

New findings of deep-sea nematodes of genus *Benthimermis* Petter, 1980 (Nematoda, Benthimermithidae) with description of seven new species

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ABSTRACT

Species of *Benthimermis* Petter, 1980 from different parts of the world ocean from depths between 630 and 5880 m were examined. This resulted in new findings of *B. filiformis* Petter, 1987, *B. bureaui* Petter, 1983, and *B. mario-nensis* Petter, 1983 and description of seven new species. The female of *B. ifremeri* n. sp. differs from *B. arnaudi* Petter, 1983 in the absence of a caudal terminal knob, a thinner body, and a longer tail; from *B. edouardensis* Petter, 1983 in a smaller body length and a longer tail; from *B. minuta* Petter, 1987 in a longer and thicker body and a shorter tail. The male of *B. improvisa* n. sp. has thin and pointed cephalic setae and a round ventral gland at the level of amphid, which opens outside. The female of *B. petterae* n. sp. differs from *B. laubieri* Petter, 1987 by pocket-shaped amphidial foveae and reflected ovaries. The male of *B. petterae* n. sp. has a small caecum in the anterior part of the posterior testis. The male of *B. platyptera* n. sp. has the fewest number of supplementary organs (two), shortest spicules, and the smallest body length. The female of *B. pseudominuta* n. sp. differs from *B. laubieri* by its rounded posterior end, smaller body length, and a thicker body. The female of *B. tchesunovi* n. sp. differs from *B. australis* Petter, 1983 and *B. bureaui* in its smaller body length, the presence of a cuticular thickening at the cephalic apex, and smaller eggs. The female of *B. turpicauda* n. sp. has a caudal terminal spine of irregular shape, transversal circular ridges of the hypodermis at the level of the junctions of trophosomal cells, and hologonic ovaries.

KEY WORDS

Nematoda,
Benthimermithidae,
Benthimermis,
parasite,
deep-sea,
new species.

RÉSUMÉ

Nouvelles découvertes sur des nématodes de mer profonde du genre Benthimermis Petter, 1980 (Nematoda, Benthimermithidae) et description de sept nouvelles espèces.

Des espèces du genre *Benthimermis* Petter, 1980 récoltées dans différentes régions océaniques du monde entre 630 et 5880 m ont été examinées. De nouvelles découvertes de *B. filiformis* Petter, 1987, *B. hureaui* Petter, 1983 et *B. marionensis* Petter, 1983 ont été réalisées. Sept nouvelles espèces sont décrites. La femelle de *B. ifremeri* n. sp. diffère de celle de *B. arnaudi* Petter, 1983 par l'absence d'une protubérance caudale terminale, un corps plus fin et une queue plus longue ; de celle de *B. edouardensis* Petter, 1983 par un corps plus court et une queue plus longue ; de celle de *B. minuta* Petter, 1987 par un corps plus long et plus épais et une queue plus courte. Le mâle de *B. improvisa* n. sp. présente des soies céphaliques fines et pointues et une glande ventrale arrondie au niveau de l'amphide qui s'ouvre sur l'extérieur. La femelle de *B. petterae* n. sp. diffère de celle de *B. laubieri* Petter, 1987 par des fovea en forme de poche et des ovaires réfléchis. Le mâle de *B. petterae* n. sp. a un petit caecum dans la partie antérieure du testicule postérieur. Le mâle de *B. platyptera* n. sp. a le plus petit nombre d'organes supplémentaires (deux), les spicules les plus courts de même que le corps. La femelle de *B. pseudominuta* n. sp. diffère de celle de *B. laubieri* par son extrémité postérieure arrondie, son corps plus court et plus épais. La femelle de *B. tchesunovi* n. sp. diffère de celles de *B. australis* et *B. hureaui* par son corps plus court, la présence d'un épaississement cuticulaire à l'apex céphalique et des œufs plus petits. La femelle de *B. turpicauda* n. sp. a une épine terminale caudale de forme irrégulière, des rides circulaires transversales de l'hypoderme au niveau des jonctions des cellules trophosomales et des ovaires hologones.

MOTS CLÉS

Nematoda,
Benthimermithidae,
Benthimermis,
parasite,
mer profonde,
nouvelles espèces.

INTRODUCTION

Nematodes of the family Benthimermithidae Petter, 1980 are known as rare and poorly studied parasites of predominantly deep-sea benthic invertebrates: the polychaetes, priapulids, various crustaceans, holothuroids, and even free-living nematodes (Hope 1977; Petter 1980, 1983b; Rubtzov 1980; Chesunov 1988). Like the real fresh-water and terrestrial mermithids (order Mermithida Hyman, 1951) the larval stages of benthimermithids parasitise the host body cavities and internal organs. Adult or late larval worms leave the host to the environment for a non-parasitic phase where they reproduce but evidently do not feed (as inferred from a strongly modified alimentary tract including lack of a mouth).

The systematic status of this family is disputable. Petter described the majority of known species of the genus *Benthimermis* Petter, 1980 (Petter 1980, 1981a, b, 1982a, b, 1983a, 1987) and established a monotypic genus *Adenodelphis* Petter, 1983. Besides, several species of benthimermithids were described by Rubtzov (1980) and Tchesunov (1988). Tchesunov (Tchesunov 1995, 1997; Chesunov 1997) proposed to include the family Benthimermithidae into the independent order Benthimermithida Tchesunov, 1995. He considered that benthimermithids were erroneously related to analogous fresh-water and soil mermithids and marine nematodes of the order Marimermithida Rubtzov, 1980 on the basis of the convergent similarity only. However, such features as the pattern of cephalic sensilla (6 + 4) and presence

of male numerous supplementary organs indicate that Benthimermithida belong to chromadorian nematodes. According to some features of larvae (the construction of mouth stylet and pharynx, the presence of caudal glands), it is possible that benthimermithids came from free-living marine nematodes close to the subfamily Camacolaiminae Micoletzky, 1924 (Leptolaimidae Örley, 1880) (Tchesunov 1997). Besides, the propensity to parasitism has been recently discovered among Camacolaiminae. Several new species were described as internal parasites of foraminiferan (Hope & Tchesunov 1999; Tchesunov *et al.* 2000), and one species was found in the body cavity of the polychaetes *Syllis* sp. (pers. obs.).

Now Benthimermithidae consist of three valid genera: *Adenodelphis* Petter, 1983, *Benthimermis* Petter, 1980 (synonym *Abos* Rubtzov, 1980), and *Trophomera* Rubtzov & Platonova, 1974. The type genus *Benthimermis* consists of 21 described species, the two other genera are monotypic.

In this work the results of the examination of a part of the material from the Muséum national d'Histoire naturelle, Paris (MNHN) collection are presented. Examined nematodes were collected in different regions of the world ocean during seven research cruises organized by the Institut français de Recherche pour l'Exploitation de la Mer, Brest (IFREMER).

ABBREVIATIONS

- “a” de Man a index: (length of body)/(maximal body diameter);
 “c” de Man c index: (length of body)/(length of tail);
 “V” de Man V index: [(length from cephalic end to vulva)/(length of body)] × 100%.

MATERIAL AND METHODS

Adult free-living nematodes were collected from sediment samples in several survey cruises in different regions of the world ocean. The Sanders dredge or box core Usnel (1/4 m²) were used for

collecting samples. Specimens were fixed on board with 4% formaldehyde in sea water. Nematodes were then rinsed in distilled water, transferred to anhydrous glycerol according to progressive evaporation method (Seinhorst 1959), mounted in a glass slide and examined with an optical microscope.

For transmission electron microscopy (TEM), specimens Nos 4 and 5 of *Benthimermis filiformis* were cut into pieces 4–6 mm long. Selected portions were postfixed with 1% osmium tetroxide in distilled water for six days at 4°C. Postfixed portions were progressively transferred through a graded distilled water/ethanol/acetone series to pure acetone, embedded in Epon resin and polymerized at 60°C for 48 hours. Ultra-thin sections (40 nm thick) were made with an ultramicrotome using a diamond knife and then stained with aqueous uranyl acetate and Reynolds lead citrate. The sections were viewed with a JEOL JEM-100B (Tokyo, Japan) at 80 kV.

All examined specimens are deposited in the collection of the MNHN. For details about material examined, refer to Tables 1–7.

SYSTEMATICS

Benthimermis filiformis Petter, 1987

(Figs 1–3; Tables 1; 2)

Benthimermis filiformis Petter, 1987: 571, 572, fig. 4.

TYPE MATERIAL. — Holotype: Norway Sea, 64°24.3'N, 1°43.9'E, 2615 m, 19.VII.1975, mature ♀ (MNHN 37 BC); paratypes: Norway Sea, 69°29.2'N, 10°11.6'E, 2957 m, 27.VII.1975, 1 juvenile ♀ (MNHN 38 BC); Norway Sea, 73°28.2'N, 10°06.6'W, 2973 m, 7.VIII.1975, 1 mature ♀ (MNHN 54 BC).

MATERIAL EXAMINED. — 7 fertile ♀♀ (see Tables 1 and 2 for details).

DESCRIPTION

Measurements are presented in Table 2. Only females were found. Body cylindrical, long. Anterior end in shape of rounded cone. Posterior end conical, possessing a terminal spine from 60 to 110 µm long. For most of the specimens,

TABLE 1. — Coordinates, depth and dates of collecting of the samples where females of *Benthimermis filiformis* Petter, 1987 were found.

No. of specimen	1	2	3	4	5	6	7
Collection No.	MNHN 314 BF	MNHN 326 BF	MNHN 359 BF	MNHN 360 BF	MNHN 364 BF	MNHN 377 BF	MNHN 379 BF
Cruise	MD 32	DEMERABY	WALVIS	WALVIS	WALVIS	BIOVEMA	BIOVEMA
Station	DS 151	KG 10	KG 06	KG 10	CP 06	KG 15	KG 16
Date of collecting	5.IX.1982	16.IX.1980	26.XII.1978	27.XII.1978	30.XII.1978	20.XI.1977	25.XI.1977
Region	Western part of the Indian Ocean	Western Atlantic	Southeastern Atlantic	Southeastern Atlantic	Southeastern Atlantic	Western Atlantic	Western Atlantic
Coordinates	20°51.0'S 56°03.3'E	8°10.31'N 49°02.98'W	33°54.2'S 05°09.2'E	33°54.7'S 05°09.2'E	33°22.5'S 02°35.9'E	10°47.6'N 42°40.88'W	11°35.8'N 32°51.4'W
Depth	3240- 3300 m	4440 m	5210 m	5210 m	4550 m	5100 m	5880 m

TABLE 2. — Measurements (in μm) of females of *Benthimermis filiformis* Petter, 1987.

No. of specimen	1	2	3	4	5	6	7
Body length	4094.0	5516.0	4094.0	4000.0	5375.0	4828.0	4922.0
Maximal body diameter	106.0	111.0	88.0	75.0	136.0	91.0	111.0
Diameter at the level of cephalic sensilla	21.0	17.0	18.0	15.0	22.0	21.0	18.0
Diameter at the level of amphids	60.0	68.0	46.0	44.0	70.0	60.0	59.0
Diameter at the middle of the body	106.0	111.0	83.0	75.0	136.0	88.0	110.0
Diameter at the level of the anus	40.0	43.0	36.0	41.0	64.0	55.0	56.0
Distance from the cephalic end to the amphids	42.0	80.0	56.0	121.0	63.0	83.0	83.0
"a"	38.6	49.7	46.8	53.3	39.5	53.1	44.3
"c"	42.2	43.0	53.9	50.6	37.3	41.6	36.2
"V", %	55.3	51.8	53.1	52.7	52.6	53.7	55.5

terminal caudal spine completely cuticular with a longitudinally or obliquely striated core, but terminal spine of the specimen No. 6 having a cytoplasmic core with some vesicle-like inclusions. Cuticle about 2.5 μm thick at anterior and posterior body part, and about 1.5 μm thick at mid-body. Cuticle of apical cephalic part thinner (about 1 μm) in some specimens. Stratification of cuticle usually visible at anterior part of caudal spine. Mouth opening absent. Four mediolateral papilloid cephalic setae (1.5-2.0 μm long) inserted in tiny pits. Amphids non-spiral. Amphidial aperture looking like a transversally oriented

ovals of about 2.0 μm width. Amphidial fovea tubiform. Somatic sensilla appearing as pores connected with hypodermal glands in lateral chords. Such sensilla only found in several specimens. Pharynx looking like a non-muscular string devoid of internal lumen. Midgut a multicellular trophosome devoid internal lumen and consisting of four cells at cross-section (Fig. 3). Cell borders of trophosome clearly visible. Rectum looking like a tube with thin walls. Anus appearing as narrow channel inside cuticle or absent. Female reproductive system didelphic, amphidelphic, occupying about one quarter of all body length.

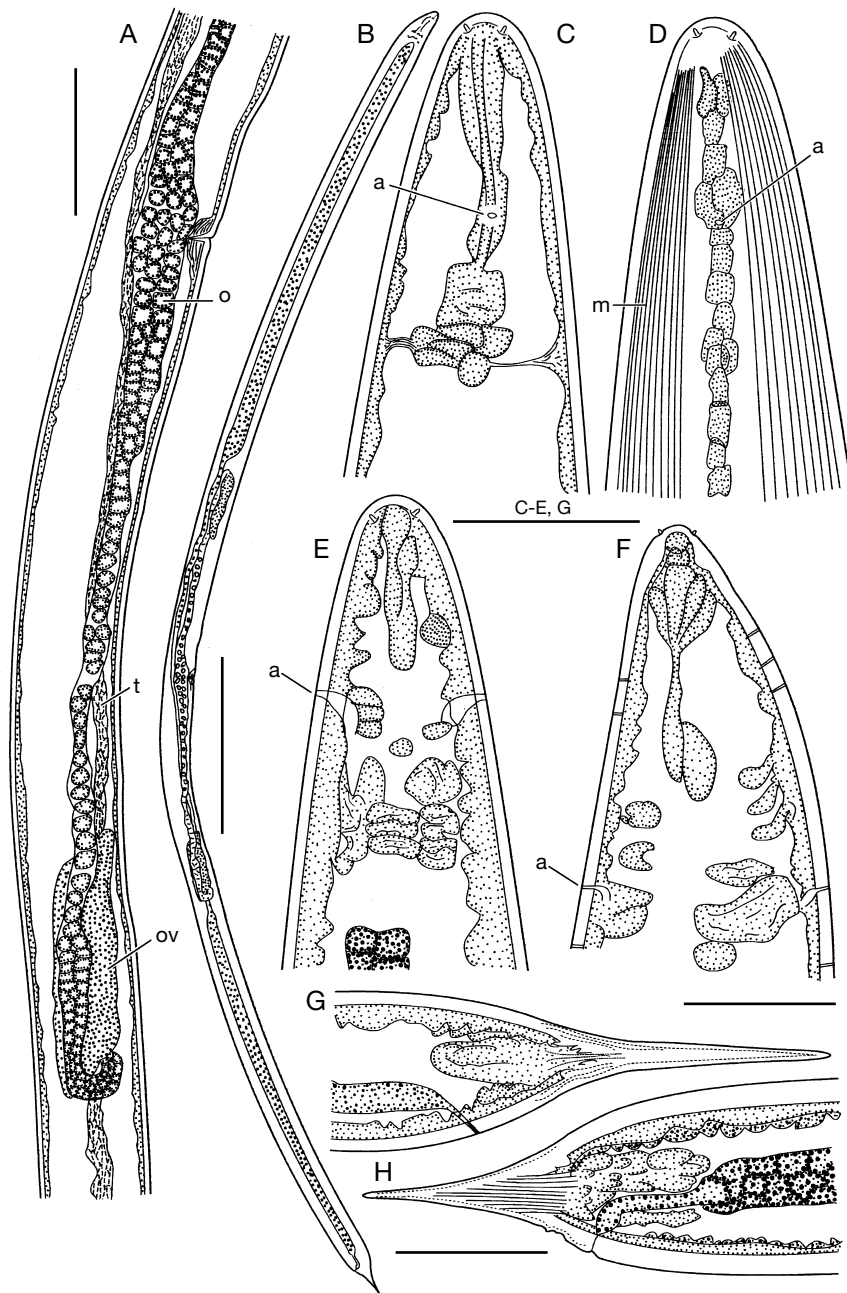


FIG. 1. — *Benthimermis filiformis* Petter, 1987, ♀ (see Tables 1 and 2 for locations and measurements of specimens); **A**, reproductive system of specimen No. 3; **B**, total view of specimen No. 3; **C-E**, cephalic end of specimen No. 3; **F**, cephalic end of specimen No. 4; **G**, tail of specimen No. 4; **H**, tail of specimen No. 3. Abbreviations: **a**, amphid; **m**, somatic musculature; **o**, oocytes or eggs; **ov**, ovary; **t**, trophosome. Scale bars: **A**, 100 μ m; **B**, 500 μ m; **C-H**, 50 μ m.

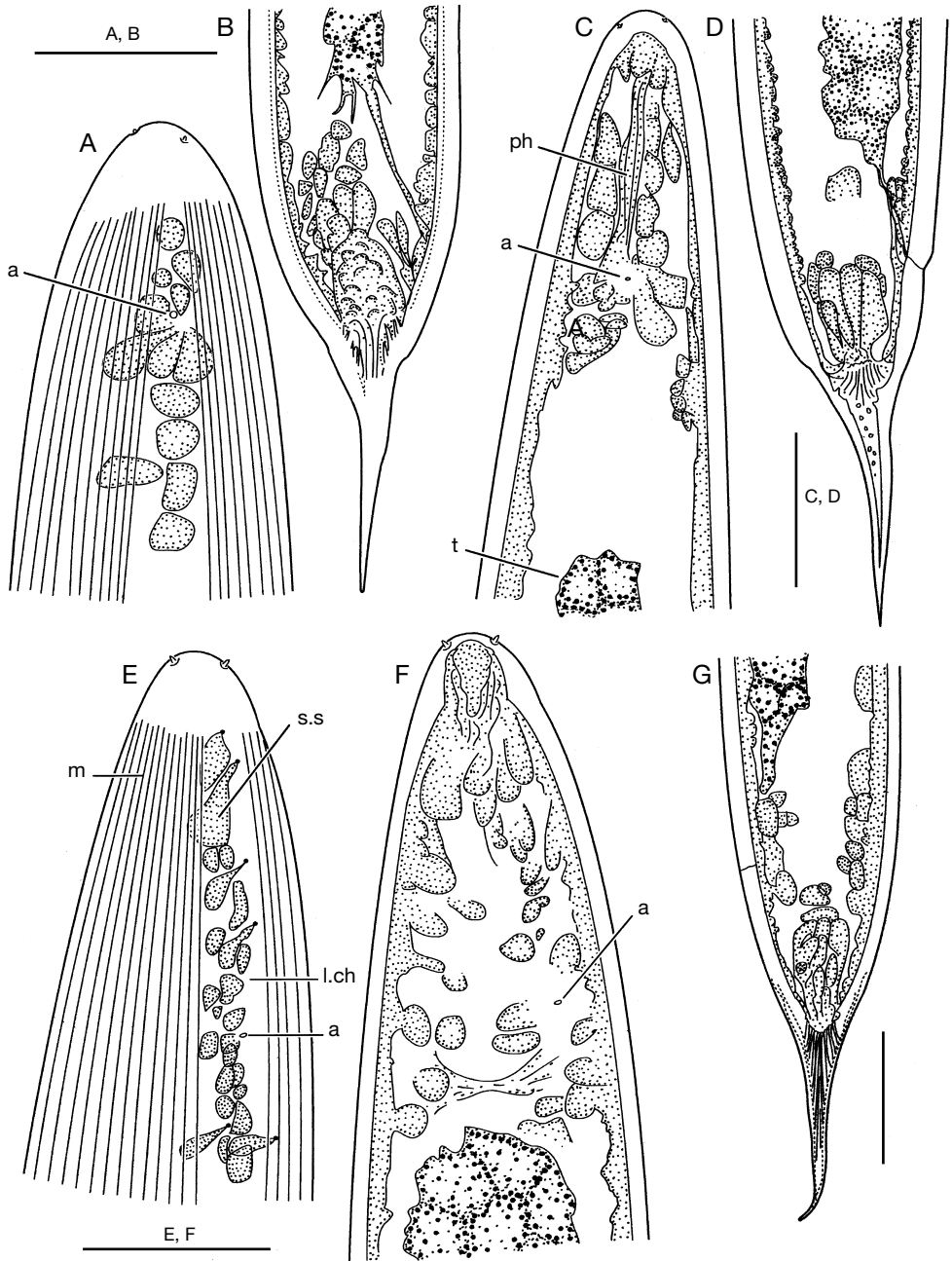


FIG. 2. — *Benthimermis filiformis* Petter, 1987, ♀ (see Tables 1 and 2 for locations and measurements of specimens); **A**, cephalic end of specimen No. 1; **B**, tail of specimen No. 1; **C**, cephalic end of specimen No. 6; **D**, tail of specimen No. 6; **E**, **F**, cephalic end of specimen No. 2; **G**, tail of specimen No. 7. Abbreviations: **a**, amphid; **l.ch**, lateral hypodermal chord; **m**, somatic musculature; **ph**, vestigial pharynx; **s.s.**, hypodermal gland connected with somatic sensillum; **t**, trophosome. Scale bars: 50 µm.

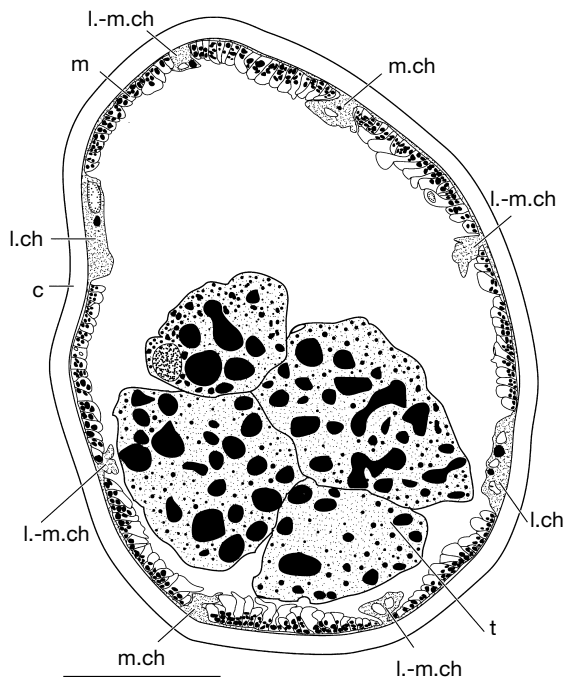


FIG. 3. — *Benthimermis filiformis* Petter, 1987, ♀ (see Tables 1 and 2 for locations and measurements), cross-section at level of trophosome of specimen No. 4 (reconstruction based on TEM-photos). Abbreviations: **c**, cuticle; **l.ch**, lateral hypodermal chord; **l.-m.ch**, lateromedian hypodermal chord; **m**, somatic musculature; **m.ch**, median hypodermal chord; **t**, trophosome. Scale bar: 10 mm.

Ovaries reflected. Egg diameter about 10.0 mm. Neither morphologically differentiated spermatheca nor spermatzoa nor vulvar glands observed.

REMARKS

B. filiformis was described on three specimens (two mature and one juvenile females) from the Norwegian Sea (64°-73°N, 10°W-10°E, depth 2615-2957 m). The present new specimens were found in very distant regions, but they agree with the original description of *B. filiformis* in shape of the tail, construction of the gonad and the trophosome, in the body length and "V" index (3700-4700 mm and 46.8-56.8% respectively in the original description). But the new nematodes do not correspond with the original description for "a" and "c" (38.6-53.3 and 36.2-53.9 respectively vs 46.3-58.8 and 49.5-74.0 respectively).

TABLE 3. — Coordinates, depth and dates of collecting of the samples where females of *B. hureaui* Petter, 1983 were found.

No. of specimen	1	2
Collection No.	MNHN 320 BF	MNHN 325 BF
Cruise	MD 32	DEMERABY
Station	DC 18	KG 08
Date of collecting	14.VIII.1982	15.IX.1980
Region	Western part of the Indian Ocean	Western Atlantic
Coordinates	21°19.0'S 55°15.6'E	8°09.2'N 49°02.6'W
Depth	3150-3225 m	4434 m

TABLE 4. — Measurements (in µm) of females of *B. hureaui* Petter, 1983.

Specimen No.	1	2
Body length	3078.0	3172.0
Maximal body diameter	100.0	98.0
Diameter at the level of cephalic sensilla	25.0	20.0
Diameter at the level of amphids	46.0	45.0
Diameter at the middle of the body	100.0	98.0
Diameter at the level of the anus	—	41.0
Distance from the cephalic end to the amphids	29.0	31.0
"a"	30.8	32.4
"c"	—	62.2
"V", %	56.3	52.2

Besides, the distance from the anterior end to the amphids varies, and is less than in original description (42-121 vs 100-110 µm). The body length is greater than in the original description in most new specimens (4000-5516 vs 3700-4700 µm). It seems to the author, in spite of these distinctions, that establishment of a new species is not rational, because there are no gaps between ranges of character measurements of new and earlier described specimens.

Benthimermis hureaui Petter, 1983 (Fig. 4; Tables 3; 4)

Benthimermis hureaui Petter, 1983a: 7, 8, fig. 4.

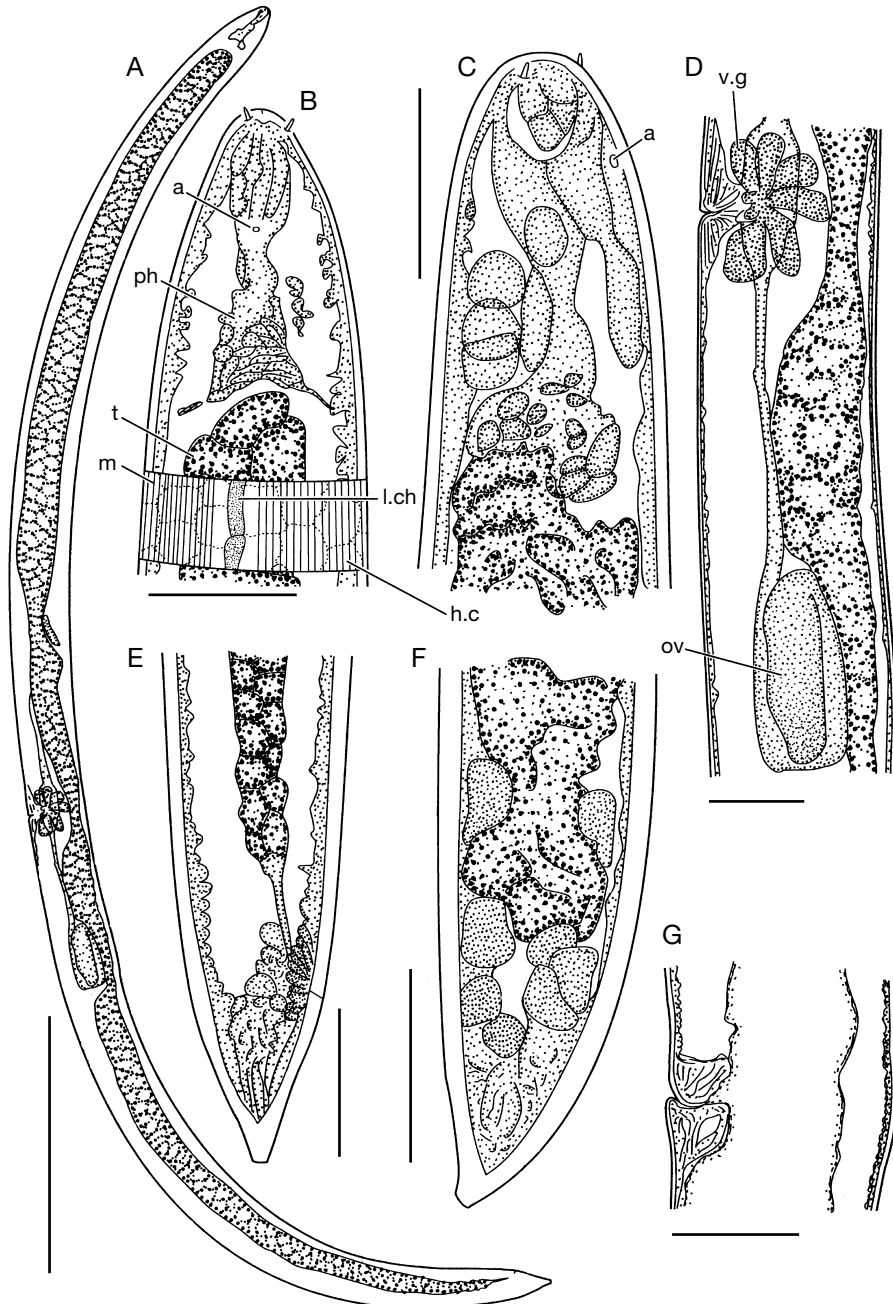


FIG. 4. — *Benthimermis hureai* Petter, 1983, ♀ (see Tables 3 and 4 for locations and measurements of specimens); **A**, total view of specimen No. 2; **B**, cephalic end of specimen No. 2; **C**, cephalic end of specimen No. 1; **D**, reproductive system of specimen No. 2; **E**, tail of specimen No. 2; **F**, tail of specimen No. 1; **G**, region of the vulva of specimen No. 1. Abbreviations: **a**, amphid; **h.c**, hypodermal cells; **l.ch**, lateral hypodermal chord; **m**, somatic musculature; **ov**, ovary; **ph**, vestigial pharynx; **t**, trophosome; **v.g**, vulvar glands. Scale bars: A, 500 μ m; B-G, 50 μ m.

TYPE MATERIAL. — Holotype: S Indian Ocean, 46°02.0'S, 49°08.5'E, 980 m, 28.IV.1976, ♀ (MNHN 153 BB); paratypes: same locality, 5 ♀♀ (MNHN 154 BB).

MATERIAL EXAMINED. — 2 immature ♀♀ (see Tables 3 and 4 for details).

DESCRIPTION

Measurements are presented in Table 4. Body cylindrical, slightly narrower at anterior and posterior ends. Posterior end in shape of a truncated cone. Amphids non-spiral. Amphidial apertures pore-like, about 2 µm in diameter. Four medio-lateral papilloid cephalic setae 3–4 µm long inserted in tiny pits. Pharynx looking like a non-muscular string devoid of an internal lumen. Specimen No. 2 possessing slight channel in cuticle instead of mouth, as well as vestigial rectum and anus. Cuticle of this specimen thicker at cephalic apex; borders between trophosomal cells distinct. Borders between trophosomal cells of specimen No. 1 indistinct, rectum and anus absent. Cuticle gradually thickened from 2–3 µm at anterior part of body to 4–5 µm at posterior part. Female reproductive system didelphic, amphidelphic, occupying about one quarter of total body length. Ovaries reflected. Neither morphologically differentiated spermatheca nor spermatozoa nor vulvar glands discovered.

REMARKS

B. bureaui was originally described from six specimens collected in the more western French Southern and Antarctic Islands (southern part of the Indian Ocean, 46°2'S, 49°8.5'E, 980 m depth). The new specimens were found in other regions remote from one another. Nevertheless, there is an evident close similarity between them and type specimens, except an absence of sclerotic ring around the vagina, which is mentioned in the original description. Besides, there are no rectum and anus in one specimen, whereas all specimens described by Petter (1983a) possess it. However, basing on these distinctions, an establishment of a new species is not rational.

Benthimermis ifremeri n. sp.

(Fig. 5)

TYPE MATERIAL. — Holotype: Western Atlantic, cruise DEMERABY, stn CP 14, 10°24.32'N, 46°46.02'W, 4800 m depth, 28.IX.1980, immature ♀ (MNHN 335 BF).

ETYMOLOGY. — In honour of the Institut français de Recherche pour l'Exploitation de la Mer (IFREMER).

DIAGNOSIS. — The new species has a rounded tail without a terminal process like *B. arnaudi* Petter, 1983, *B. edouardensis* Petter, 1983, and *B. minuta* Petter, 1987. *B. ifremeri* n. sp. differs from *B. arnaudi* in a smaller body length (5.3 vs 6.7–6.8 mm); by the absence of caudal terminal knob; by a thinner body ("a" = 32.7 vs 23.9–24.3); by a longer tail ("c" = 70.8 vs 80–335); by the absence of optically dense ring around the vagina. The new species has a smaller body length than *B. edouardensis* (5.3 vs 8.6–9.35 mm) and a longer tail ("c" = 70.8 vs 107.5–311.7). The new species possesses a body length twice longer than *B. minuta*; a thinner body ("a" = 32.7 vs 17.7–20.0); a longer tail ("c" = 70.8 vs 93.0–162.5). Besides, the trophosome of *B. minuta* consists of one row of cells whereas the trophosome of *B. ifremeri* n. sp. consists of several rows of cells. The three species compared with the new species were described from other regions of the world ocean.

DESCRIPTION

Measurements: L = 5313 µm; "a" = 32.7; "c" = 70.8; "V" = 55.3%. Maximal body diameter = 155 µm. Diameter at level of: cephalic sensilla = 27 µm; amphids = 77 µm; midbody = 155 µm; anus = 105 µm. Distance from anterior end to amphid = 58 µm.

Body cylindrical, slightly narrower to anterior end. Anterior and posterior ends rounded. Amphids non-spiral. Amphidial aperture pore-like. Amphidial fovea tubiform. Four medio-lateral cephalic setae about 4 mm long, thin but sharply thickened basally, i.e. possessing basal cone-form part and thinner setiform distal part. Mouth opening absent, but thin axial string 47 µm length visible in anterior part of the pharynx. Short pharynx devoid of an internal lumen and ending by a glandular thickening. Midgut being a trophosome without visible internal lumen and having two or three big cells in transversal optical section. Rectum looking like a short tube with thin walls. Anus present. Cuticle width in cephalic end about 5 µm, and gradually

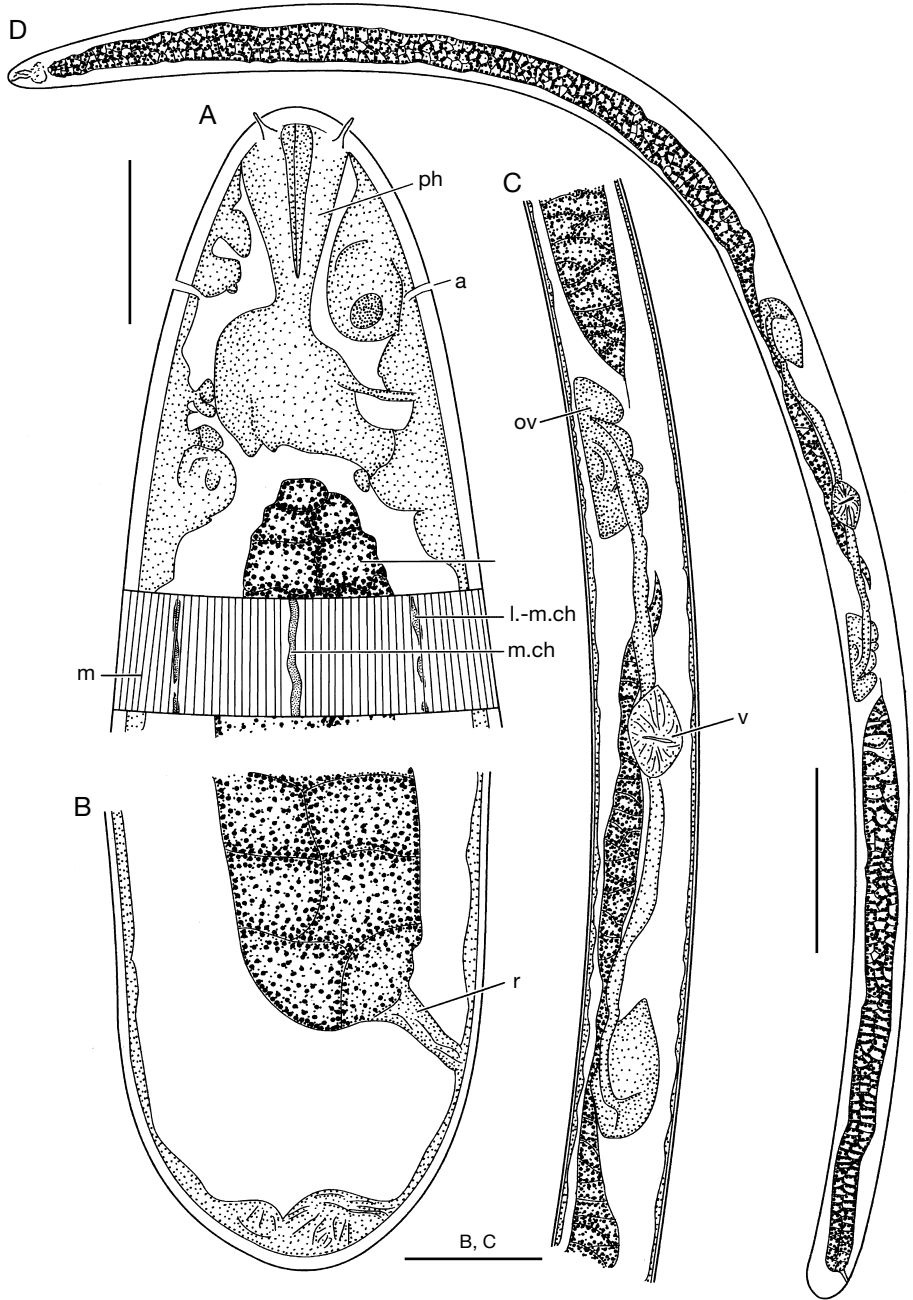


FIG. 5. — *Benthimermis ifremeri* n. sp., ♀ holotype (MNHN 335 BF); **A**, cephalic end; **B**, tail; **C**, reproductive system; **D**, total view. Abbreviations: **a**, amphid; **l.-m.ch**, lateromedian hypodermal chord; **m**, somatic musculature; **m.ch**, median hypodermal chord; **ov**, ovary; **ph**, vestigial pharynx; **r**, rectum; **v**, vulva. Scale bars: A, B, 50 µm; C, 200 µm; D, 500 µm.

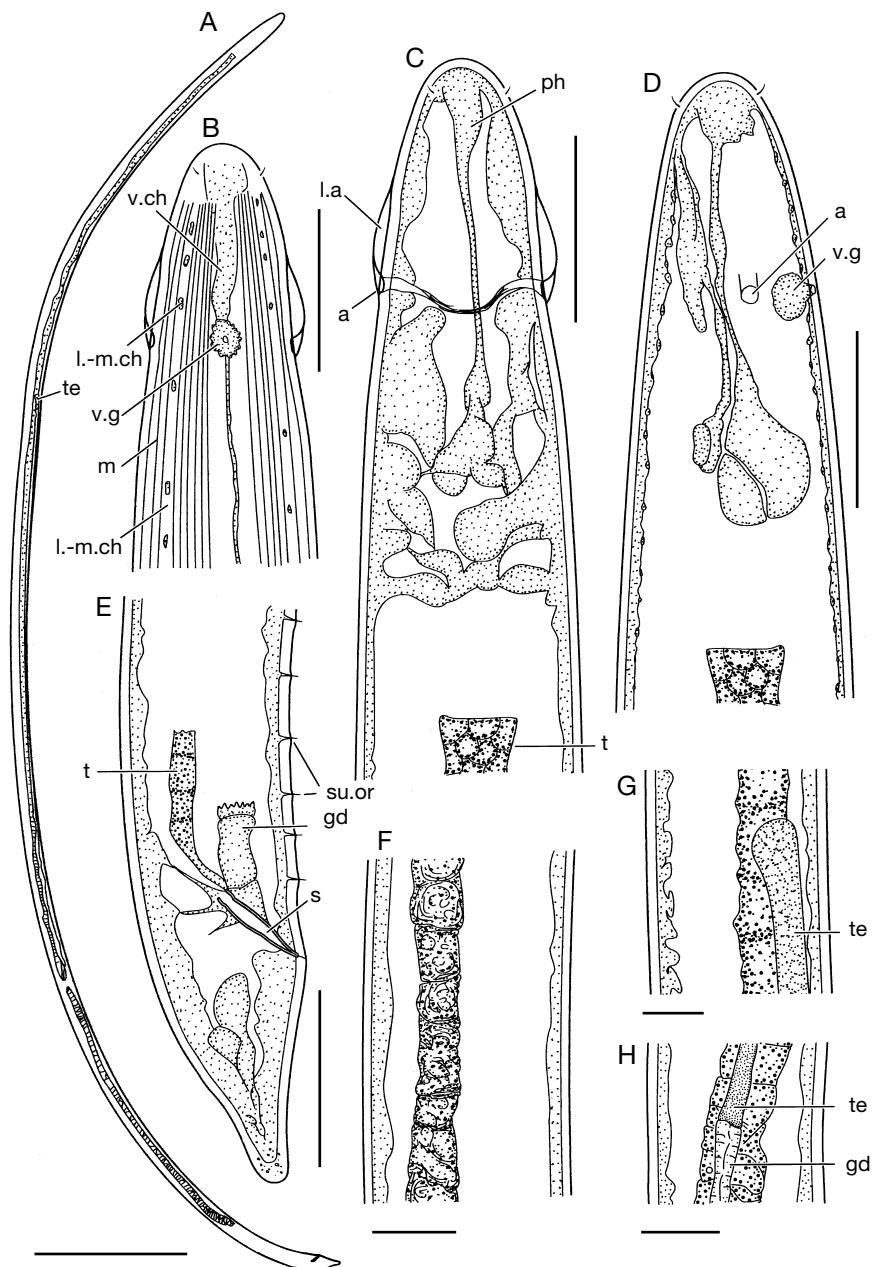


FIG. 6. — *Benthimermis improvisa* n. sp., ♂ holotype (MNHN 332 BF); **A**, total view; **B-D**, cephalic end; **E**, tail; **F**, part of the trophosome at the midbody; **G**, beginning of the testis; **H**, end of the testis. Abbreviations: **a**, amphid; **gd**, gonoduct; **l.a**, lateral alae; **l.-m.ch**, lateromedian hypodermal chord; **m**, somatic musculature; **ph**, vestigial pharynx; **s**, spicule; **su.or**, supplementary organ; **t**, trophosome; **te**, testis; **v.ch**, ventral chord; **v.g**, vulvar glands. Scale bars: A, 500 μ m; B-E, 50 μ m; F-H, 20 μ m.

decreasing to 4 μm at posterior end. Female reproductive system didelphic, amphidelphic, occupying about one fifth of all body length. Ovaries reflected. Vagina short. Neither morphologically differentiated spermatheca nor vulvar glands discovered.

REMARKS

The structure of cephalic setae of the new species (basal cone-form part and thinner setiform distal part, absence of pits around setae) is unique for the genus *Benthimermis*.

Benthimermis improvisa n. sp.

(Fig. 6)

TYPE MATERIAL. — Holotype: Western Atlantic, cruise DEMERABY, stn KG 27, 10°23.02'N, 46°45.08'W, 4800 m, 28.IX.1980, mature ♂ (MNHN 332 BF).

ETYMOLOGY. — From Latin *improvisus* (surprising, unexpected).

DIAGNOSIS. — Described male differs from all other known males of *Benthimermis* by the shape of cephalic setae which are thin and acute; by the structure of the male reproductive system consisting of one long non-paired terminal testis and gonoduct, while males of the other *Benthimermis* species possess two testes. Besides, this male has a round ventral gland at the level of amphid, which opens outside.

DESCRIPTION

Measurements: L = 4844 μm ; "a" = 88.1; "c" = 92.3. Maximal body diameter = 55 μm . Diameter at level of: cephalic sensilla = 24 μm ; amphids = 45 μm ; midbody = 50 μm ; anus = 45 μm . Distance from anterior end to amphid = 66 μm . Length of lateral cervical alae = 31 μm , maximal height of lateral cervical alae = 4 μm . Spicules 28 μm long. Body thread-like, cylindrical. Anterior end in shape of a rounded cone. Posterior end conical. Amphids non-spiral. Amphidial aperture round, about 4.5 μm in diameter. Amphidial fovea tubiform. Four very thin acute bristle-shaped medio-lateral cephalic setae about 2.5-3.0 μm long. Cuticle width about 3.0 μm . Lateral cervical alae anterior to amphids. Their length about a half of distance from anterior end to amphids. Mouth opening absent. Pharynx looking like a non-

muscular string devoid of an internal lumen with a thickening on posterior end. Small spherical gland at level of amphid on ventral side of the body, possessing a short canal ended by a distinct outlet 1.5 μm wide on ventral side. Midgut being a trophosome without visible internal lumen. Trophosome consisting of several rows of cells at posterior part of body. But in middle part of body, trophosome formed by a chain of rather large cells. Anus present. Male reproductive system about 3 mm long, consisting of one long non-paired terminal testis and long vas deferens. Spicules straight, distally acuted, without a gubernaculum. Nine midventral supplementary organs present anterior to anus.

REMARKS

The cephalic thin and acute setae are not found in any other species of *Benthimermis*. Setae of such shape may be considered as a primitive feature, which is peculiar to free-living nematodes. The ventral round gland at the cervical part of the body represents a vestigial renetta (excretory organ of free-living nematodes).

Benthimermis marionensis Petter, 1983

(Fig. 7)

Benthimermis marionensis Petter, 1983a: 9, 10, fig. 5. — Tchesunov 1988: 15-17, figs 3, 4.

TYPE MATERIAL. — Holotype: S part of Indian Ocean, 46°52.5'S, 37°53.5'E, 110 m, 25.III.1976, ♀ (MNHN 166 BB); paratypes: same data, 6 ♀ ♀ (MNHN 166 BB).

MATERIAL EXAMINED. — Western Atlantic, cruise DEMERABY, stn KG 03, 8°7.88'N, 49°3.71'W, 4440 m depth, 12.IX.1980, 1 immature ♀ (MNHN 322 BF).

DESCRIPTION

Measurements: L = 9000 μm ; "a" = 64.3; "V" = 53.5%. Maximal body diameter = 140 μm . Diameter at level of: cephalic sensilla = 33 μm ; amphids = 86 μm ; midbody = 140 μm . Distance from anterior end to amphid = 84 μm . Body thread-like, cylindrical. Anterior end in shape of a rounded cone. Posterior end conical, possessing terminal spine 130 μm long. Core (apparently cytoplasmic) with granular inclusions

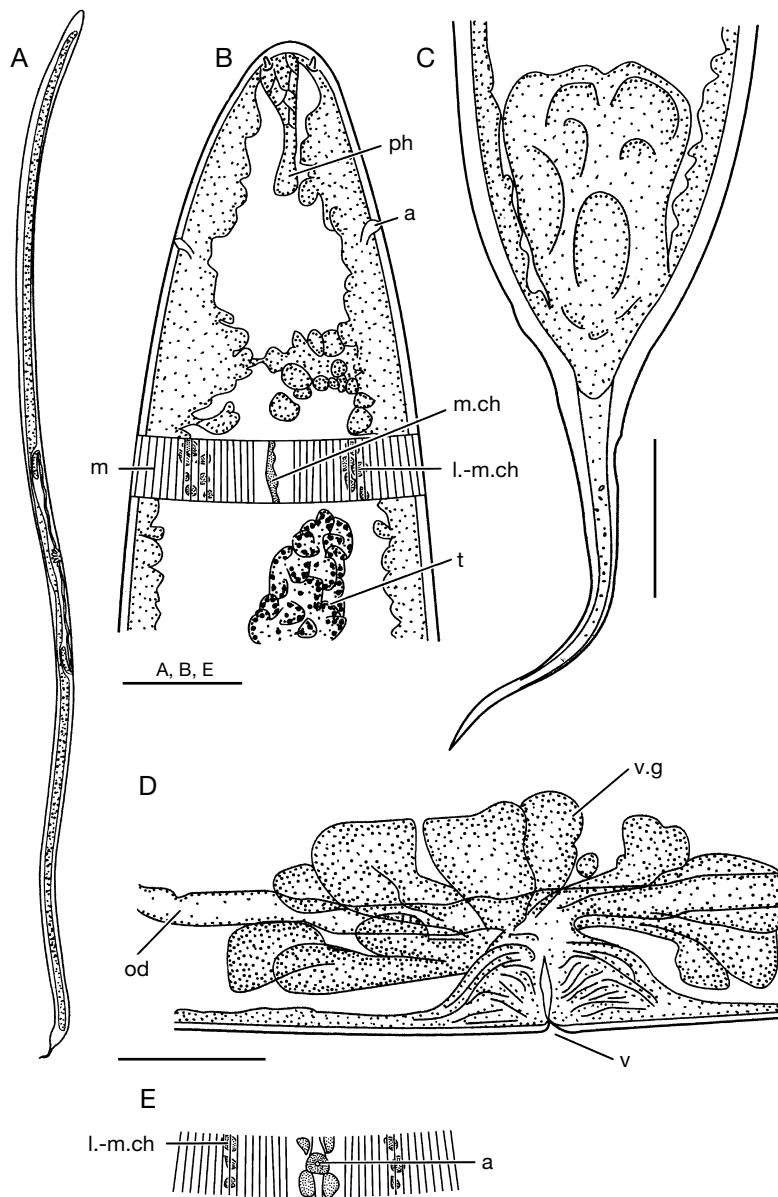


FIG. 7. — *Benthimermis marionensis* Petter, 1983, ♀; **A**, total view; **B**, cephalic end; **C**, tail; **D**, region of vulva; **E**, body wall at the anterior end, laterally. Abbreviations: **a**, amphid; **l-m.ch**, lateromedian hypodermal chord; **m**, somatic musculature; **m.ch**, median hypodermal chord; **od**, oviduct; **ph**, vestigial pharynx; **t**, trophosome; **v**, vulva; **v.g**, vulvar glands. Scale bars: A, 1000 µm; B-E, 50 µm.

inside terminal spine. Cuticle width is 3-6 µm. Mouth opening absent. Four mediolateral papilloid cephalic setae about 3.0 µm long inserted in tiny pits. Amphids non-spiral. Amphidial

aperture pore-like. Amphidial fovea tubiform, slightly wider than aperture. Pharynx looking like a non-muscular string without an internal lumen. Midgut being a multicellular trophosome

without visible internal lumen. Rectum and anus absent. Female reproductive system amphidelphic, occupying about one fifth of total body length. Ovaries reflected. Vagina short. Neither morphologically differentiated spermatheca nor spermatozoa nor vulvar glands discovered.

REMARKS

B. marionensis was described upon eight mature females from the southern part of the Indian Ocean, 46°52'S, 37°51'E, 31-110 m depth (Petter 1983a). The other findings were made in the Southern Atlantic, 57°09'S, 26°09'W from depth 1729 m (Tchesunov 1988). The new finding is from absolutely another region and a much greater depth. The new specimen agrees with the original description of *B. marionensis* in shape of the tail with the terminal spine possessing cytoplasmic core; construction of the gonad and the trophosome. Body length, the de Man "V" index, and the distance from the anterior end to the amphid are in accordance with the original description too (9.0 mm, 53.5%, and 84 µm vs 9.3-14.8 mm, 46.5-74.0%, and 70-85 µm respectively). However the terminal spine of the new specimen is twice shorter than in the original description (130 vs 200-320 µm). Besides, there is no evident anus in the new specimen contrary to type specimens (Petter 1987). As the new specimen was found far from the place of the first finding, it is possible that it can belong to another population of *B. marionensis*. This suggestion can explain the size differences in several morphological features.

Benthimermis petterae n. sp.

(Figs 8; 9; Table 5)

TYPE MATERIAL. — Holotype: Western Atlantic, cruise DEMERABY, stn KG 24, 10°22.7'N, 46°44.7'W, 4800 m, 26.IX.1980, mature ♂ (MNHN 330 BF); allotype: stn KG 04, 8°8.62'N, 49°4.65'W, 4436 m, 12.IX.1980, 1 immature ♀ (MNHN 323 BF); paratype: same station as holotype, 1 immature ♀ (MNHN 330 BF).

ETYMOLOGY. — In honour of Dr Annie Petter (MNHN), who first discovered and described the family Benthimermithidae.

DIAGNOSIS. — Females of *B. petterae* n. sp. are distinguished from females of *B. laubieri*, the most resembling species, in the absence of anus and rectum, and in the absence of optically dense ring around the vagina. The amphidial fovea of *B. petterae* n. sp. is pocket-shaped, while the amphidial fovea of *B. laubieri* is tubiform. The cuticle of the female of *B. petterae* n. sp. thickens at the anterior and posterior ends unlike that of *B. laubieri*. The ovaries of *B. petterae* n. sp. are reflected, whereas the ovaries of *B. laubieri* are outstretched.

The male of the new species shows some resemblance to *B. diploptera* Petter, 1981, *B. leptosoma* Petter, 1981, *B. aptera* Petter, 1982, *B. australis* Petter, 1983, *B. rosaliae* Tchesunov, 1988 in shape of tail and construction of the male reproductive system (two testes arranged consecutively). However, the new species differs from those species in number of supplementary organs (10 vs 18-68, 14-38, 19, 15-24, and 11-15, respectively) and in the morphology of the posterior testis possessing a small caecum in its anterior part. Furthermore, the male of the new species differs from the male of *B. diploptera* in absence of postamphidial part of cervical alae; from male of *B. leptosoma* in absence of cervical alae at the apical part of the head. The cervical alae of male of *B. australis* are less wide than the cervical alae of the new species. The male of *B. aptera* has no cervical alae at all. The male of *B. petterae* n. sp. also resembles the male of *B. improvisa* n. sp. in the shape of the tail and the number of supplementary organs (10). However, the male of *B. petterae* n. sp. differs from the male of *B. improvisa* n. sp. in morphology of the male reproductive system (two testes vs one testis); in spicule length (49 vs 28 µm); in absence of the small round gland at the level of the amphids on the ventral side of the body, which is present in the male of *B. improvisa* n. sp.

DESCRIPTION

Male

Measurements: L = 5812 µm; "a" = 77.5; "c" = 70.0. Maximal body diameter = 75 µm. Diameter at level of: cephalic sensilla = 28 µm; amphids = 63 µm; midbody = 75 µm; anus = 50 µm. Distance from anterior end to amphid = 85 µm.

Body thread-like, cylindrical. Anterior end in shape of a rounded cone. Posterior end conical and acute. Mouth opening absent. Four medio-lateral cephalic setae about 5 µm long inserted in tiny pits. Amphids non-spiral. Amphidial aperture resembling a pore of 5 µm in diameter. Amphidial fovea tubiform. Cuticle width 4-5 µm along entire body. Cervical alae of 64 µm length

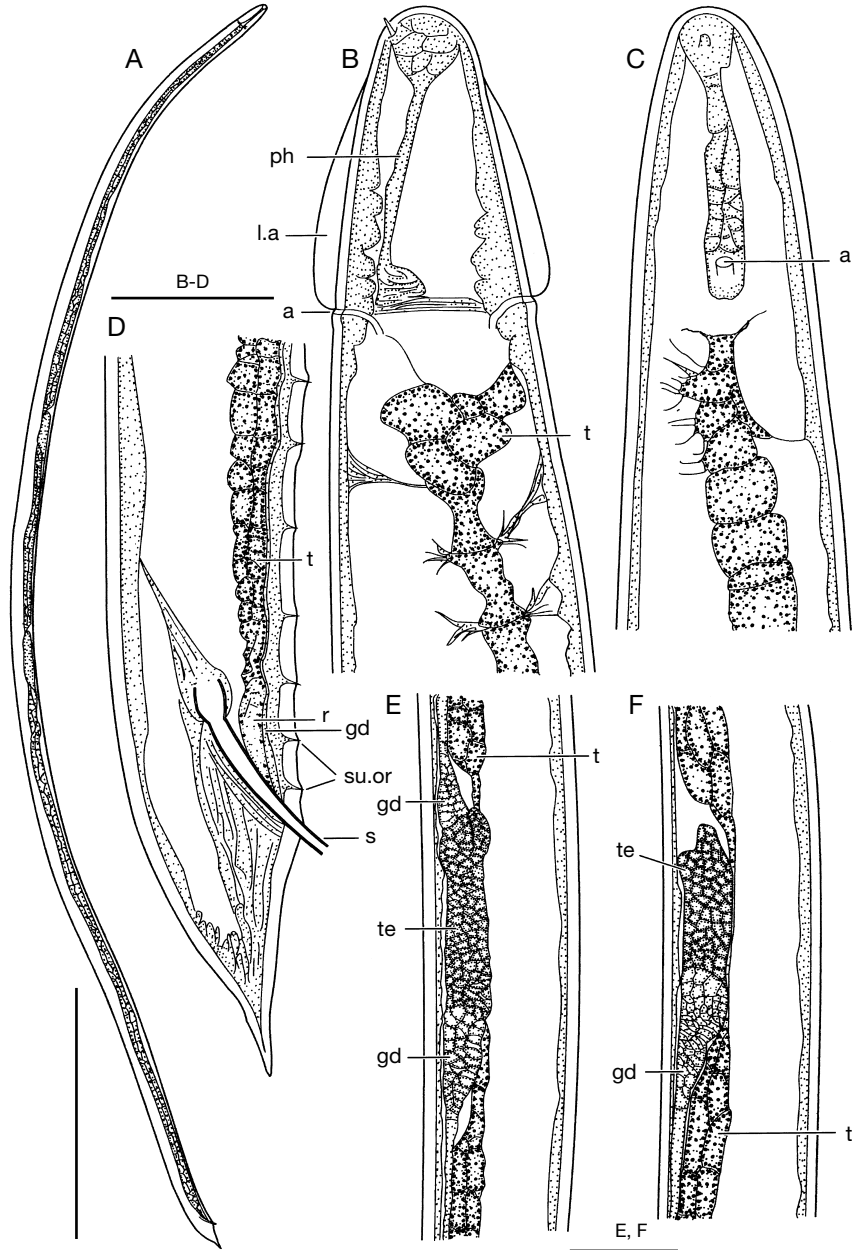


FIG. 8. — *Benthimermis petterae* n. sp., ♂ holotype (MNHN 330 BF); **A**, total view; **B**, **C**, cephalic end; **D**, tail; **E**, posterior testis; **F**, anterior testis. Abbreviations: **a**, amphid; **gd**, gonoduct; **l.a.**, lateral alae; **ph**, vestigial pharynx; **r**, rectum; **s**, spicule; **su.or**, supplementary organ; **t**, trophosome; **te**, testis. Scale bars: A, 1000 µm; B-F, 50 µm.

and 8 µm height right ahead amphids. Pharynx looking like a non-muscular string devoid of internal lumen. Midgut being a trophosome

without visible internal lumen and at midbody consisting of one or several rows of big cells. Rectum and anus present. Male reproductive

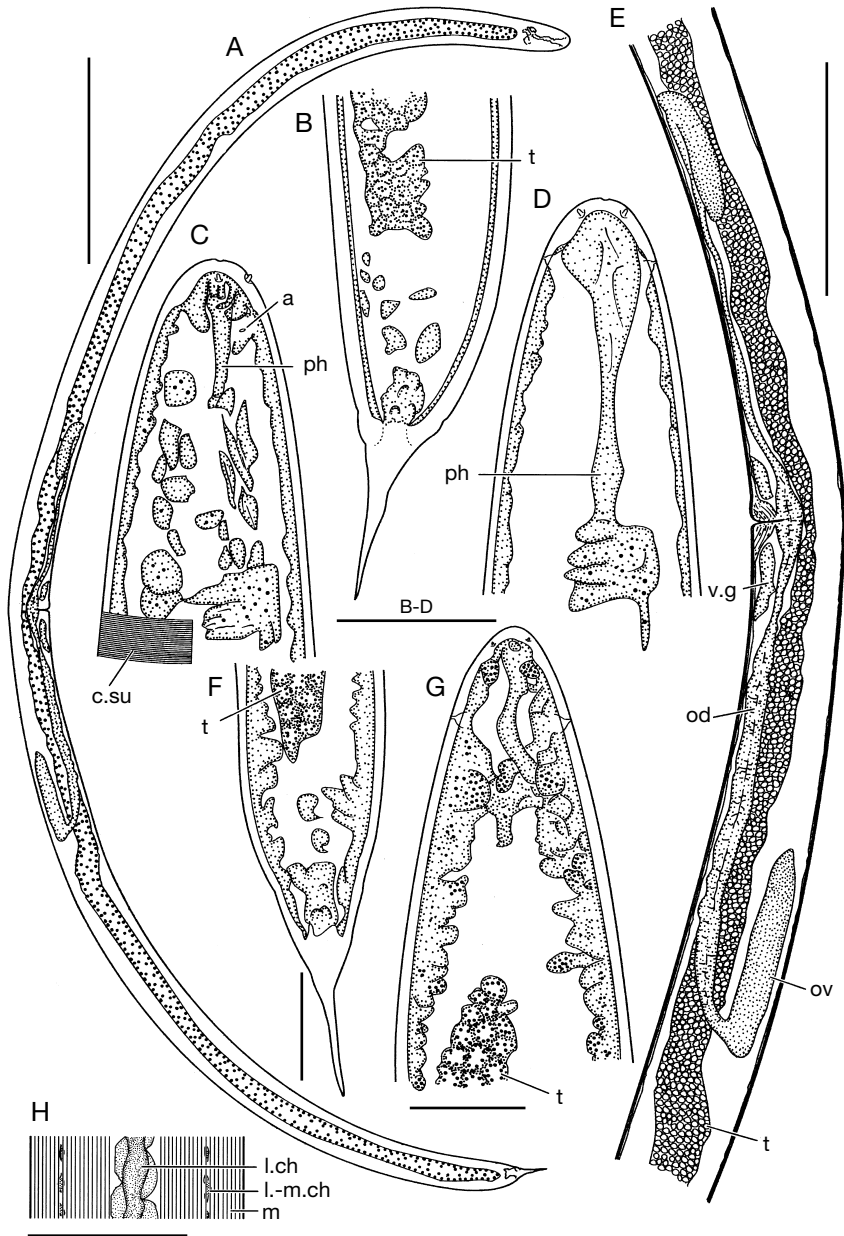


FIG. 9. — *Benthimermis petterae* n. sp., ♀; **A-E, H**, allotype (MNHN 323 BF); **F, G**, paratype (MNHN 330 BF); **A**, total view; **B**, tail; **C, D**, cephalic end; **E**, reproductive system; **F**, tail; **G**, cephalic end; **H**, body wall at the anterior end, laterally. Abbreviations: **a**, amphid; **c.su**, cuticle surface; **l.ch**, lateral hypodermal chord; **l.-m.ch**, lateromedian hypodermal chord; **m**, somatic musculature; **od**, oviduct; **ov**, ovary; **ph**, vestigial pharynx; **t**, trophosome; **v.g**, vulvar glands. Scale bars: A, 500 µm; B-D, F-H, 50 µm; E, 200 µm.

system long, its anterior end almost reaching anterior end of trophosome. Two testes placed one after the other and linked together by

joint spermaduct. Posterior testis at its anterior part having a small caecum directed forward. Spicules straight, 49 µm long, without a gubernaculum.

TABLE 5. — Measurements (in μm) of females of *B. petterae* n. sp.

Specimen	Allotype	Paratype
Body length	4406.0	5156.0
Maximal body diameter	83.0	113.0
Diameter at the level of cephalic sensilla	20.0	22.0
Diameter at the level of amphids	46.0	56.0
Diameter at the middle of the body	83.0	113.0
Distance from the cephalic end to the amphids	23.0	43.0
"a"	53.4	45.8
"V", %	52.8	50.6

culum. Ten supplementary organs anterior to anus.

Female

Measurements are presented in the Table 5. Body cylindrical, slightly narrowed to anterior and posterior ends. Anterior end in shape of a rounded cone. Posterior end conical and acute, terminal part of tail elongated, completely cuticular, without any longitudinal or oblique striae. Amphidial aperture in shape of a transversally oriented oval of about 2 μm width. Amphidial fovea funnel-shaped. Four mediolateral cephalic setae about 3 μm long set in small foveae. Mouth opening absent, but tiny apical pit visible at cephalic end. Short pharynx devoid of an internal lumen and looking like a thin string ending by a glandular thickening at posterior end. Midgut resembling a trophosome without visible internal lumen and consisting of about 10 rows of big cells. Neither rectum nor anus found. Cuticle width about 8 μm in apical part of head, from 3 to 5 μm at level of midbody, and from 6 to 8 μm in posterior part of tail. Regular fine annulation observable with an optical microscope. Female reproductive system didelphic, amphidelphic, occupying about one quarter of total body length. Ovaries reflected. Vagina short. Vulvar glands present around vagina. Morphologically differentiated spermatheca not observed.

Benthimermis platyptera n. sp. (Fig. 10)

TYPE MATERIAL. — Holotype: Western Atlantic, cruise DEMERABY, stn KG 25, 10°22.41'N, 46°46.74'W, 4800 m, 27.IX.1980, mature δ (MNHN 331 BF).

ETYMOLOGY. — From Greek *platyptera* (wide-wing).

DIAGNOSIS. — The male of *B. platyptera* n. sp. differs from all other described males of the genus *Benthimermis* in the fewest number of supplementary organs (2 vs 4-68 in other species), the shortest spicules (19 vs 28-160 μm in other species), and the smallest body length (2953 vs 3300-15000 μm in other species).

DESCRIPTION

Measurements: L = 2953 μm ; "a" = 84.4; "c" = 101.8. Maximal body diameter = 35 μm . Diameter at level of: cephalic sensilla = 12 μm ; amphids = 32 μm ; midbody = 35 μm ; anus = 33 μm . Distance from anterior end to amphid = 43 μm . Spicules 19 μm long.

Body thread-like, cylindrical. Anterior end shaped as a rounded cone. Posterior end rounded. Four mediolateral cephalic setae about 1.5 μm long, inserted in small pits. Amphids non-spiral. Amphidial aperture present as pore of 4 μm in diameter. Amphidial fovea tubiform. Cuticle width 1.5 μm at anterior part, 1.5 μm at midbody, and 6 μm at extremity of posterior end. Cervical alae of 4.5 μm maximal width, beginning right ahead amphids and reaching cephalic apex. Right and left alae join each other at cephalic apex. Mouth opening vestigial, present as an apical light trace in cuticle. Pharynx looking like a non-muscular string devoid of an internal lumen with a thickening at distal end. Midgut being a trophosome consisting of one row of big cells. At midbody, trophosome looking like a backbone. Rectum and anus present. Male reproductive system of 1700 μm length consisting of two testes arranged one after the other and connected by a short spermatheca. Spicules straight, without a gubernaculum. Two very small supplementary organs anterior to anus.

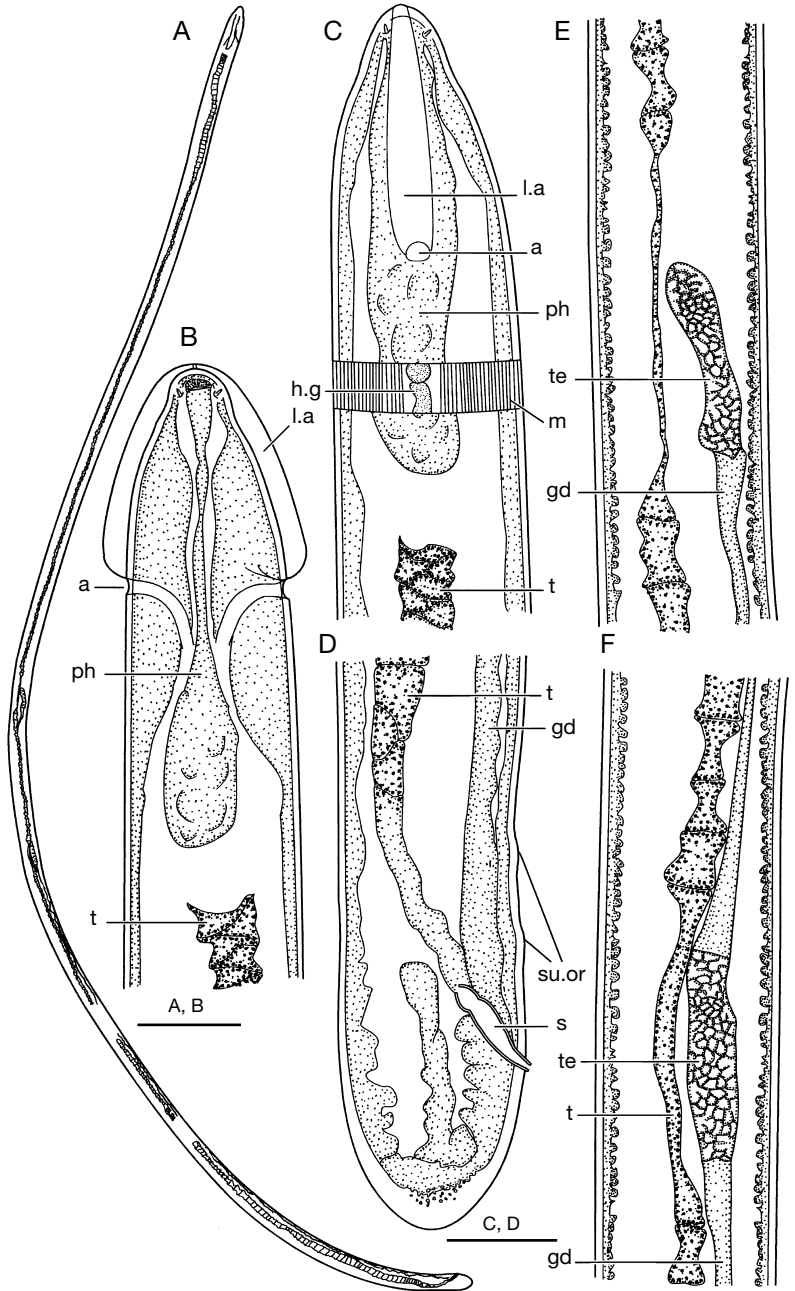


FIG. 10. — *Benthimermis platyptera* n. sp., ♂ holotype (MNHN 331 BF); **A**, total view; **B, C**, cephalic end; **D**, tail; **E**, anterior testis; **F**, posterior testis. Abbreviations: **a**, amphid; **gd**, gonoduct; **h.g**, hypodermal gland; **l.a**, lateral alae; **m**, somatic musculature; **ph**, vestigial pharynx; **s**, spicule; **su.or**, supplementary organ; **t**, trophosome; **te**, testis. Scale bars: A, 2000 µm; B-F, 20 µm.

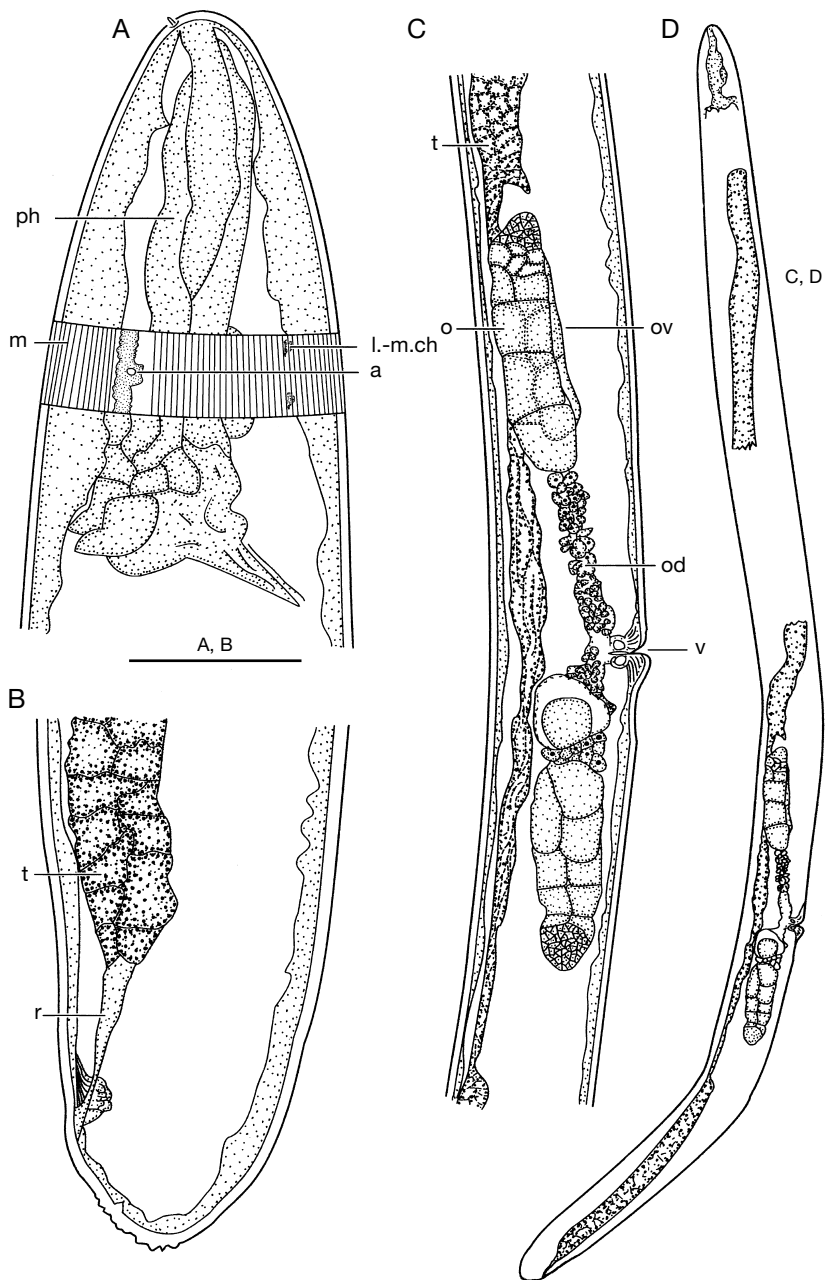


FIG. 11. — *Benthimermis pseudominuta* n. sp., ♀ holotype (MNHN 329 BF); **A**, cephalic end; **B**, tail; **C**, reproductive system; **D**, total view. Abbreviations: **a**, amphid; **l-m.ch**, lateromedian hypodermal chord; **m**, somatic musculature; **o**, oocytes or eggs; **od**, oviduct; **ov**, ovary; **ph**, vestigial pharynx; **r**, rectum; **t**, trophosome; **v**, vulva. Scale bars: A, B, 50 µm; C, 200 µm; D, 500 µm.

Benthimermis pseudominuta n. sp.
(Fig. 11)

TYPE MATERIAL. — Holotype: Western Atlantic, cruise DEMERABY, stn KG 21, 10°24.85'N, 46°46.65'W, 4800 m, 25.IX.1980, 1 ♀ (MNHN 329 BF).

ETYMOLOGY. — The name points to the superficial resemblance with *B. minuta* Petter, 1987.

DIAGNOSIS. — Until now the single species *B. laubieri* was known to possess outstretched ovaries in the genus *Benthimermis*. *B. pseudominuta* n. sp. differs from *B. laubieri* in the shape of the posterior end (rounded vs pointed respectively), body length (2781 vs 5200-6700 µm respectively), and thicker body ("a" = 23.2 vs 32.0-55.8 respectively).

DESCRIPTION

Measurements: L = 2781 µm; "a" = 23.2; "c" = 86.9; "V" = 66.3%. Maximal body diameter = 120 µm. Diameter at level of: cephalic sensilla = 22 µm; amphids = 86 µm; midbody = 120 µm; anus = 61 µm. Distance from anterior end to amphid = 109 µm. Length of: female reproductive system 606 µm; anterior ovary = 206 µm; posterior ovary = 243 µm; anterior oviduct = 25 µm; posterior oviduct = 140 µm. Maximal size of oocytes inside ovary 50 × 50 µm.

Body stout and sausage-shaped, slightly narrowed at anterior and posterior ends. Anterior and posterior ends rounded. Amphidial apertures pore-like, about 2.5 µm in diameter. Four mediolateral cephalic setae about 3.5 µm long, inserted in small pits. Mouth opening absent. Short pharynx devoid of an internal lumen and looking like a thin string. Midgut resembling a trophosome without visible internal lumen and consisting of two to four rows of cells. Rectum in the form of short tube with thin walls. Anus present. Cuticle width about 4.0 µm at midbody, and slightly decreasing to anterior and posterior ends. Female reproductive system didelphic, amphidelphic, occupying about one fifth of total body length. Ovaries outstretched. Vagina short. Optically dense ring visible around vagina. No distinct uterus. Eggs inside oviducts absent. Neither morphologically differentiated spermatheca nor vulvar glands observed.

REMARKS

Oocytes of the new species are not numerous and very large. The size of the eggs of *B. pseudominuta* n. sp. is only comparable with the size of eggs of *B. megala* Petter, 1987, the biggest species of genus *Benthimermis*, which reaches 17 cm long. The hosts of *B. pseudominuta* n. sp. are unknown. However, the small number of eggs in this species suggests that successful invasion of hosts is only possible in relatively dense host population.

Benthimermis tchesunovi n. sp.
(Fig. 12)

TYPE MATERIAL. — Holotype: Southeastern Atlantic, cruise WALWIS, stn DS 01, 33°53.9'S, 05°05.9'E, 5205 m, 24.XII.1978, mature ♀ (MNHN 362 BF).

ETYMOLOGY. — In honour of Dr A. V. Tchesunov, Department of Invertebrate Zoology, Faculty of Biology, Moscow State University.

DIAGNOSIS. — The female of *B. tchesunovi* n. sp. is similar to *B. australis* and *B. bureauui* in shape of the tail. The new species differs from *B. australis* in the body length (1953 vs 4380-9400 µm), presence of a cuticular thickening at the cephalic apex, number of trophosomal cells at the cross-section (2-4 vs about 10 [Chesunov 1988]), absence of the distinct uterus, and smaller and oval eggs (15 × 9 vs 30 × 30 µm). The new species differs from *B. bureauui* in the body length (1953 vs 2500-3800 µm), presence of the cuticular thickening at the cephalic apex, the body thickness ("a" = 38.3 vs 25.0-32.4), the thick cuticular walls of the vagina, and smaller and oval eggs (15 × 9 vs 25 × 25 µm). The new species is similar to *B. minuta* in its body length, but differs from *B. minuta* by the shape of the tail (conical vs rounded).

DESCRIPTION

Measurements: L = 1953 µm; "a" = 38.3; "c" = 55.8; "V" = 52.0%. Maximal body diameter = 51 µm. Diameter at level of: cephalic sensilla = 16 µm; amphids = 35 µm; midbody = 51 µm; anus = 37 µm. Distance from anterior end to amphid = 36 µm. Maximal size of eggs 15 × 9 µm. Body cylindrical, slightly narrowed to anterior end. Anterior end in shape of a rounded cone. Posterior end conical and angular. Amphidial apertures pore-like, about 1.5 µm in diameter. Four mediolateral cephalic setae about 1 mm long inserted in small pits. Mouth opening

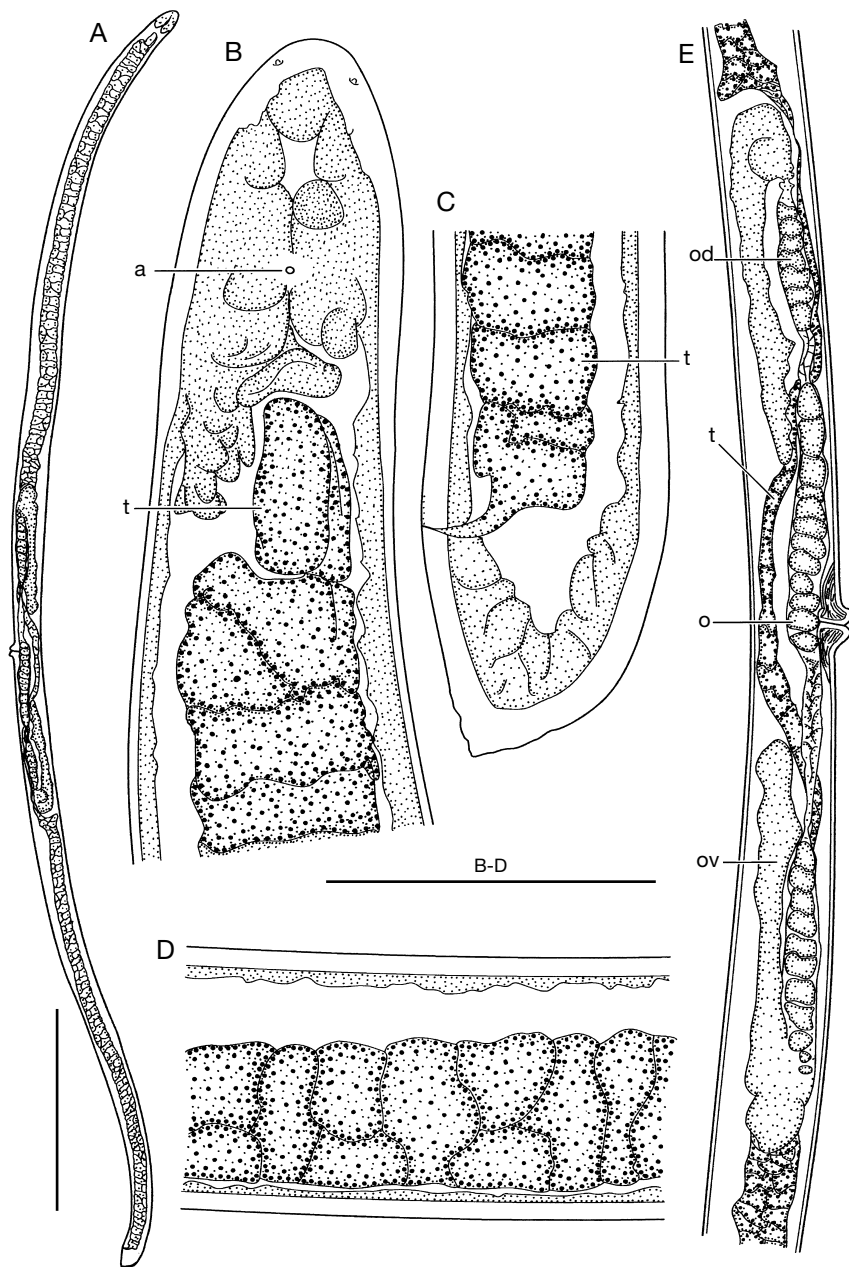


FIG. 12. — *Benthimermis tchesunovi* n. sp., ♀ holotype (MNHN 362 BF); **A**, total view; **B**, cephalic end; **C**, tail; **D**, part of the trophosome at the midbody; **E**, reproductive system. Abbreviations: **a**, amphid; **o**, oocytes or eggs; **od**, oviduct; **ov**, ovary; **t**, trophosome. Scale bars: **A**, 400 µm; **B-D**, 50 µm; **E**, 100 µm.

absent. The pharynx devoid of an internal lumen and looking like a shapeless cellular agglomeration. Midgut being a trophosome without visible

internal lumen and consisting of two rows of big cells at level of midbody. Generally, dorsoventrally oriented pair of cells alternates with

laterally oriented pair of cells. Trophosome consists of only one row of cells at posterior and anterior ends. Rectum resembling a short tube with thin walls. Anus present. Cuticle width about 1.5 μm at midbody, slightly increasing up to 4 μm at anterior end and up to 6 μm at posterior end. Apical cap-like cuticular thickening of 6 μm present at cephalic apex. Female reproductive system amphidelphic, occupying about one third of entire body length. Ovaries reflected. The oviducts long, about 200 μm . Vagina short. Thickness of vaginal walls comparable with thickness of body cuticle. No distinct uterus. Neither morphologically differentiated spermatheca nor spermatozoa nor vulvar glands observed.

Benthimermis turpicauda n. sp.
(Fig. 13; Tables 6; 7)

TYPE MATERIAL. — Holotype: mature ♀; paratype: immature ♀ (see Tables 6 and 7 for details).

ETYMOLOGY. — From Latin *turpis* (ugly, deformed) and *cauda* (tail).

DIAGNOSIS. — Females of *B. turpicauda* n. sp. differ from all other species of *Benthimermis* in the irregular shape of their caudal terminal spine. The ovaries of the mature female *B. turpicauda* n. sp. are hologonic. The ovaries of such construction are only known in *B. megala* Petter, 1987, the biggest known species of genus *Benthimermis* (Miljutin & Tchesunov 2001). The new species differs from *B. megala* in the body length (3.4 and 6.1 vs 65-170 mm), the structure of the trophosome (one row of big cell vs multicellular trophosome), the shape of the caudal terminal spine, and many other parameters.

DESCRIPTION

Measurements are presented in Table 7. Body cylindrical, slightly narrowed at anterior end. Anterior end in shape of rounded cone. Posterior end rounded, possessing terminal cuticular process of irregular shape. Amphids non-spiral. Amphidial apertures pore-like, about 4 μm in diameter. Four mediolateral cephalic setae about 4 μm long inserted in small pits. Small pores connected with hypodermal glands in sublateral chords. Mouth opening absent. Pharynx devoid of an internal lumen and terminated posteriorly

TABLE 6. — Coordinates, depth and dates of collecting of the samples where females of *B. turpicauda* n. sp. were found.

Specimen	Holotype	Paratype
Collection No.	MNHN 317 BF	MNHN 333 BF
Cruise	MD 32	DEMERABY
Station	DR 62	DS 02
Date of collecting	28.VIII.1982	13.IX.1980
Region	Western part of the Indian Ocean	Western Atlantic
Coordinates	21°08.0'S, 55°11.8'E	8°09.23'N, 49°04.37'W
Depth	630-710 m	4400 m

TABLE 7. — Measurements (in μm) of females of *B. turpicauda* n. sp.

Specimen	Holotype	Paratype
Maturity	Mature	Immature
Body length	3422.0	6125.0
Maximal body diameter	125.0	141.0
Diameter at the level of cephalic sensilla	29.0	31.0
Diameter at the level of amphids	70.0	78.0
Diameter at the middle of the body	125.0	141.0
Diameter at the level of the anus	77.0	93.0
Distance from the cephalic end to the amphids	105.0	102.0
Length of caudal terminal spine	16.0	40.0
Female reproductive system length, % of body length	15.0	6.0
Eggs size	19.0 x 16.0	—
"a"	27.4	43.4
"c"	72.8	71.2
"V", %	49.3	48.0

by a shapeless cellular agglomeration. Trophosome consisting of one row of big cells. Peripheral cytoplasm of trophosomal cells light and without any inclusions, but middle parts of the trophosomal cells filled with numerous vesicles and granules. Generally, transversal circular ridges of hypodermis present around joining trophosomal cells. Rectum looking like a thin-walled tube. Anus subterminal and hardly seen.

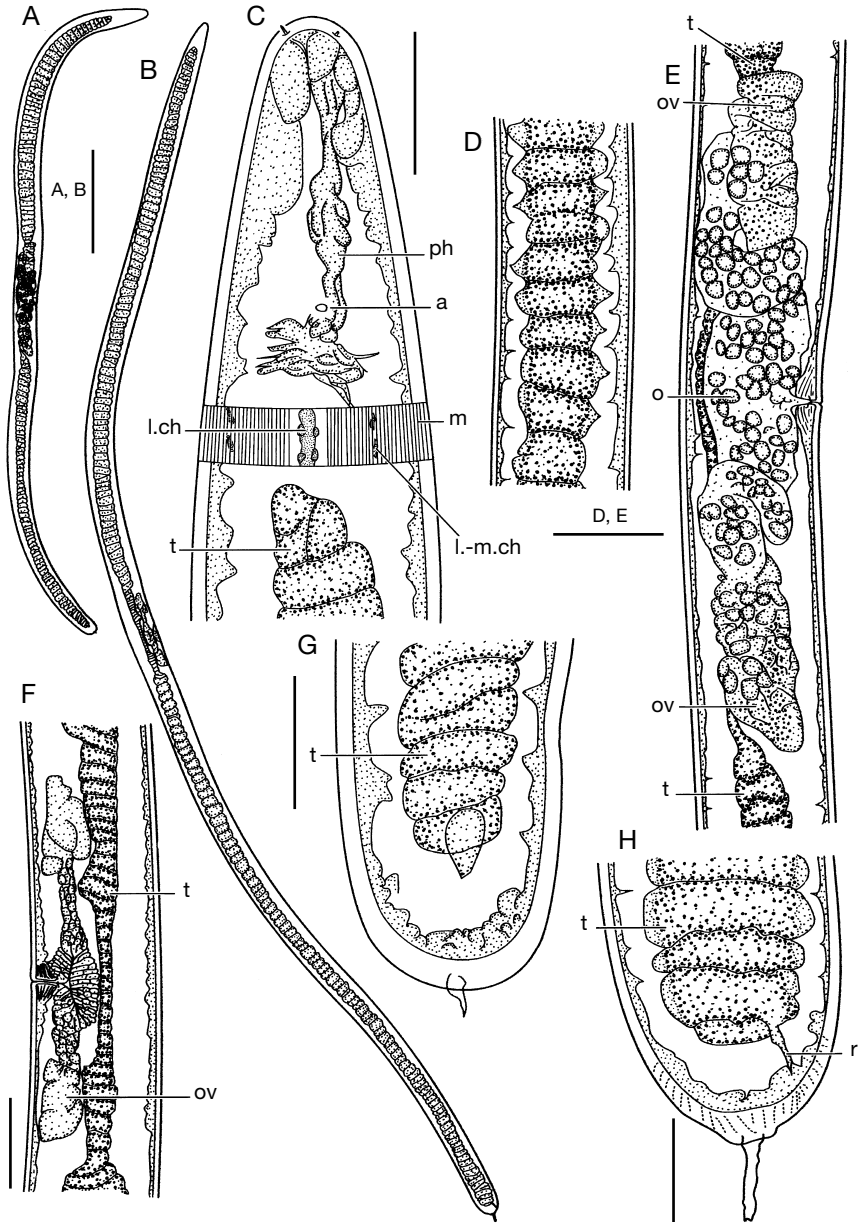


FIG. 13. — *Benthimermis turpicauda* n. sp., ♀; **A, C-E, G**, holotype (MNHN 317 BF); **B, F, H**, paratype (MNHN 333 BF); **A**, total view; **B**, total view; **C**, cephalic end; **D**, a part of the trophosome at the midbody; **E**, reproductive system; **F**, reproductive system; **G**, tail; **H**, tail. Abbreviations: **a**, amphid; **l.ch**, lateral hypodermal chord; **l.-m.ch**, lateromedian hypodermal chord; **m**, somatic musculature; **o**, oocytes or eggs; **ov**, ovary; **ph**, vestigial pharynx; **r**, rectum; **t**, trophosome. Scale bars: A, B, 500 µm; C, G, H, 50 µm; D-F, 100 µm.

Cuticle width about 5 µm at midbody, slightly increasing at terminal part of posterior end. Female reproductive system amphidelphic, very

short. Ovaries short, hologonic (germinal zone extending throughout entire length of gonads). In mature female, oviducts short, twisted, very

wide in their proximal parts, and containing eggs. No distinct uterus. Vagina is short, with thin cuticular walls. Neither morphologically differentiated spermatheca nor spermatozoa nor vulvar glands were observed.

REMARKS

The holotype and the paratype have been found in different parts of the world ocean very distant from each other. The paratype is almost twice longer than the holotype. However, these specimens are similar in body proportions, morphology of the trophosome, transversal circular ridges of the hypodermis around the places of the junction of the trophosomal cells, and, undoubtedly, belong to the same species.

Morphology of the female reproductive system in *B. turpicauda* n. sp. (hologonic ovaries) is different from that of most other *Benthimermis* species. The ovaries of *Benthimermis* typically are telogonic (the germinal zone confined to the distal ends) (Petter 1980, 1983a, 1987; Chesunov 1988; Tchesunov 1988). Only one exception has been known before: the giant (up to 17 cm in length) species *B. megalia* Petter, 1987, having hologonic ovaries too (Miljutin & Tchesunov 2001).

The caudal terminal spine of *B. turpicauda* is of variable and irregular shape and, evidently, is vestigial.

DISCUSSION

It is known that nematodes, in comparison to many other animals, possess only a few features, which can be used in species discrimination. However such features are still fewer in number in benthimermithids. The works on this family indicate that the best features are: de Man indices, the shape of the tail (variations are possible for some species), the structure and the size of the gonads in mature specimens, the size of eggs in mature females, the length of spicules and the number of preanal supplementary organs in males, the distance from the cephalic end to the amphids (variations are possible for some species), and the shape and length of the cephalic

sensilla. Yet it is not clear if it is possible to use presence or absence of the sclerotized ring around the vagina as a specific feature, since this might depend on maturity of females. Features like the presence or absence of the vestigial mouth opening, anus, rectum, and vulvar glands, the distance from the cephalic end to the beginning of the trophosome or from the posterior end to the end of the trophosome, and the size of the gonads in immature specimens, have a lower value for diagnosis. Firstly, the trophosome often shrinks after the fixation, and it leads to the detachment of the trophosome ends from their native places. Secondly, in immature specimens, the size of the gonads may differ from that in mature specimens. Thirdly, in the specimens of the same species, a vestigial mouth opening, or an anus, or a rectum may be absent or present. Fourthly, it was shown (Miljutin & Tchesunov 2001), that, at the free-living stage, young mature females of *B. megalia* Petter, 1987 have well developed vulvar glands, while these glands almost disappear in old females.

In connection with the adjustment to the parasitic way of life, the morphology of the nematodes of genus *Benthimermis* has been subjected to fundamental reconstruction. The mouth opening is either completely absent or in the form of the small apical pore. The pharynx of the adult specimens represents a cellular mass devoid of the internal lumen, the muscular envelope, and any internal cuticular structures. However, the early parasitic larvae possess a mouth opening, and there is a small stylet in the anterior part of their pharynx (Chesunov 1997). The pharyngeal stylet was also described in the free-living immature male of *B. rotundicauda* possessing three cuticles (Petter 1981b).

The midgut is modified to the trophosome, which serve as a depot of the nutrients (Chesunov 1997; Miljutin & Tchesunov 2001). There are two main types of the trophosome structure. The first type is a multicellular trophosome (five cells or more at the cross-section) with the cells oriented radially around an axial narrow internal lumen. The internal lumen, however, is devoid of microvillous layer (Miljutin & Tchesunov 2001). Such type of the trophosome is known, for example, in *B. arnaudi*

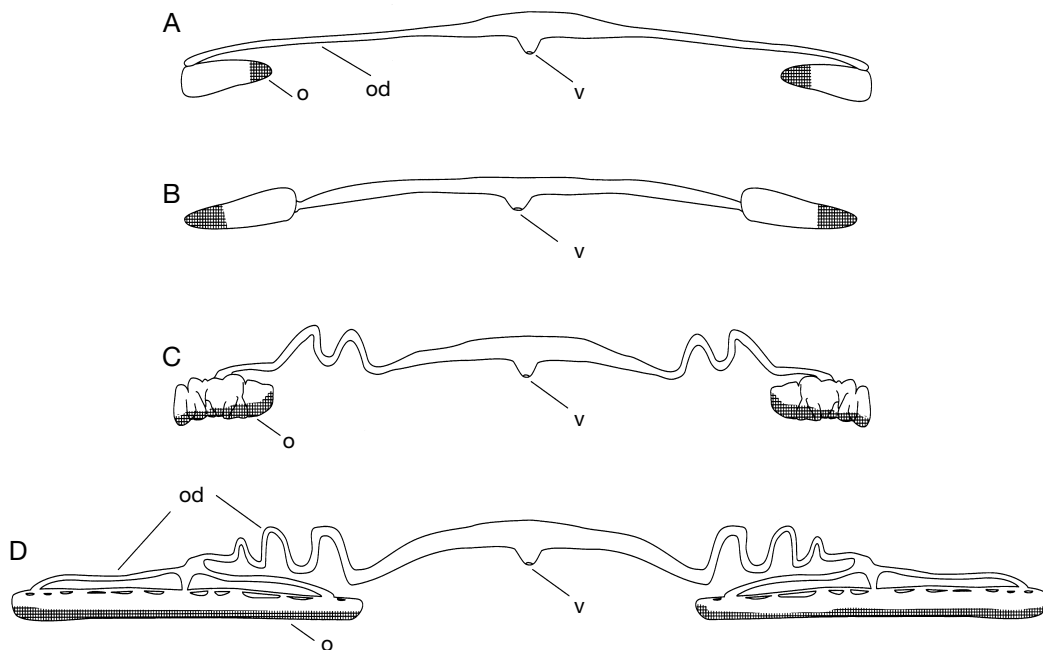


FIG. 14. — Main types of *Benthimermis* Petter, 1980 female reproductive systems (germinal zones are indicated by the hatching); **A**, telogonic reflected ovaries (most species); **B**, telogonic outstretched ovaries (two known species); **C**, hologonic ovaries of *B. turpicauda* n. sp.; **D**, hologonic ovaries of *B. megala* Petter 1987. Abbreviations: o, oocytes or eggs; od, oviduct; v, vulva.

and *B. marionensis* (Tchesunov 1988), *B. diploptera*, and *B. megala* (Miljutin & Tchesunov 2001). The second type is an oligocellular trophosome (from one to four cells at cross-sections) without an internal lumen, for example, *B. filiformis* (Fig. 3) and many small species. Apparently, the first type is most primitive (as such trophosome is similar to the midgut of free-living nematodes), and the second type is a result of the reduction. Rectum and anus are either present or vestigial or completely absent. The excretory system is not found in this genus except in *B. improvisa* n. sp., the cervical ventral spherical gland of which can be treated as a vestigial renetta.

The sensilla of the cephalic end are in shape of short papillae except *B. improvisa* n. sp. possessing setiform cephalic sensilla. The labial papillae are usually subcuticular (Miljutin & Tchesunov 2001). The somatic setae, as a rule, corresponding to hypodermal glands in the lateral chords were found in almost all earlier described speci-

mens. However, in the present investigation, such setae have not been found in the majority of specimens, in spite of the presence of hypodermal glands in the lateral chords.

The female ovaries are of three types in genus *Benthimermis* (Fig. 14). The most species have reflected telogonic ovaries, two known species (*B. laubieri* and *B. pseudominuta* n. sp.) have outstretched telogonic ovaries, and, at last, *B. megala* (Miljutin & Tchesunov 2001) and *B. turpicauda* n. sp. have hologonic ovaries. It is interesting, that hologonic ovaries are only found in parasitic nematodes (Foor 1983). Apparently, the reflected telogonic ovary should be considered as a plesiomorphy, as such type of ovaries is peculiar to Camacolaiminae, a supposed sister group of Benthimermithidae.

The male reproductive system consists of testes, paired outstretched spicules without gubernaculum, and a row of preanal medioventral supplementary organs (from two to several tens). The

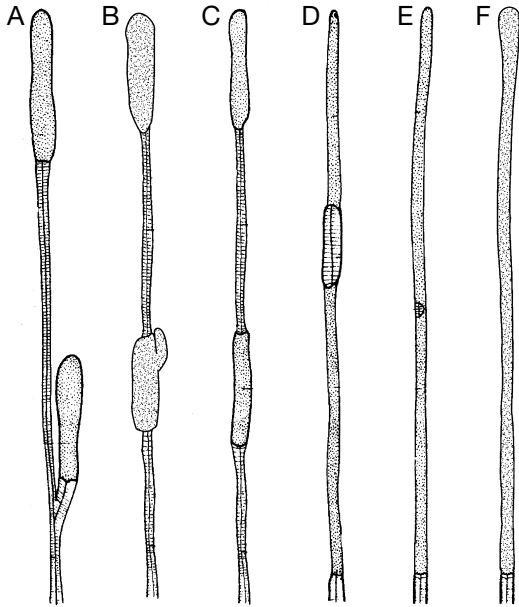


FIG. 15. — Morphological series of the testes of the male of genus *Benthimermis* Petter, 1980 (based on Petter [1982b: fig. 3], modified and supplied); **A**, *B. breviptera* Petter, 1982; **B**, *B. petterae* n. sp.; **C**, *B. leptosoma* Petter, 1981; **D**, *B. gracilis* Petter, 1982; **E**, *B. diploptera* Petter, 1981; **F**, *B. improvisa* n. sp.

testicle arrangement is rather diverse (Fig. 15). Apparently, the plesiomorph state is the paired testes, both directed anterior (*B. breviptera* and *B. crosetensis*). Male gonads of the majority of *Benthimermis* species are paired, arranged one after the other, and consecutively connected by the joint spermaduct. The structure of the gonad of *B. petterae* n. sp. demonstrates a transitional stage between these two types. Further, the testes of *B. diploptera* may be almost fused. And, finally, the male *B. improvisa* n. sp. has a long non-paired testis. So, by the example of genus *Benthimermis* we can prove that unpaired testis is the result of the junction of two testes.

Caudal glands are not known in adult specimens. However, the terminal canal is found in the tail of the early larva (Chesunov 1997), which may be interpreted as a duct of vestigial caudal glands. Evidently, the caudal glands are reduced during the growth of the larva.

Generally, plesiomorph features of *Benthimermis* species are setiform cephalic sensilla, a presence

of excretory system, a trophosome with radially oriented cells and an internal lumen, reflected ovaries, paired testes directed anterior and parallel-connected.

The male of *B. petterae* n. sp. resembles little the females of the same species. However, they were found in the same sample, have comparable body lengths and tail shapes. Therefore they probably belong to the same species. Generally, until recently, both sexes had been only known for *B. australis* in the genus *Benthimermis*. In the remaining species, only either males or females had been described. Evidently, the considerable sexual dimorphism occurs for many species of this genus. The benthimermithids are rare deep-sea nematodes, and it is a very seldom case when females and males are found in the same sample. That is why the females and the males of the same species are identified as different species. For example, in *B. australis*, for which females and males were described, the male is thinner, and its amphids are situated at the closer distance from the anterior end than in females.

Apparently, in connection with the great diversity of reproductive systems of *Benthimermis* species, the division into several new genera should be realized. On the other hand, the future synonymization of many species described on only males or females is probable.

Hosts of majority *Benthimermis* species are unknown (only for three species). The most part of known benthimermithids are free-living adult specimens or parasitic larvae, which cannot be identified. Larval stages were found in the body cavity of marine free-living nematodes, polychaetes, priapulids, various crustaceans, and holothuroids. Small larvae were also discovered in the gonads of the holothuroids. Late parasitic stages can occupy all body of their hosts and, evidently, can result in the host death.

Apparently, late parasitising stages feed through their cuticle, as they have neither mouth opening, nor muscular pharynx with internal lumen, nor midgut of the ordinary structure. Adult free-living specimens do not feed and use the reserve nutrients accumulated during the parasitising larval stage.

Nematodes of genus *Benthimermis* are known at a depth from 31 to 5880 m from the Atlantic and

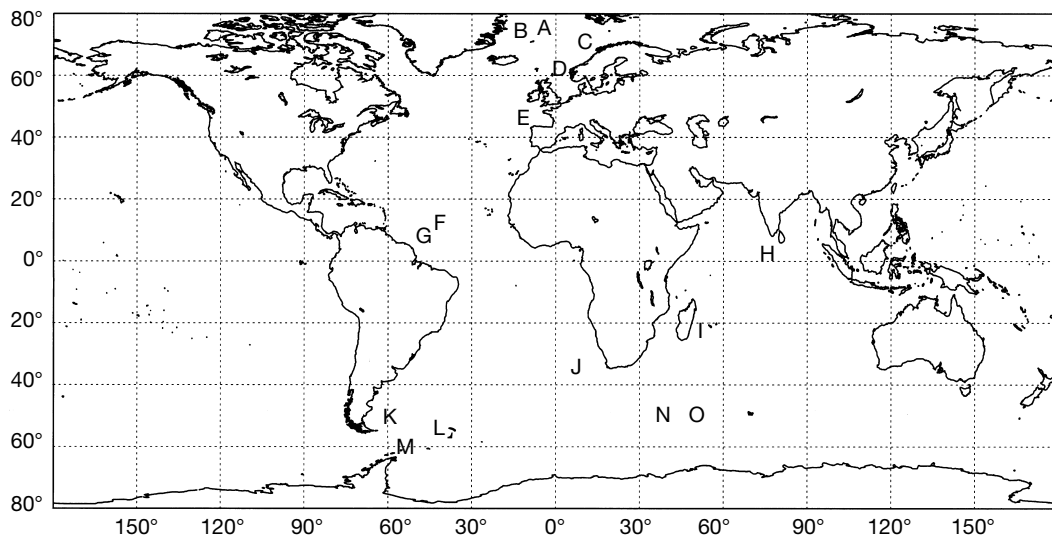


FIG. 16. — Known locations of *Benthimermis* Petter, 1980 species; **A**, *B. laubieri* ♀ and *B. leptosoma* ♂; **B**, *B. acuticauda* ♂, *B. filiformis* ♀, *B. gracilis* ♂ and *B. megala* ♀; **C**, *B. conicauda* ♀, *B. diploptera* ♂, *B. filiformis* ♀, *B. minuta* ♀ and *B. rotundicauda* ♂; **D**, *B. conicauda* ♀, *B. filiformis* ♀, *B. laubieri* ♀ and *B. megala* ♀; **E**, *B. hopei* ♀ and *B. leptosoma* ♂; **F**, *B. acuticauda* ♂ and *B. minuta* ♂; **G**, *B. arnaudi* ♀, *B. edouardensis* ♀, *B. filiformis* ♀, *B. hureaui* ♀, *B. improvisa* n. sp. ♂, *B. marionensis* ♀, *B. petterae* n. sp. ♂ and ♀, *B. platyptera* n. sp. ♂, *B. pseudominuta* n. sp. ♀ and *B. turpicauda* n. sp. ♀; **H**, *B. bathycola* ♀; **I**, *B. filiformis* ♀, *B. hureaui* ♀, *B. marionensis* ♀ and *B. turpicauda* n. sp. ♀; **J**, *B. aptera* ♂, *B. breviptera* ♂, *B. filiformis* ♀ and *B. minuta* ♀; **K**, *B. arnaudi* ♀; **L**, *B. australis* ♀, *B. marionensis* ♀ and *B. rosaliae* ♂; **M**, *B. australis* ♀; **N**, *B. australis* ♂ and ♀, *B. edouardensis* ♀ and *B. marionensis* ♀; **O**, *B. arnaudi* ♀, *B. crosetensis* ♂ and *B. hureaui* ♀.

the Indian oceans (Fig. 16). Most of the species were found at a depth from 2000 to 4000 m.

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REFERENCES

- CHESUNOV A. V. 1988. — A case of nematode parasitism in nematodes. A new find and redescription of a rare species *Benthimermis australis* Petter, 1983 (Nematoda: Marimermithida: Benthimermithidae) in South Atlantic. *Helminthologia* 25: 115-128.
- CHESUNOV A. V. 1997. — Marimermithids (Nematoda): anatomy, taxonomy, and phylogeny. *Russian Journal of Zoology* 1 (4): 440-455.
- FOOR W. E. 1983. — Nematoda, in ADIYODI K. G. & ADIYODI R. G. (eds), *Reproductive Biology of Invertebrates*. Vol. 1: *Oogenesis, Oviposition, and Oosorption*. John Wiley & Sons Ltd, Chichester: 223-256.
- HOPE W. D. 1977. — Gutless nematodes of the deep-sea. *Mikrofauna des Meeresboden* 61: 307-308.
- HOPE W. D. & TCHESUNOV A. V. 1999. — *Smithsoninema inaequale* n. g. and n. sp. (Nematoda, Leptolaimidae) inhabiting the test of a foraminiferan. *Invertebrate Biology* 118 (2): 95-108.
- MILJUTIN D. M. & TCHESUNOV A. V. 2001. — On the histological anatomy of *Benthimermis megala* Petter, 1987, a giant nematode from the Norwegian deep-sea (Nematoda: Benthimermithidae). *Nematology* 3 (6): 491-502.
- PETTER A.-J. 1980. — Une nouvelle famille de nématodes parasites d'invertébrés marins, les Benthimermithidae. *Annales de Parasitologie humaine et comparée* 55 (2): 209-224.
- PETTER A.-J. 1981a. — Description des mâles d'une nouvelle espèce de nématode marin de la famille des Benthimermithidae. *Annales de Parasitologie humaine et comparée* 56 (3): 285-295.

- PETTER A.-J. 1981b. — Description des mâles de trois nouvelles espèces de nématodes de la famille des Benthimermithidae. *Bulletin du Muséum national d'Histoire naturelle* 4^e sér., 3, section A (2): 455-465.
- PETTER A.-J. 1982a. — *Benthimermis gracilis* n. sp., nouveau mâle de la famille des Benthimermithidae (Nematoda). *Bulletin du Muséum national d'Histoire naturelle* 4^e sér., 9, section A (1-2): 71-74.
- PETTER A.-J. 1982b. — Description de deux nouveaux mâles de la famille des Benthimermithidae (Nematoda) de l'Atlantique sud-oriental. *Bulletin du Muséum national d'Histoire naturelle* 4^e sér., 9, section A (3-4): 397-403.
- PETTER A.-J. 1983a. — Quelques nouvelles espèces du genre *Benthimermis* Petter, 1980 (Benthimermithidae: Nematoda) du Sud de l'océan Indien. *Systematic Parasitology* 5: 1-15.
- PETTER A.-J. 1983b. — Description d'un nouveau genre de Benthimermithidae (Nematoda) présentant des utérus munis de glandes annexes. *Annales de Parasitologie humaine et comparée* 58 (2): 177-184.
- PETTER A.-J. 1987. — Quelques nouvelles espèces de femelles du genre *Benthimermis* Petter, 1980 (Benthimermithidae: Nematoda) des grands fonds de la mer de Norvège. *Bulletin du Muséum national d'Histoire naturelle* 4^e sér., 9, section A (3): 565-578.
- RUBTZOV I. A. 1980. — [New marine parasitic nematode, *Abos bathycola*, from priapulids and a taxonomic position of the family Marimermithidae in the class Nematoda]. *Parazitologiya* 14: 177-181 (in Russian with English summary).
- SEINHORST J. W. 1959. — A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. *Nematologica* 4: 67-69.
- TCHESUNOV A. V. 1988. — [New finding of deep-sea nematodes of the family Benthimermithidae in the South Atlantic, with description of a new species]. *Vestnik Zoologii* 6: 12-22 (in Russian with English summary).
- TCHESUNOV A. V. 1995. — New data on the anatomy of marimermithid nematode *Marimermis maritima*, and a review of the system of Marimermithida. *Nematologica* 41 (3): 347.
- TCHESUNOV A. V. 1997. — On the histological anatomy of *Marimermis maritima* Rubtzov & Platonova, 1974 (Nematoda: Enoplia: Marimermithida), parasite of a sea urchin. *Fundamental and Applied Nematology* 20 (4): 349-356.
- TCHESUNOV A. V., MILJUTIN D. M. & EVSEEV A. V. 2000. — [Metazoan parasites of Protozoa]. *Priroda* 3: 6-12 (in Russian).

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