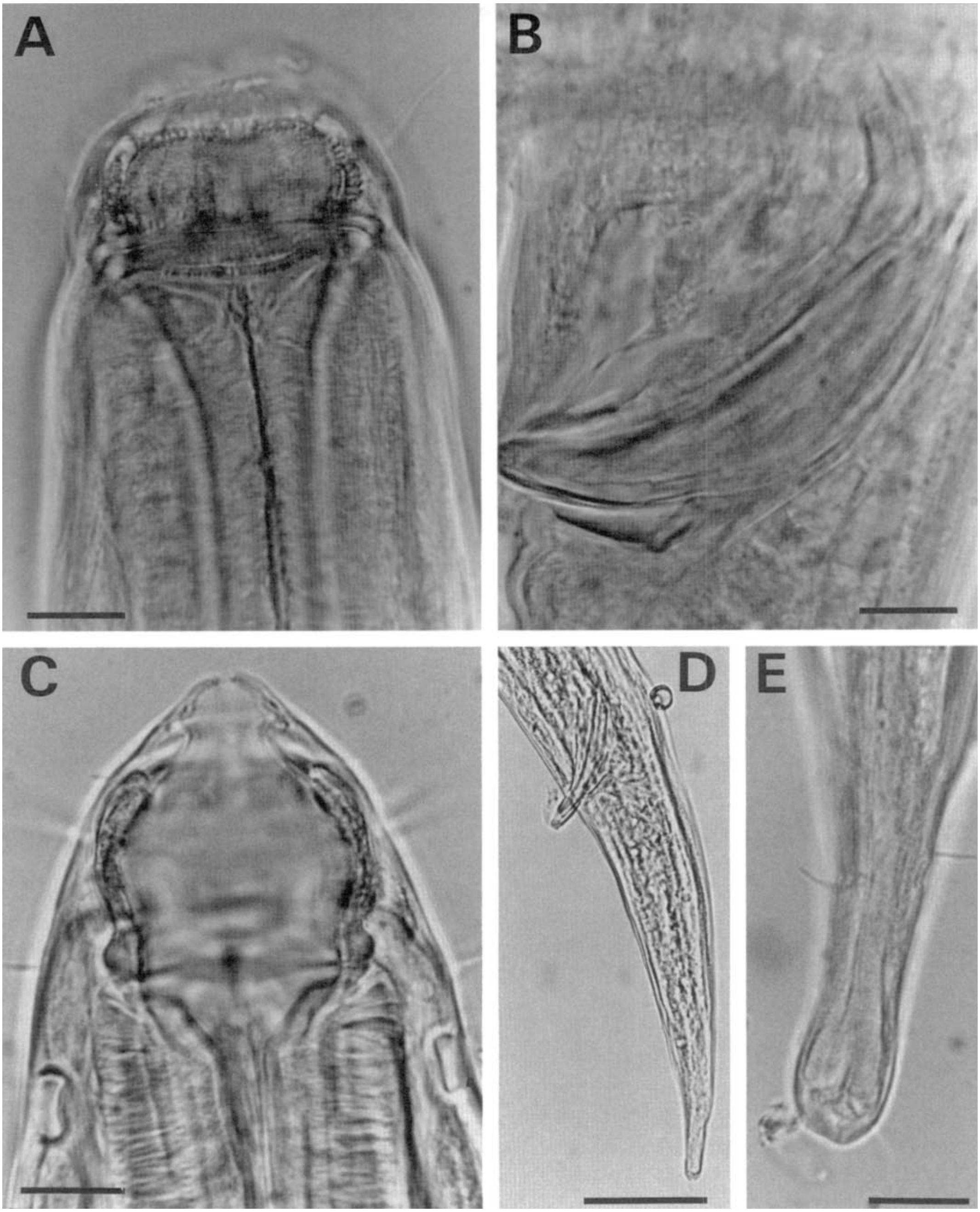

FIG. 3. Photomicrographs of males of *Sphaerolaimus occidentalis* n. sp. A) Head showing two sclerotized rings in buccal cavity. B) Copulatory apparatus. C) Head. D) Tail. E) Tail tip. Scale bars: A–C,E = 10 μm; D = 50 μm.

than in midbody. Three setae at tail tip, 5–8 μm long (Fig. 2D). Six inner labial papillae, 5–6 μm from anterior end (Fig. 5D,E). Six outer labial setae, 1.5–2.0 μm long (Fig. 5D,E); four cephalic setae, 3–4 μm long (Fig. 5D,E). Outer labial setae and cephalic setae in one circle, 10–11 μm from anterior end. Subcephalic setae 14–15 μm from anterior end, arranged as four sublateral groups of three or four setae 18, 13, 9, and 7 μm long, and four submedian groups of three setae, one 15–16 μm long and two 7–9 μm long (Fig. 5D). Sclerotized cheilostomal ridges or perioral platelets numerous, 5–6

TABLE 2. Measurements, ratios, and percentages of holotype male, paratype males (n = 4), and paratype females (n = 2) of *Sphaerolaimus occidentalis* n. sp.

Character	Holotype male	Paratype males Mean	Paratype males Range	Paratype female	Paratype female
		Measurements (µm)			
Body length	1,589	1,472	1,304–1,600	1,588	1,640
Esophagus length	312	302	275–316	316	332
Tail length	165	158	137–184	148	156
Body width	73	77.5	65–85	70	74
Head width	25	27.3	25–31	25	32
Body width at end of esophagus	70	66.3	57–70	64	70
Anal width	51	52.3	45–59	40	42
Spicule length	71	71	68–74		
		Ratios			
a	21.8	19.1	17.4–20.1	21.8	23.4
b	5.1	4.9	4.7–5.1	4.8	5.2
c	9.6	9.4	8.7–9.5	10.2	11.1
		Percentages			
V				72.9	73.8

µm long, anterior to buccal capsule. Oral opening surrounded by six triangular lips, each with wide ridges (Fig. 5D). Buccal cavity 21–22 µm wide, 16–18 µm long, with sides 2–3 µm thick (Fig. 3A,C). Posterior end of buccal cavity encircled by sclerotized zone, 4–5 µm wide, consisting of two rings (Fig. 3A,C). Buccal cavity ending just behind buccal rings (Fig. 3A). Extrabuccal projections of buccal wall present, 6–7 µm long, at posterior end of buccal capsule (Fig. 3A,C). Amphid circular, 7–8 µm in diameter, 15–18% of corresponding body diameter, posterior to buccal cavity, 32–40 µm (1.3–1.6 head diameters) from head end (Fig. 3C). Esophagus 24–32 µm wide at nerve ring, 36–47 µm at base. Esophageal lumen triradiate, strongly sclerotized (Fig. 7A), 9–10 µm wide at nerve ring, 14–18 µm wide at base. In TEM two different types of muscles connected to lumen: heavy, more transverse muscles attached to central lumen; more oblique muscles connected to peripheral, triradiate endings of lumen (Fig. 7A). Cardia conoid, 24 µm wide, 19 µm long. Renette cell 27–32 µm long, 23–25 µm wide, posterior to esophagus; duct diameter 3 µm. Duct leading into ampulla and ventral pore, situated behind nerve ring, 184–235 µm (70–75% of the length of esophagus) from anterior end. Testes opposed, diorchic, anterior testis left (n = 3) or right (n = 2) of intestine, posterior testis always on opposite side of the anterior testis. Ejaculatory gland cells present laterally on both sides of intestine. Precloacal papillae present. Spicules arcuate, slender, thick-walled, 68–74 µm long, 1.2–1.5 times cloacal body diameter (Figs. 2D;3B,D). Spicules widest in middle tapering distally to a narrowly rounded tip, proximally with a cylindrical or ovoid head (Figs. 2D;3B,D). Gubernaculum small, triangular in lateral view, 14–17 µm long, 3–4 µm thick (Figs. 2D;3B,D). Tail conoid-cylindrical (Figs. 2D,3D); terminus short, clavate, sometimes cylindrical, 16–18 µm long, 12–14% of tail length (Figs. 2D,3D). Caudal glands present, opening through separate pores (Fig. 3E).

Female (n = 6): Similar to male in general morphological characters (Fig. 2A–C). Gonad monodelphic, antepudendal, outstretched, lying either to right or left side of intestine (of four females, three with ovary on right side of intestine, one on left side) (Fig. 2A). Prevulval spermatheca extending into base of ovary (Fig. 2A), swollen, 45 µm in diameter, connected to uterus at region of sphincter muscles, 15–20 µm wide, 25 µm long. Vaginal sphincter muscles indistinct, 15 µm thick, 20 µm wide. Vaginal gland postvulval, 20–22 × 28–35 µm (Fig. 2A).

Type locality

Collected in mud at 80-m depth in Bothnian Bay, northern Baltic Sea, water salinity 3–4‰.

Type specimens

Holotype male slide BBe 72, paratype male slide BBl 4, paratype male slide BBj 29, paratype male slide BBe 31, paratype male slide BBb 85, paratype male slide BBd 65, paratype female slide BBc 55, paratype female slide BBj 29, paratype female slide BBc 34, paratype female slide BBd 65. Holotype male slide BBe 72, paratype slides BBc 55, BBj 29, and BBl 4 deposited in the Zoological Museum, University of Helsinki; remaining slides deposited in the Nematode Collection of the Instituut voor Dierkunde, Ledeganckstraat 35, B-9000 Gent, Belgium.

Diagnosis

Free-living nematode of the family Sphaerolaimidae characterized by stout body (a = 20.2–23.4), 10 cephalic setae (six outer labial setae + four cephalic setae), subcephalic setae in eight groups, 3–4 setae in each; two sclerotized, 3–5 µm-wide rings at posterior end of buccal cavity; amphid posterior to buccal cavity; slender, almost equally thickened somatic setae; esophageal lumen strongly sclerotized; spicule slender, arcuate; gubernaculum small, triangular in lateral view; females with weakly developed vaginal sphincter muscles; tail terminus short, clavate, sometimes cylindrical.

Relationships

Of those species of *Sphaerolaimus* having 10 cephalic setae (six outer labial setae, four cephalic setae) and the amphid posterior to the buccal cavity (Freudenhammer, 1975), *S. occidentalis* n. sp. is most similar to *S. crenellatus* Warwick, 1973, which differs from *S. occidentalis* n. sp. by its larger body size (2.4–2.7 mm) and presence of triangular sclerotizations (buttresses [Warwick, 1973]) at the posterior end of the buccal cavity (Warwick, 1973). *Sphaerolaimus gracilis* also has the amphid posterior to the buccal cavity, but it has 6 setose cephalic sense organs while *S. occidentalis* n. sp. has 10. *Sphaerolaimus gracilis* also lacks the sclerotized posterior rings and outer posterior projection of the buccal cavity of *S. occidentalis* n. sp. The luminal lining of the esophagus in *S. gracilis* is narrower and not as sclerotized as the lining in *S. occidentalis* n. sp. *Sphaerolaimus gracilis* differs from *S. occidentalis* n. sp. in having an apophysis on the gubernaculum of the male and having the female with more strongly developed vaginal dilator sphincter muscles.

Both *Sphaerolaimus makrolasius* Schulz, 1932 and *S. sabulosus* Schulz, 1932 are considered *species inquirendae* by Lorenzen (1978) and Wieser (1956). The male of the latter species is unknown, but the female is larger (2.76–2.96 mm) than *S. occidentalis* n. sp. Buccal cavities in *S. makrolasius* and *S. occidentalis* n. sp. resemble each other. *Sphaerolaimus makrolasius* can be differentiated from *S. occidentalis* n. sp. by its larger body size (2.0–2.4 mm vs. 1.3–1.6 mm), longer spicules (100–110 µm vs. 60–72 µm), and larger gubernaculum. *Sphaerolaimus makrolasius* and *S. occidentalis* n. sp. seem to be closely related to *S. hirsutus* Bastian, 1865 (Gourbault, 1987). They all have a shallow buccal cavity, a structurally distinct zone at the posterior end of buccal cavity, slender spicules, and a triangular gubernaculum without apophyses. The esophageal lumen of *S. hirsutus* appears to be as sclerotized (Bastian, 1865) as the lumen of *S. occidentalis* n. sp. and ultrastructurally similar to that of *S. occidentalis* n. sp. and *S. gracilis* (Gourbault, 1987). *En face* views of *S. balticus* Jensen, 1979 (Malakhov and Ovchinnikov, 1980) and *S. occidentalis* n. sp. were similar in the topography of the head region. Each had six well-separated, triangular lips with wide ridges (possibly perioral platelets of Jacobs and Heyns, 1992), relatively small labial papillae, six outer labial setae, four cephalic setae, three submedian subcephalic setae, and four sublateral subcephalic setae. In *S. balticus,* Jensen (1979) also found four subcephalic sublateral setae and six setose outer labial setae. Female reproductive organs of *S. occidentalis* n. sp. and *S. hirsutus* resemble each other in having poorly developed vaginal sphincter muscles (Bastian, 1865; Gourbault, 1987).

Remarks

Gut content analysis (n = 10; 5 males, 5 females): Three of 10 specimens had empty guts. Three specimens had spines, 2–3 µm long, in the foregut, and one of them also had spines in the posterior gut. In three different specimens there were 1–2 whole, partly digested nematodes in the gut. In two of them the ingested prey was in the posterior gut, and in one in the anterior gut. One of these specimens, a gravid female of *S. occidentalis* n. sp., had eaten an entire male *Eleutherolaimus schneideri* Turpeenniemi, 1996 tail-end first (Fig. 8B). The prey was in the posterior gut, with the tail end close to the rectum. Internal, soft parts of the victim were partly digested, but cuticle, amphid, and spicule were undigested. One specimen of *S. occidentalis* n. sp. had a rather large nematode in the posterior gut. This prey had sediment particles in its gut and was probably a member of Xyalidae.

Sphaerolaimus gracilis de Man 1876 (Form 2) (Figs. 4A–H;5A–C,F;6A,B;7B;8A,C)

Measurements of males and females are given in Table 3, and measurements of J4 are given in Table 4.

Redescription

Males (n = 14): Body slender, tapering anteriorly to conoid head end (Figs. 4A,5A), light yellow in LM. Cuticle finely striated (10–12 annules/10 µm) (Fig. 5B). Somatic setae in 8 longitudinal rows (Fig. 5A). Somatic setae considerably more numerous in cervical and tail regions than in midbody region (Figs. 4A,D;5A). In cervical region somatic setae 6–17 µm long (Fig. 5A,B), in midbody 6–7 µm long, and in tail 5–9 µm long (Fig. 4D). Oral opening of two chambers, with numerous ridges (Fig. 4A). Lips bearing many fine ridges (perioral platelets) (Fig. 5C). Six inner labial papillae, about 0.5 µm long (Figs. 4A,5C). Six outer labial papillae and four cephalic setae in one circle, anterior to buccal cavity (Figs. 4A,5C). Cephalic setae 5.5–6.5 µm long, about one-third the head diameter (Figs. 4A;5A,C). Subcephalic setae in eight groups: submedian group with one 15–16 µm-long seta and two 7–8 µm-long setae (Figs. 4A,5B); sublaterally four setae of different lengths (Figs. 4A,5B). Buccal cavity composed of a thick-walled anterior part and a sclerotized, thin-walled posterior part, the borders of the overlapping zones appearing as two weak lines (Fig. 4A).

Amphids circular, posterior to buccal cavity, width 7.3 ± 0.7 µm (5.6–8.0; n = 11), 24–29% of body diameter, 36.3 ± 2.0 µm (29.6–36.0; n = 11) (1.6–1.8 head diameters) from head end (Figs. 4A;5A,B). Esophagus cylindrical, anterior to nerve ring, gradually widening posteriorly. Luminal lining strongly sclerotized, triradiate in cross-section (Figs. 4A,7B). In electron microscopy two different sets of muscles connected to luminal lining of esophagus (Fig. 7B); transverse, strongly developed muscles connected to central lumen, more oblique muscles connected to triradiate endings of lumen (Fig. 7B). Renette pore posterior to nerve ring, 173.6 ± 14.8 µm (152–190; n = 11) from anterior end. Cardia conoid, 12–19 µm wide, 9–12 µm long (Fig. 4B–C). Renette cell 110.8 ± 15.5 µm (88–144; n = 9) posterior to end of esophagus (Fig. 4B). Renette cell 13.9 ± 5.1 µm (8.0–21.6; n = 5) × 31.5 ± 5.6 (24–36; n = 5) in diameter. Two pairs of coelomocytes (Fig. 3B,C): first pair 62.0 ± 16.1 µm (44–88; n = 6) and 102.6 ± 18.5 µm (76–128; n = 7) posterior to end of esophagus; second pair on other side of intestine 141.6 ± 11.7 µm (124–158; n = 9) and 194.2 ± 13.2 µm (172–212; n = 9) posterior to end of esophagus.

Testes opposed, diorchic, outstretched, position variable; anterior and posterior testes always on opposite sides of intestine. In two aberrant males testes parallel, directed anteriorly, on opposite lateral sides of intestine. Ejaculatory gland cells present. Precloacal papillae 7–9, about 1 µm wide, 1 µm long, at intervals of 21–45 µm (Fig. 5F). Spicule walls strongly sclerotized, proximal and distal part of about equal length forming an angle of about 135 degrees (Fig. 4D). Spic-

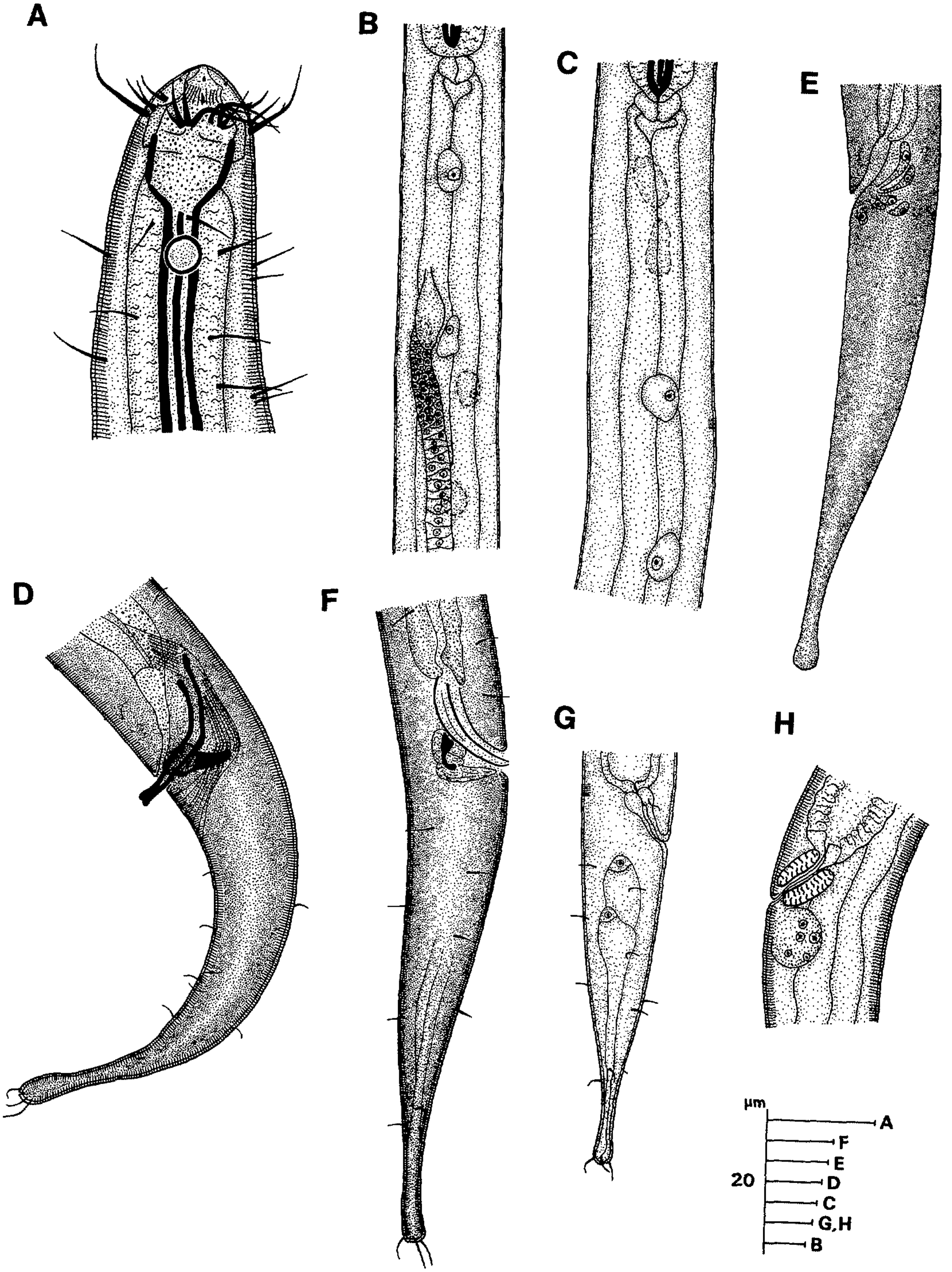

FIG. 4. Drawings of *Sphaerolaimus gracilis.* A) Anterior end of male. B) Midbody of female showing two pairs of coelomocytes, ovary, and renette cell. C) Midbody of male. D) Tail of male. E) Tail of J4 male. Note cells around cloacal opening. F) Posterior end of intersex female showing right spicule and median accessory piece. G) Tail of female. H) Vulva of female. Note heavily muscled sphincter around vagina and postvulvar gland with many nuclei.

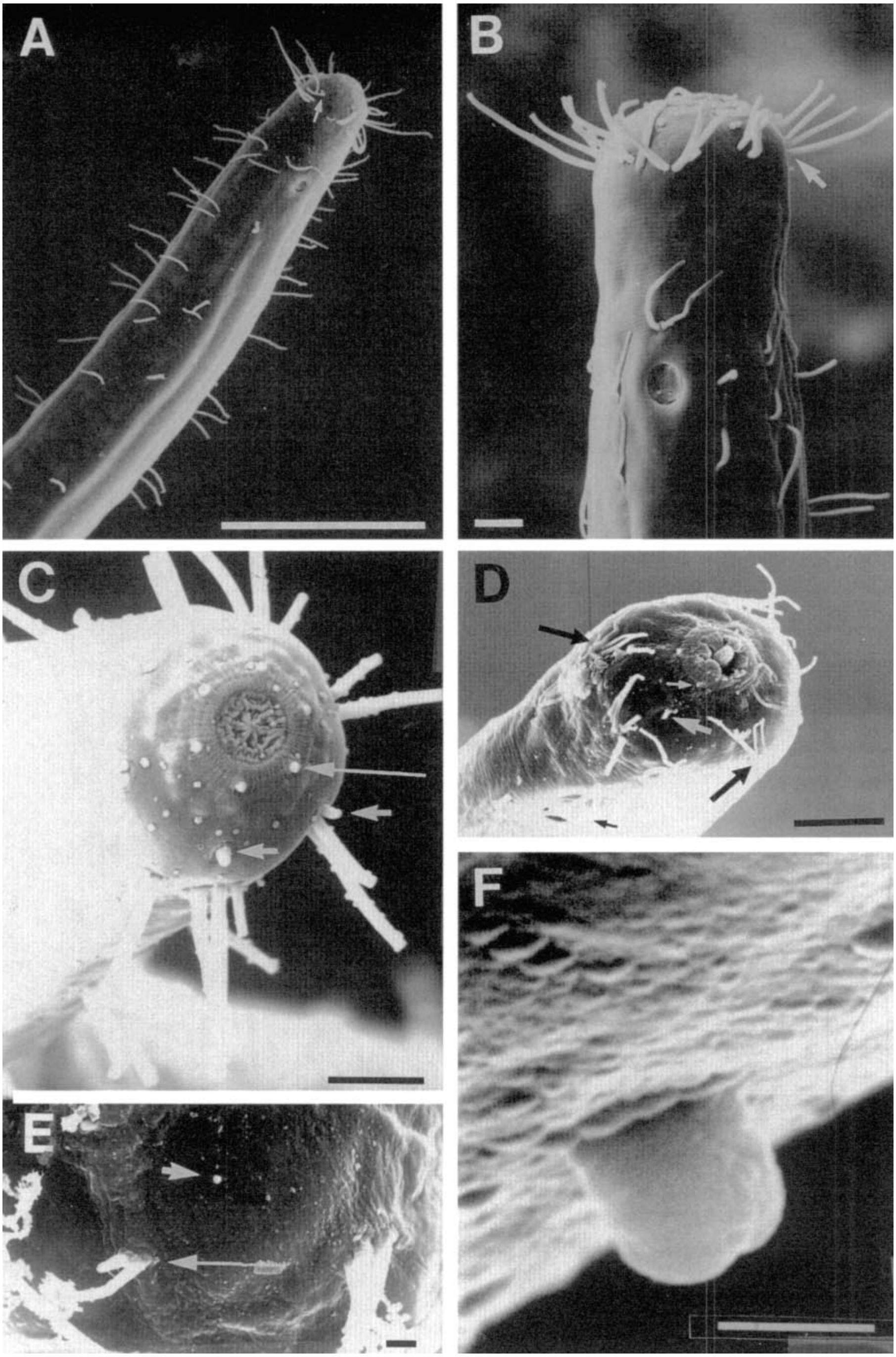

FIG. 5. Scanning electron micrographs of *Sphaerolaimus gracilis* (A–C,F) and *S. occidentalis* n. sp. (D–E). A) Anterior end of *S. gracilis* showing arrangement of somatic setae. Note outer labial papilla and cephalic seta (arrow), long subcephalic seta, and amphid. B) Head of *S. gracilis* showing three setae in submedian group of subcephalic setae (arrow). C) Inner (long arrow) and outer (short arrows) labial papillae of *S. gracilis*. D) *En face* view of *S. occidentalis* n. sp. showing six lips divided into perioral platelets. Note inner labial papilla (small white arrow), lateral outer labial seta (large white arrow), three submedian subcephalic setae (large black arrows), and amphid (small black arrow). E) High magnification of Fig. D. Note small inner labial papilla (short arrow) and grouping of labial seta and cephalic seta (long arrow). F) Precloacal papilla of *S. gracilis*. Scale bars: A = 100 µm; B–D = 10 µm; E,F = 1 µm.

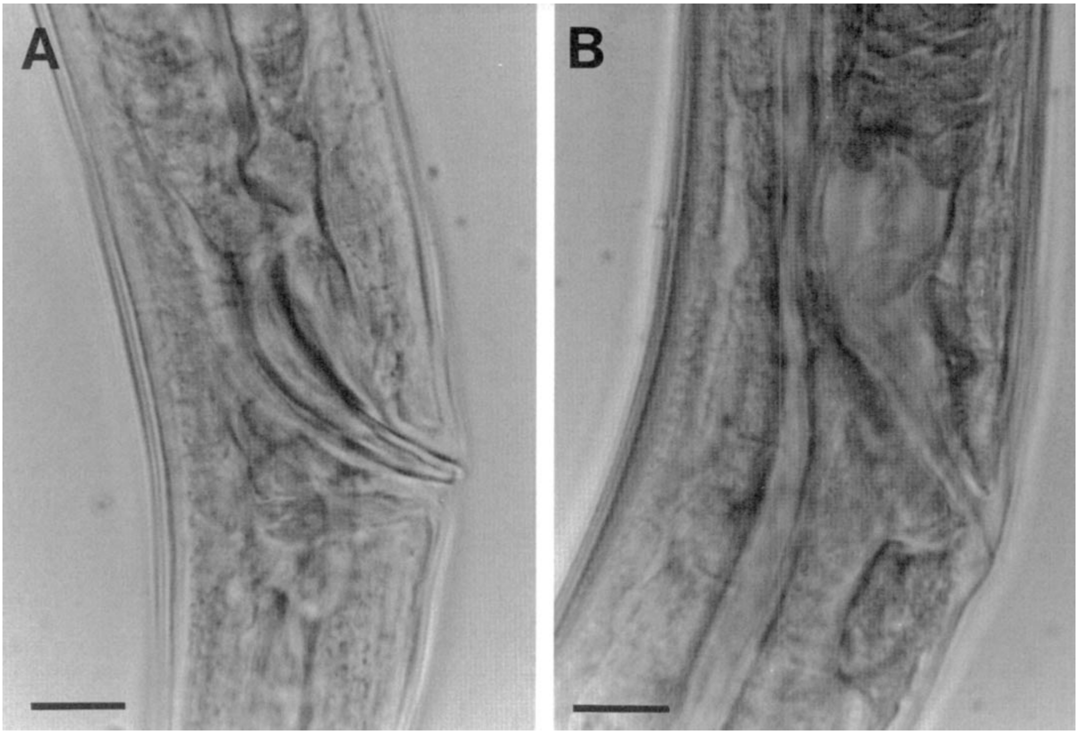

FIG. 6. Photomicrographs of intersex of *Sphaerolaimus gracilis*. A) Right spicule. B) Vulva region. Scale bars = 10 µm.

ules converging distally. Spicules 55.4 ± 5.6 µm (47.2–64.0; n = 14) long, 1.4 times cloacal body diameter (Fig. 4D). Gubernaculum between spicules, quadrangular in shape, apophysis 18.2 ± 2.7 µm (12–20; n = 10) long, with lateral sclerotized plates extending on lateral sides of both spicules (Fig. 4D).

Tail length 3.8–3.9 times cloacal body diameter (Fig. 4D). Tail end clavate, 15–20% of total tail length. Three tail tip setae, 8–12

TABLE 3. Measurements, ratios, and percentages of adult specimens of *Sphaerolaimus gracilis*.

Character	Males (n = 14)			Females (n = 22)		
	Mean	Range	SD	Mean	Range	SD
		Measurements (µm)				
Body length	1,182	1,046–1,424	111	1,212	972–1,668	150
Esophagus length	261	224–335	30.6	259	192–340	31.9
Tail length	151	130–185	13.2	148	120–184	15.3
Body width	46.9	34–76	10.4	48.0	35–76	10.8
Head width	19.2	17.6–26.0	2.2	18.8	16.0–24.0	2.0
Body width at end of esophagus	43.1	32.0–65.0	8.4	44.1	32.0–72.0	8.9
Anal width	39.1	32–55	6.2	34.0	27.2–53.6	5.5
Spicule length	55.4	47.2–64.0	5.6			
		Ratios				
a	25.9	18.2–33.1	4.2	25.9	18.0–31.7	3.6
b	4.6	4.2–5.0	0.2	4.7	4.2–5.1	0.3
c	7.7	7.3–8.6	0.3	8.2	7.1–9.1	0.5
		Percentages				
V				67.3	64.5–71.6	1.7

TABLE 4. Measurements, ratios, and percentages of J4 *Sphaerolaimus gracilis.*

Character	J4 Males (n = 12) Mean	Range	SD	J4 Females (n = 8) Mean	Range	SD
		Measurements (μm)				
Body length	1,004	834–1,144	94	981	872–1,185	99
Esophagus length	226	186–254	21.2	215	190–280	28.0
Tail length	130	112–150	10.0	135	100–140	13.2
Body width	38.6	30–43	4.5	34.4	28.8–46.0	5.2
Head width	15.7	12.8–18.0	1.8	16.0	13.6–19.0	1.8
Body width at end of esophagus	34.3	28.8–40.0	3.4	34.2	30.4–44.0	4.2
Anal width	29.2	23.2–33.0	3.1	27.7	24–36	3.8
Length of anterior testis	78	47–160	34.9			
Length of posterior testis	45	16–110	29.3			
Length of ovary				204	40–301	79.1
		Ratios				
a	26.2	22.0–30.9	2.6	29.1	24.9–35.1	3.5
b	4.4	4.0–4.9	0.2	4.6	4.2–4.9	0.2
c	7.6	7.1–8.5	0.4	7.9	7.1–8.7	0.6
		Percentages				
V				67.5	65.2–71.7	2.0

μm long (Fig. 4D). Caudal glands opening through separate pores.

Females (n = 22): In most respects similar to the males. Amphid slightly smaller than in males, 6.1 ± 0.4 μm (5.6–6.4; n = 5) in diameter, 20.3% ± 1.1 (19–22; n = 5) of the corresponding body diameter. Renette cell 111.3 ± 28.3 μm (61–144; n = 10) posterior to esophagus, 19.8 ± 3.3 μm (16.0–25.6; n = 8) × 45.5 ± 9.1 μm (36–64; n = 8) in diameter. Renette pore 173.6 ± 22.3 μm (140–220; n = 18) from anterior end. Gonad monodelphic, antepudendal, outstretched, lying either to right or left side of intestine (of 14 females, six with ovary on left side of intestine; eight, including intersex, on right side). Dilatory vaginal sphincter muscles well developed (Fig. 4H).

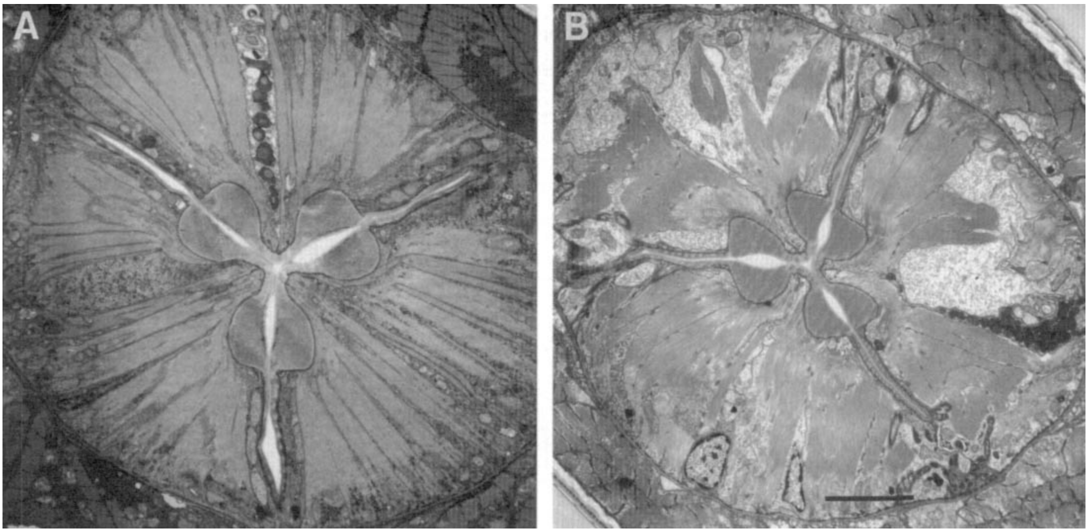

FIG. 7. Transverse electron micrographs of esophagus of *Sphaerolaimus* spp. A) *S. occidentalis* n. sp. B) *S. gracilis.* Note wider and more sclerotized lumen of *S. occidentalis.* Scale bar = 5 μm.

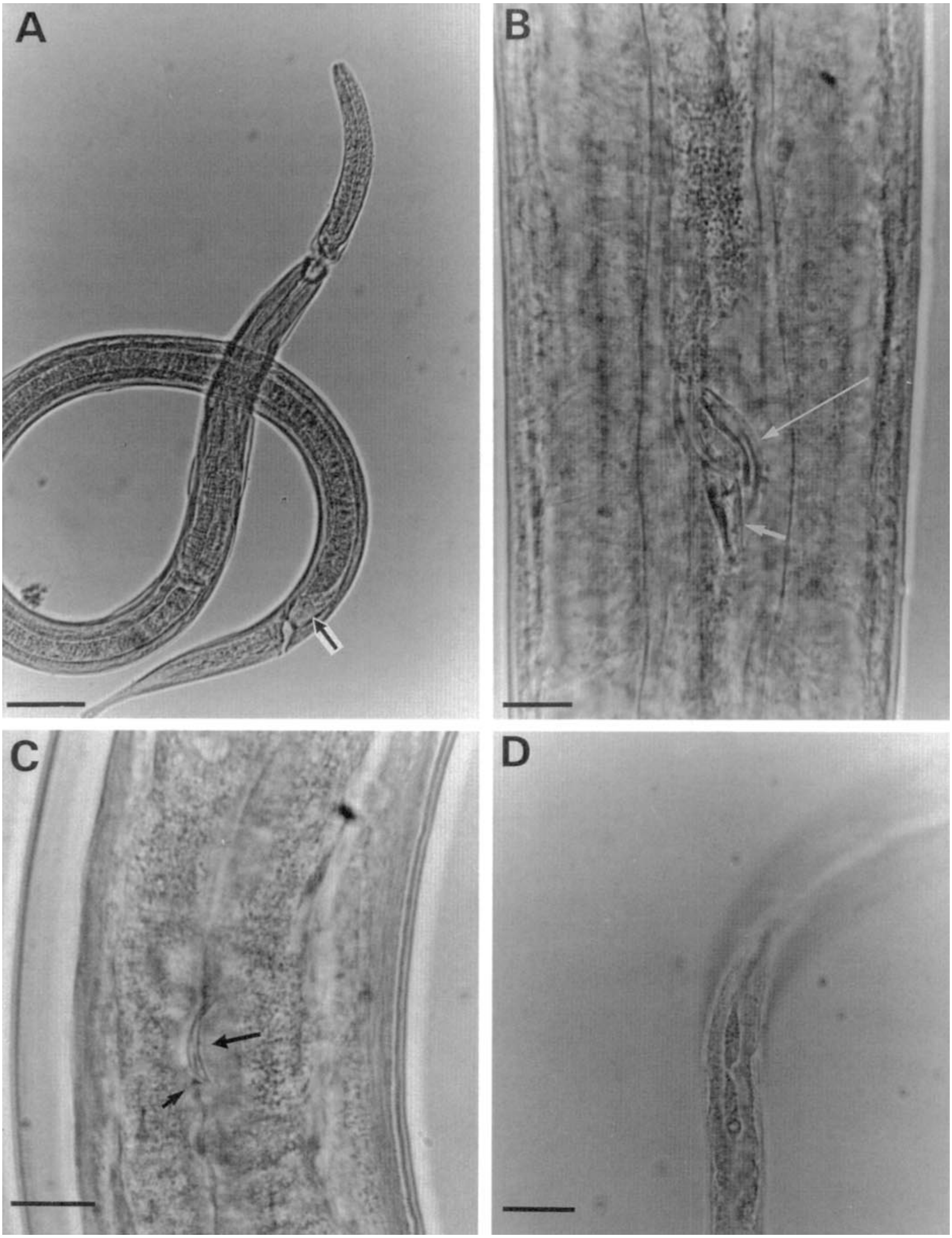

FIG. 8. Feeding habits of *Sphaerolaimus gracilis*, *S. occidentalis* n. sp., and *Eumonhystera borealis* n. sp. A) *S. gracilis* actively feeding on *Monhystera* sp. Two pairs of spicules of *E. borealis* n. sp. indicated by arrow. B) *Eleutherolaimus schneideri* in posterior gut of *S. occidentalis* n. sp. Note spicules (long arrow) and gubernaculum (small arrow). C) Spicule (long arrow) and gubernaculum (small arrow) of *E. borealis* n. sp. in posterior gut of *S. gracilis*. D) Two possible unicellular zooflagellates in the gut of *E. borealis* n. sp. Scale bars: A = 50 µm, B–D = 10 µm.

Postvulval vaginal gland about 20 µm in diameter (Fig. 4H).

J4 males (n = 7): Renette pore 152.0 ± 16.7 µm (120.8–166.4; n = 7) from anterior end. Renette cell 80.0 ± 28.5 µm (36–116; n = 6) posterior to esophagus, 16.9 ± 4.9 µm (16–

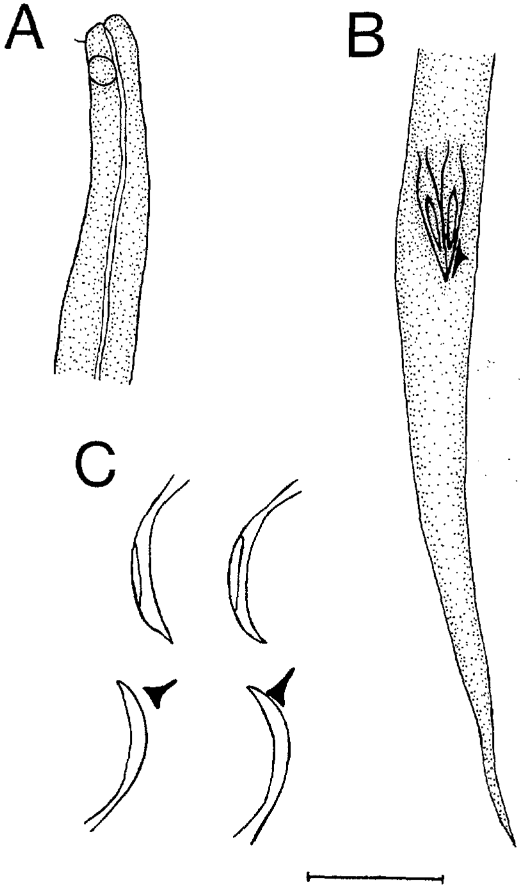

FIG. 9. Drawings of male of *Eumonhystera borealis* n. sp. occurring in gut of *Sphaerolaimus gracilis*. A) Anterior body. B) Posterior body. C) Spicules from different guts. Scale bar = 10 μm.

20.8; n = 4) × 31.0 ± 11.5 μm (10–40; n = 4). Spicules not developed, but cells forming copulatory apparatus present. Anterior testis larger than posterior testis.

Intersexual female (n = 1) (Figs. 4F;6A,B): Length = 1,128 μm; head width 19 μm; body width at end of esophagus 37 μm, at vulva 41 μm, at anus 34 μm. Ratios: a = 28.8, b = 4.3, c = 7.6, V = 66.1. Six inner labial papillae; six outer labial papillae and four cephalic setae in one circle; outer labial papillae about 1.5 μm long, cephalic setae 5 μm long (26.3% of head diameter). Subcephalic setae arranged as four sublateral groups of four unequal setae and four submedian groups of two setae 9 and 19 μm long. Somatic setae at midbody 6–7 μm long. Buccal cavity 14.4 μm wide and 19.0 μm long (anterior part 10 μm long, posterior portion 9.0 μm long). Renette pore 156 μm from anterior end, ampulla 3.2 × 6.0 μm in diameter, renette cell on right side of intestine, 80 μm from end of esophagus, 12 × 40 μm in diameter. Gonad on the right side of intestine, 40 μm from the renette, 140 μm from the base of esophagus, 341 μm long. Dilator sphincter of vulva 24 μm long, wall 5.6 μm thick in middle, postvulvar gland 16 × 8 μm in diameter (Fig. 6B). Spicules arcuate, unequal in length; right spicule 34 μm long, left spicule 43 μm long (Figs. 4F,6A). Gubernaculum median, rounded, 4–5 μm in diameter, with 5-μm-long apophysis (Fig. 4F). Preanal papillae present. Tail conoid-cylindrical, cylindrical part about 20% of tail length (Fig. 4F).

Remarks

The observed morphological characters of *S. gracilis* agreed well with those of other descriptions (De Man, 1922; Gerlach, 1965; Lorenzen, 1969, 1978). Ridges of the head end, seen with SEM, may be homologous with perioral platelets in *Monhystera* and *Eumonhystera* spp. (Jacobs and Heyns, 1992). The head topographies of *S. gracilis* and *Monhystera coomansi* Jacobs and Heyns, 1992 resemble each other. In SEM the head region of *S. gracilis* differed from that of *S. balticus* and *S. occidentalis* n. sp. in having narrower perioral platelets, relatively larger labial papillae, and more papilliform outer labial sense organs (Malakhov and Ovchinnikov, 1980). Configuration of subcephalic setae appeared to be similar. Lorenzen (1969) described three morphologically distinct male forms in *S. gracilis,* designated as 1, 2, and 3. The Bothnian Bay material studied was dominated by form 2. Presence of large specimens (length of female of present material 1.67 mm, length of male from Spitzbergen 1.56 mm) (Gerlach, 1965) may indicate that *S. gracilis* has a long generation time. A spermatheca, present in *S. gracilis,* is known from other species of *Sphaerolaimus* and is commonly present in Sphaerolaimidae (Gourbault, 1987). An anteriorly directed posterior testis in two fertile males of *S. gracilis* is unique. In a longer male the renette cell was normally developed, whereas in a shorter male the renette cell was poorly developed. Occurrence of anterior testis or ovary and renette cell always on the same side of the body suggests that the renette cell determines gonad orientation.

The intersex female resembled the J4 male. The intersex specimen had shorter cephalic setae (26% vs. 44% of head diameter), longer anterior part of buccal cavity (10 vs. 8 μm), and longer cylindrical part of tail (23% vs. 15%).

The Baltic Sea region now has three known *Sphaerolaimus* spp. (Schneider, 1927; Schiemer et al., 1983; present study). They have different colors in LM: *S. gracilis* is light yellow, *S. occidentalis* n. sp. is white, and *S. balticus* G. Schneider, 1906 is dark with a black gut (Schneider, 1927).

Gut content analysis of S. gracilis (n = 50: 21 females, 12 males, 17 J4): The gut was empty in half the specimens studied and full in three specimens. Nematode prey were observed in the guts of *S. gracilis* as whole specimens (Fig. 9A,B), as fragments (Fig. 8A), or as sclerotized parts of specimens (Fig. 8C). The latter included buccal structures, amphid apertures, and spicules (Figs. 8C,9C). Clusters of 2–3 μm-long spines were rarely encountered, probably belonging to members of Oligochaeta. Occasionally, actively feeding specimens were seen ingesting nematodes (Fig. 8A). One *S. gracilis* was observed eating a large *Monhystera* sp. (Fig. 8A). The intestine of *S. gracilis* was filled, apparently with the prey, nearly to the anus, where two pairs of spicules of earlier prey had accumulated (Fig. 8A). These spicules were identical to those of *E. borealis* n. sp., which appeared to be the preferred food source of *S. gracilis* (Figs. 8C,9). Spicules of *E. borealis* n. sp. were present in the guts of 10 of 24 *S. gracilis*. Undigested specimens were in the foreguts of two specimens of *S. gracilis*, and one entire specimen was in the midgut of one specimen of *S. gracilis*. Three digested bodies, including spicules and remnants of cuticles, were in the posterior guts of three specimens of *S. gracilis*. In the gut of one female were eight pairs of spicules of *E. borealis* n. sp. and in another female, 10 pairs of spicules. Spicules usually occurred in pairs and only rarely were well separated. In both of these specimens the gut lumen was unusually wide and also contained spines. A sclerotized jaw-like structure, 3 × 8 μm, and provided with numerous teeth each about 0.5 μm long, was in one of these guts, possibly indicating oligochaete prey. Occasionally the gubernaculum and apophysis of spicules *E. borealis* n. sp. were not displaced. The occurrence of whole specimens of *E. borealis* n. sp. in the guts of *S. gracilis* indicated that this prey was swallowed whole. Buccal cavities (lengths 9, 12, 16 μm) of *Axonolaimus spinosus* (Bütschli, 1874) were present in each of three specimens of *S. gracilis*. One unidentified buccal cavity and an amphid of *Leptolaimus* sp. was seen. Anterior parts of *S. gracilis* buccal cavities, with outer diameters of 11.2 and 12.8 μm, were present in the intestine of two *S. gracilis*. The smaller capsule was in the gut of an 870-μm-long J4 (gonad 16 μm long). The buccal cavity was at the posterior end of the intestine; anteriorly the gut was filled with digested material. In the anterior part of the intestine was a pair of arcuate spicules, unequal in length (right spicule 24 μm, left spicule 28 μm). In ventral view, associated with the spicules was a concave gubernaculum, 4 μm long, distally 4 μm wide, 0.5 μm thick, proximally 1.5 μm wide, 0.5 μm thick. A 6-μm-long apophysis was attached to the distal end of the gubernaculum. If the spicules and the buccal cavity were of the same specimen, the species eaten by *S. gracilis* form 2 was *S. gracilis* form 1. Form 1 and form 2 occur in different biotopes in the North Sea coast; the small form lives in the subtidal zone and the large form in the intertidal zone (Lorenzen, 1969). *S. gracilis* form 1 has not yet been collected from the Bothnian Bay. Presence of digestible material close to the *S. gracilis* buccal cavity in the gut of *S. gracilis* clearly indicates that *S. gracilis* consumed at least part of another *S. gracilis*.

Discussion

The material studied indicated that *S. gracilis* is a predacious species. The predacious character of *Sphaerolaimus* spp. is well known (Jensen, 1987; Wülker and Schuurmans Stekhoven, 1933), and *Monhystera* and *Axonolaimus* spp. are known prey (Schulz, 1932; Wülker and Schuurmans Stekhoven, 1933). Some species of *Mononchus* Bastian, 1866 feed on small microscopic animals such as protozoa, rotifers, and nematodes (Cobb, 1917). Feeding behavior resembles that of *S. gracilis* in that prey is fragmented or swallowed whole (Cobb, 1917). When prey was swallowed whole, unicellular algae could be seen in the gut of the prey (Cobb, 1917). One food item of *E. borealis* n. sp. also appeared to be a 7–10 µm-long unicellular organism, found in some specimens. A similar unicellular organism also was seen in the gut of a young *S. gracilis*. Three pairs of these cells occurred in the guts of two *E. borealis* n. sp. eaten by a *Monhystrella anophthalma* Lorenzen 1976, which occurs in Bothnian Bay. It is evident that protozoa or algae (Cobb, 1917) are significant food objects for some monhysterids. Tietjen and co-workers (Heip et al., 1985) found that certain nematodes feed selectively on bacteria and algae, and there is evidence that *Sphaerolaimus* spp. are selective predators (Nicholas, 1984). The occurrence of *E. borealis* n. sp. in the guts of so many *S. gracilis* specimens is indicative of selective predative behavior. The mass occurrence of *E. borealis* n. sp. in the guts of two different *S. gracilis* specimens suggests that these nematodes may not be swallowed whole. The occurrence of small spines in the guts possibly means that *S. gracilis* consumed a member of Oligochaeta that had eaten *E. borealis* n. sp.

When eating a large nematode, *S. gracilis* apparently grasps the prey with the ridges of the vestibulum, comparable to the inner lip armature of Mononchida (Cobb, 1917). Both *Sphaerolaimus* and *Mononchus* spp. have a strongly developed esophageal luminal lining (Cobb, 1917). Electron micrographs of the esophagus of *S. gracilis* and *S. occidentalis* n. sp. demonstrated that the lumen is triradiate and strongly sclerotized. It appears that the heavy transverse musculature is used to open the lumen, while the more oblique and less dense musculature is used to pull in the prey. The wide mouth and esophageal lumen of *S. occidentalis* n. sp. clearly allows swallowing of large nematodes, such as members of Eleutherolaimidae and Xyalidae. However, *S. gracilis,* which has a narrower esophageal lumen and buccal cavity, did not ingest members of these families. Oligochaeta were more common in the guts of *S. occidentalis* n. sp. than in the guts of *S. gracilis.*

The prey of *S. gracilis* (nematodes) and *Mononchus* sp. (rotifers) often are ingested tail-first. *S. gracilis* is also reported to attack prey behind the esophago-intestinal junction (Schulz, 1932). Members of Sphaerolaimidae have a broad oral opening for catching prey, whereas other predators (Thoracostomopsidae, Enoplidae, Selachinematidae) use buccal claws or mandibles (Jensen, 1987). The diameter of buccal cavity and esophageal lumen likely is important in determining whether prey is swallowed whole. *Sphaerolaimus occidentalis* n. sp. can ingest large species such as *Eleutherolaimus schneideri* Turpeenniemi 1996, which was not found in the guts of *S. gracilis.* It is not known how important *Eleutherolaimus schneideri* or other prey are for *S. occidentalis* n. sp. The feeding behaviors of the two *Sphaerolaimus* spp. are different, and may explain their different gut colors.

Remarks

Sphaerolaimus gracilis de Man, 1876 probably is not the only nematode species feeding on *Eumonhystera borealis* n. sp. A partially digested nematode in the gut of a *Monhystrella anophthalma* Lorenzen, 1969 from Bothnian Bay had circular amphids, 3 µm in diameter, about 5 µm from its head end. Posteriorly the internal tissue of the victim was almost completely digested. Indistinct remnants of cuticle were present. Three pairs of granulated cells, 7–10 µm long, 3–5 µm wide, and still intact, occurred at intervals of about 70 µm in the gut region of the victim. The size of the amphid and the width of the body indicate that this nematode prey likely was *E. borealis* n. sp. *Monhystrella anophthalma* is clearly a predator or predator-omnivore and thus differs from other *Mon-*

hystrella spp., which are known as bacterial feeders (Jacobs, 1987).

Profundal bottom temperatures of Bothnian Bay, in the northern part of the Baltic Sea, are close to summer water temperatures of a shallow arctic tundra pond at Barrow, Alaska, where small zooflagellates are the most important single group of bacterial grazers (Fenchel, 1975). Unicellular organisms eaten by *E. borealis* n. sp. resemble zooflagellates. Predators of *E. borealis* n. sp. (e.g., *S. gracilis, M. anophthalma,* and probably some Oligochaeta) may play an important role in keeping *E. borealis* n. sp. populations in an active phase of growth.

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