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Free-living marine nematodes from the Southern Bight of the North Sea. III. Species of the Monoposthiidae, Filipjev, 1934

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Abstract : The intraspecific variations of *Monoposthia mirabilis* Schulz, 1932 are examined. Different morphotypes are present in different habitats. The morphological variation is correlated with an environmental gradient, *i.e* the median grain size of the sand fraction. A new species of the Monoposthiidae, *Nudora gourbaultae* sp. nov., is described; it is characterized by the broadened first and second cuticular annule, the presence of 12 costae, two pre-anal cuticular modifications and the shape of the gubernaculum.

Résumé : Observation des variations intraspécifiques des *Monoposthia mirabilis* Schulz, 1932 ; existence de morphotypes différents selon le biotope. La variabilité morphologique est corrélée aux paramètres de l'environnement et plus précisement à la médiane de la fraction sableuse. Description de *Nudora gourbaultae* sp. n.; cette espèce est caractérisée par la taille des premiers anneaux corporels, la présence de douze côtes et de deux expansions cuticulaires préanales, ainsi que par la forme du gubernaculum.

INTRODUCTION

Recently, more attention has been paid to the intraspecific variability of marine nematodes, especially as a consequence of extensive ecological studies. Examination of many specimens of a single species from a restricted geographical area demonstrated a large intraspecific variability inside the genera *Neochromadora* and *Sabatieria* (Vincx, 1986).

Meiobenthos of the Southern Bight of the North Sea has been investigated on a large spatial scale from 1971 to 1976 (Govaere *et al.*, 1980). The Belgian near shore waters have been sampled regularly from 1976 onwards (Herman *et al.*, 1985). The Dutch Delta region was studied over two years ('84-'85) in 20 stations. In all these study areas, *Monoposthia mirabilis* Schulz, 1932 is common in the sandy stations, but usually not very dominant. The morphology of specimens from different sites has been compared. Although obvious differences were found between specimens from different localities, these cannot be considered as diagnostic at species level.

A new species of the Monoposthiidae, *Nudora gourbaultae* sp. nov., only lives in the coarser sands, together with *Monoposthia mirabilis*.

MATERIAL AND METHODS

The Southern Bight is divided in two study areas, respectively the Southern part with the Belgium coast and the Northern part with the Dutch Delta region. The description of the Southern part, sampling methods and general characteristics of the nematode assemblages are given in Herman *et al.* (1985).

In the Dutch Delta region, samples were taken with a box corer (0.07 m^2) or a Van Veen grab (0.2m^2) in 20 stations during three periods : autumn 1984, spring 1985 and autumn 1985. Subsamples (10 cm^2) were drawn to study the meiofauna. After fixation with warm (70 °C) 4% formaldehyde-sea-water solution, the nematodes were transferred into pure glycerine (cf. Seinhorst, 1959). All measurements (except ratio's) are in micrometers. Spicules (spic) and other curved structures are measured along the arc. Values in the formula indicate :

level of	nerve	pharynx	vulva	anus		
ceph. setae	ring		Μ	cloaca	total	
	corresponding body diameter					

a = bodylength divided by greatest body width, b = bodylength divided by pharyngeal length, c = bodylength divided by tail length, c' = tail length divided by anal body width, V = position of the vulva as percentage of total body length from the anterior, c.b.d. = corresponding body diameter, c.h.d. = corresponding head diameter.

The nematod material is deposited in the Nematode collection of the Instituut voor Dierkunde, Gent, Belgium.

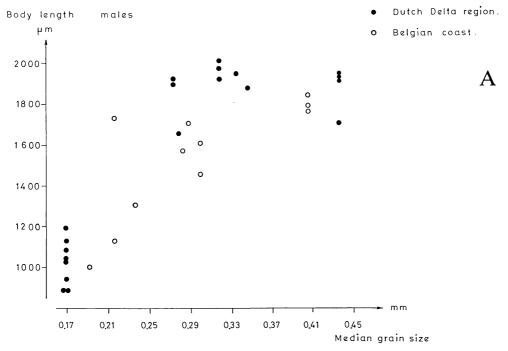
MONOPOSTHIA MIRABILIS Schulz, 1932 (Fig. 2-3, Plate 1)

The specimens of *M. mirabilis* from different localities in the Southern Bight of the North Sea differ in total body length, body width, head diameter, coarseness of the cuticular ornamentation and length of the gubernaculum. Even the juveniles can be distinguished by their habitus and the coarseness of the cuticular ornamentation.

In the Dutch Delta region, the specimens can be subdivided in two groups: the specimens belonging to the first group (Fig. 2 A-I, Plate 1 A-G) can be distinguished from the specimens of the second group (Fig. 3 A-G, Plate 1 H-N) by their smaller and more slender general habitus. The smaller form ($L\delta$ = 889-1189 µm; gub. = 21-23 µm) is present in stations characterized by a fine sandy substrate (0.160 mm < Median of the sand fraction < 0.200 mm) with 1.1 to 4.1 % silt, and more robust specimens ($L\delta$ = 1653-2005 µm; gub. = 30-36 µm) are found in eight stations, characterized by a medium sand sediment (0.237 mm < Median < 0.436 mm).

The hypothesis that two discrete habitat specific morphological groups exist was rejected because intermediate morphotypes of *Monoposthia mirabilis* were found in intermediate substrates from the Belgian coast. The morphological variation is continuous and seems to be correlated with an environmental gradient, which is best expressed by the median grain size, taking into account the sorting of the sediment and the amount of silt. For all the specimens studied of the Southern Bight (Dutch Delta region and Belgian coast), the body length is highly correlated with the median grain size of the sandfraction : for the males, r = 0.7909, n = 31 and for the females r = 0.8821, n = 26 (Fig. 1).

Up to now, *M. mirabilis* has been described from several localities. *Monoposthia mirabilis* was first described by Schulz (1932). He found one male with a body length of 1800 μ m and a gubernaculum length of 40 μ m. Allgen (1935) found 5 males and 2 females of *M. mirabilis*, described as *M. longiseta*, in a substrate consisting of sand and shells. Measurements are 1320 μ m for the male and 1150 μ m for the female. Allgen (1959) mentioned more specimens (14 $\delta \delta$ and 33 9 9) of *M. mirabilis*, still described as *M. longiseta*. Measurements are 1088 and 1275 μ m respectively. Gerlach (1953) found 2 small males, 887 and 1015 μ m long, in a sandy beach of Italy. The specimens (4 $\delta \delta$ and 3 9 9) described by Luc and De Coninck (1959) are bigger than the holotype (L δ = 2016 - 2660 μ m and L9 = 1450 - 2 143 μ m; gubernaculum = 40 μ m). The *M. mirabilis* male of the East coast of North America, described by Wieser and Hopper (1967) measures 1600 μ m. The gubernaculum is 38 μ m long.



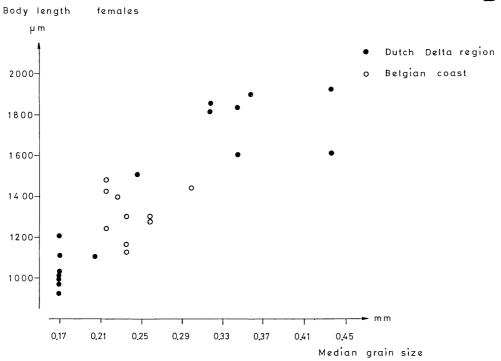


Fig. 1 - Correlation of body length with median grain size : A. Monoposthia mirabilis males, B. M. mirabilis females.

	MALES N = 31	FEMALES N = 26
	X (MIN - MAX)	X (MIN - MAX)
L l.tail w.max l.pharynx w.cardia l.bulb.post. l.bulb.ant. w.head.post. w.head.ant. l.ceph.set. w.cut.ring. w.vulva gub. a b	1 494 (889 - 2005) 109 (70 - 166) 32 (23 - 47) 175 (74 - 234) 30 (22 - 39) 41 (31 - 55) 21 (19 - 36) 17 (14 - 22) 13 (10 - 16) 15 (13 - 19) 2.5 (1.8 - 3.5) 33 (21 - 36) 38.2 (32.3 - 45.1) 7.2 (5.7 - 8.3)	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
c	13.7 (10.9 - 15.4)	13.6 (10.9- 16.2)

TABLE 1 - Measurements of Monoposthia mirabilis (in µm).

L = length; w = width; max = maximum; bulb = bulbus; cut = cuticula; ceph = cephalic; set. = setae; gub = gubernaculum; ant = anterior; post = posterior.

Β

REDESCRIPTION

Extreme size range of the discriminative morphological characters are given special attention. Measurements are presented in table 1.

Males

Body cylindrical, slightly narrowing anteriad from the cardia and more so posteriad from just before the cloacal opening (Plate 1 C - L). The body is ventrally flattened over a distance of two anal body diameters in front of the attenuated caudal region when the tail is curved (Fig. 3 F). Tail conical.

Cuticle (Fig. 2 D - E, 3 E) coarsely annulated (3 and 4 annuli per 10 μ m resp.); the annulation starts at the level of the cephalic setae. Only the tip of the tail is not annulated. The first two body rings are enlarged and demarcate the head region (Fig. 2 B, 3 A). The second ring is higher (5 - 8 μ m) than the first one (3 - 5 μ m). V - shaped structures (costae) are present from head end to cloacal opening; they are arranged in 6 longitudinal rows (Fig. 2 H). In the pharyngeal region the annuli have an anteriorly directed margin; the costae are posteriorly directed. The direction of the annuli margins and the costae changes posteriorly from the pharyngeal region, between the 80th and the 90th bodyring (Fig. 2 E, 3 E). The longitudinal differentiation is also present on the two cephalic rings, although the costae are no longer recognizable. The annuli contain very small vacuoles. These are less obvious in the smaller specimens because of the smaller cuticular rings.

The six internal labial sensilla are papilliform. The six external labial sensilla (3 μ m) are setiform. Four cephalic setae (11 - 19 μ m, according to body size) are situated at the anterior border of the cephalic capsule. No subcephalic setae. Somatic setae are present over whole body. The amphideal fovea (12% of the c.h.d.) is circular and situated on the second head annule. The corpus gelatum is sometimes extruded (Fig. 3 A). Buccal cavity large and deep (21 & 28 μ m resp. for the small and the large form), strongly sclerotized and surrounded by pharyngeal muscles. A large solid dorsal tooth and two small ventrosublateral teeth are present. Additional very small denticles can be observed in the anterior part of the buccal cavity. The anterior part of the pharynx is very muscular and forms a stomatal bulb. The dorsal pharyngeal gland opens close to the dorsal tooth. The terminal pharyngeal bulb is very prominent and consists of two equal compartments. The lumen is strongly cuticularized, especially in the posterior bulb. No ventral gland and no excretory pore observed. Nerve ring at 60% of the pharynx. Cardia (Fig. 2 A) very small. Intestine with low wall cells and broad lumen.

Diorchic, with outstretched testes, both on the right side of the intestine. Sperm cells large $(2 \ \mu m \ \emptyset)$, oval structures. Spicules absent; gubernaculum stout, strongly sclerotized. Its proximal part is enlarged with an anteriorly and a posteriorly directed protrusion. Distal part anteriorly directed and hook-like (Fig. 2 F, 3 F - G). Body annuli, anterior to cloacal opening, modified in a cuticular plate with a posteriorly directed hook. Three preanal supplements are situated on this ventral

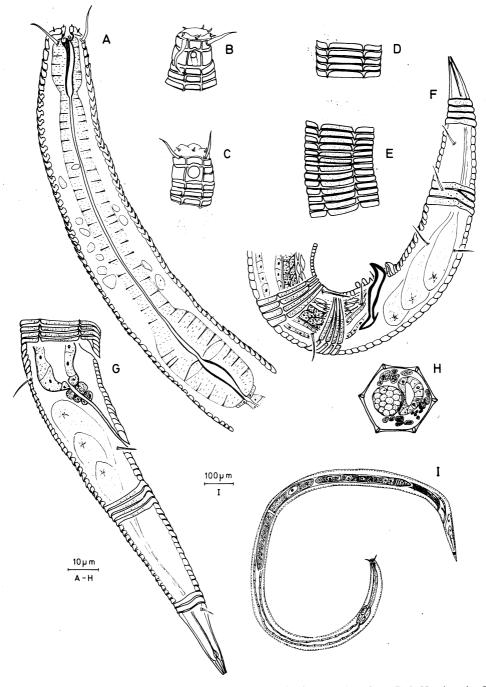


Fig. 2 - Monoposthia mirabilis: group I "small type". A.♂ Pharyngeal region; B.♂ Head end; C.♀ Head end; D. Cuticle in pharyngeal region; E. Cuticle in pharyngeal region, with change in orientation of V-markings; F.♂ Tail; G.♀ Vulvar region and Tail; H.♂ Cross section at mid-body; I.♀ Habitus.

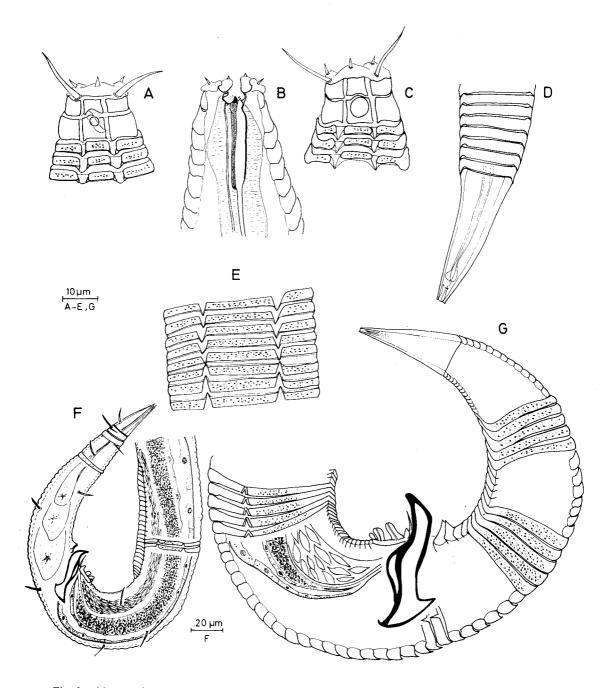


Fig. 3 - Monoposthia mirabilis: group II "large type". A.♂ Head end, surface view; B.♂ Head end; C.♀ Head end, median view; D.♂ Tail end; E.♂ Cuticle in pharyngeal region; F.♂ Posterior end; G.♂ Tail region.

plate. The two body annuli behind the cloacal opening are also modified and possess two ventrally directed projections. The anterior cloacal lip bears a stout seta. Tail with three caudal glands; spinneret 5 - 7 μ m long.

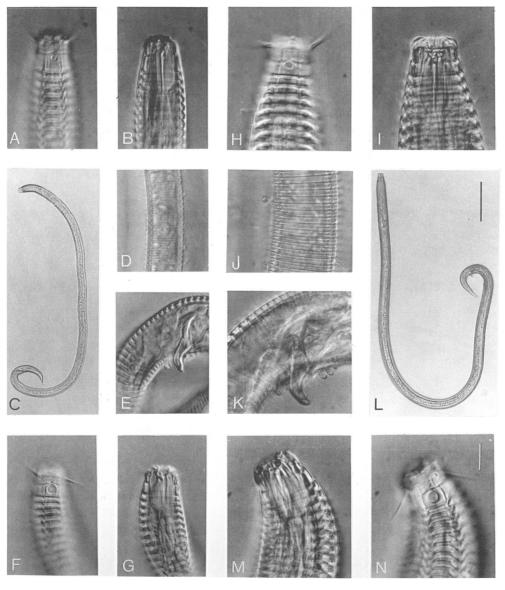


PLATE 1 - Monoposthia mirabilis A - G: "small type"; H-N: "large type".
A, H. δ Head end, surface view; B, I. δ Head end; C, L. δ Habitus; D, J. Mid region, surface view; E, K. δ Copulatory apparatus; F, N. ♀ Head end, surface view; G, M. ♀ Head end.
(Scale bar is 10 µm, except in C & L, where it is 200 µm).

Females

Only differences with the male are mentioned : somatic setae less numerous than in the male. Amphideal fovea (Fig. 2 C, 3 C) circular, larger than in the male (27% of the c.h.d.). Monodelphic and prodelphic with reflexed ovary situated at the left side of the intestine (Fig 2 I).

TAXONOMIC AND ECOLOGICAL SIGNIFICANCE

Vincx (1986) discussed the intraspecific variation of some nematode species from the Southern Bight of the North Sea; *Neochromadora paramunita* Boucher, 1976 was synonymized with *N. munita* Lorenzen, 1972 because the two morphotypes of males, with as main difference the number of preanal supplements, can be found in the same population. The females and juveniles cannot be subdivided in two types since transition forms occur. Most of the species of the *Sabatieria pulchra*-group (Platt, 1985) are considered as different ecophenotypes because they show only minor differences and because they are found in the same geographic range, although in different habitats. For *Paracyatholaimus occultus* Gerlach, 1956 differences in the cuticular ornamentation are mentioned by Riemann (1966) and Lorenzen (1972). Different morphotypes apparently occur, but transition forms also exist.

All the stations of the Southern Bight, where specimens of *M. mirabilis* are present, are characterized by a well-sorted sandy substrate with a maximum of 7%silt. Well-sorted sandy substrates (with Md > 0.125 mm) are inhabited by a true interstitial fauna, which lives in the pores. The fauna of silt and poorly-sorted silty sand is characterized by more burrowing species (McIntyre & Murison, 1973; Wieser, 1959). In well-sorted sediments the mean diameter of the interstices is approximately 30 to 40% of the mean particle diameter. Pore space is correlated with particle size. Only a silt/clay content of 7% or more should be sufficient to fill the interstices between the larger particles (Crisp & Williams, 1971). In the samples studied, the smaller morphotypes of *M. mirabilis* are present in substrates with a smaller median grain size *i.e.* smaller interstices.

The morphological variation among sites is probably due to the effects of the microenvironment on a plastic phenotype. Phenotypic plasticity in invertebrates is well known and frequently a source of taxonomic confusion (Bynum, 1980). In a study on the physical environment of interstitial organisms, and their response to it, Crenshaw, 1980 (mentioned by Vogel, 1983) emphasizes that the most important parameter for an animal, living in interstitial spaces, is shear stress. When selecting a site, an organism probably picks the right shear stress rather than some grain size.

In a coarser silt-free substrate, interstitial living nematodes can be washed out of the sediment more easily. Ward (1973) noticed that those families and genera provided with a heavily sculptured cuticle (e.g. *Monoposthia* spp.) were almost invariably associated with the coarser silt-free sediments. He proposed that the elaborate cuticular ornamentation found in *Monoposthia* may serve a dual purpose: as a protection against mechanical damage and to provide a purchase during progression through the larger interstices of coarse sediments. The presumed advantage to the animals of a more robust body is that a robust animal is stronger than a gracile animal and has a coarser cuticle which serves as a better protection against the washing out of the sediment.

NUDORA GOURBAULTAE SP. NOV. (Fig. 4, Plate 2)

MATERIAL STUDIED

Five males, five females, three juveniles.

TYPE LOCALITY

Southern Bight of the North Sea; station M14; coordinates: 51° 50' 50" N - 02° 52' 00" E; medium sand with 3 % gravel; depth 35 m. Sampled 12^{th} July 1972.

MEASUREMENTS

	-	85	212	Μ	1763
Holotype 31:					1930 (slide n° 959)
	18	37	40	42	36
		a =	45.9, b	= 9	9.1, $c = 11.7$, $c' = 4.6$, spic = 31 μ m.

Paratype

♀ 1 (allotype) :

-	110	224	1657		1820 (slide n° 960)
18	40	42	40	42	1020 (shue h 900)
	а	= 43.4,	b = 8.1	, c = 1	6.7, c' = 2.5, V = 90.8 %.

Other paratypes :

		Males $(n=4)$	Females $(n=4)$
L	:	1800-1900	1420-1810
а	:	37.9-39.3	26.9-43.7
b	:	8.7-9.5	7.3-8.5
с	:	10.6-12.0	10.8-17.5
c'	:	4.2-5.3	2.5-3.6
spic,	/V :	30-32	87-91

DESCRIPTION

Males

Body cylindrical with attenuated head end and cylindro-conical tail (Fig. 4 A).

Cuticle coarsely annulated; upper parts of the annuli are separated from each other by deeper part which have, under the light microscope, a darker colour. The annuli have the same width throughout the body length (*i.e.* 3 annuli per 10 μ m).

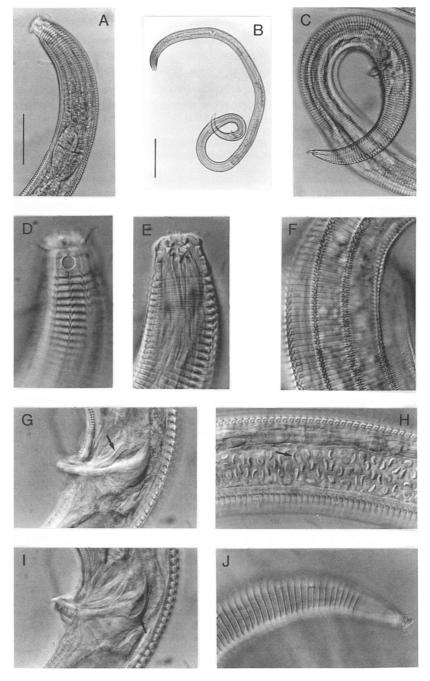


PLATE 2 - Nudora gourbaultae (\$1). A. Pharyngeal region; B. Total view; C. Tail region; D. Head end; E. Buccal cavity; F. Cuticular ornamentation; G. Left spicule (arrow indicates spi-cule); H. Sperm cells (arrow); I. Gubernaculum (arrow); J. Cuticular annules on the tail tip. (Scale bar in B is 200 μ m; scale bar is 50 μ m for A & C, and 20 μ m for D to J).

The first and second annuli are broader and form a kind of a cephalic capsule. Twelve longitudinal rows of V-markings (costae) are present; the tip of the "V" is directed posteriad in the pharyngeal region, but anteriad in the rest of the body. One dorsal, one ventral, two lateral and eight submedian rows of V-like markings are present. The longitudinal ornamentation is weakly developed on the two "cephalic" cuticular annuli (obscure in some specimens); the ornamentation stops halfway along the tail.

The lips are very well developed but not heavily cuticularized; they can be easily in- or extruded. The six internal labial papillae are very minute; the six external labial sensilla are setiform (3 μ m long) and are situated in the middle part of the lips. The four cephalic setae are 11 μ m long and are situated at the basis of the lipregion (the first cuticular annulus has sometimes a small "indentation" for the placement of cephalic setae). Somatic setae are scarce. The amphideal fovea is circular, 6 μ m diameter (28 % of the c.b.d.), and is situated on the second annulus (Fig. 4 B). The buccal cavity is well developed and heavily sclerotized; one big dorsal tooth, two smaller ventrosublateral teeth and a ventral row of denticles are present. Pharynx muscular with a prominent elongated terminal bulb which is divided into two parts; the pharyngeal tissue surrounds the buccal cavity completely and forms a pronounced swelling. Cardia 14 μ m long. Nerve ring at 40 % of the neck length. Ventral gland and pore not found.

Diorchic with both testes well developed; the anterior testis is situated at the right side of the intestine, the posterior one at the left side of the intestine. The distal parts of the testes are filled with oval sperm cells from which one border is highly refractive. An ejaculatory gland cell opens in the cloaca and is situated at the right side of the intestine. Spicules equally long (31 μ m) with a typical proximal bent. The gubernaculum is well developed and is longer (42 μ m) and stouted than the spicules (Fig. 4 C). Prominent protractor and retractor muscles are present on the gubernaculum whilst the musculature of the spicules (especially the protractors) are weakly developed (and sometimes obscure). Two preanal modifications are present, *i.e.* two rectangular cuticular structures that are probably in connection with underlying gland cells.

The tail is cylindro-conical with a non-annulated tail tip. Three caudal glands are well developed and end together in a small, round ampulla.

Females

Resemble males in most aspects.

In 1, the cephalic annuli split up in several scales due to the longitudinal rows which are continuous with the rows of "V"-like markings (Fig. 4 E). The amphideal fovea is situated on the lateral scale of the second annulus.

DIAGNOSIS

Nudora gourbaultae sp. nov. is characterized by the broadened first and second cuticular annuli; the circular amphideal fovea situated on the second annulus; 12

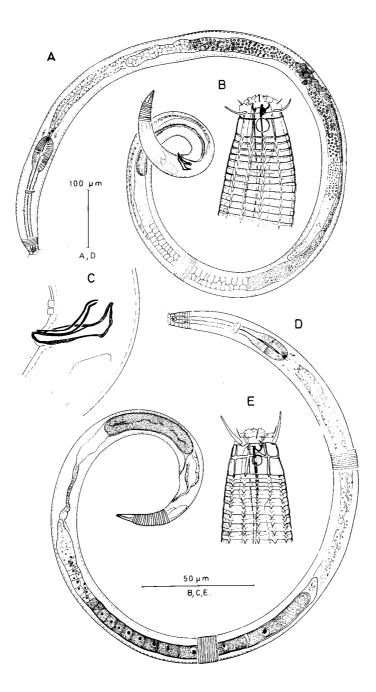


Fig. 4 - *Nudora gourbaultae* : A. \mathcal{S}_1 Total view ; B. \mathcal{S}_1 Head end ; C. \mathcal{S}_1 Copulatory apparatus ; D. \mathcal{Q}_1 Total view ; E. \mathcal{Q}_1 Head end.

longitudinal rows of V-like markings (costae) from the level of the cephalic setae to the middle of the tail; two preanal cuticular modifications in the male; shape of the gubernaculum.

DIFFERENTIAL DIAGNOSIS

Nudora gourbaultae sp. nov. is very close to *Nudora lineata* (Cobb, 1920); latter species however has "two obscure supplementary organs, of which the anterior one is located at a distance in front of the cloacal opening equal to one and one-half body diameters, the posterior one being opposite to the middle of the spicule". *Nudora lineata* is further characterized by the presence of ten costae.

Nudora bipapillata Platt, 1973 is also very close to the new species because of the presence of the two preanal supplements. A marked difference is however that the first two cuticular annuli are not broader in Nudora bipapillata (no real head present).

DISCUSSION

Up to now, 11 species are described in the genus Nudora Cobb, 1920; in only four species (*i.e. N. bipapillata* Platt, 1973, *N. campbelli* (Schulz, 1935), *N. crepidata* Wieser, 1954 & *N. steineri* (Steiner, 1921)) are the anterior cuticular annuli not broader than the other annuli. In the other species of the genus (*i.e. N. armillata* Wieser, 1959, *N. besnardi* (Gerlach, 1956), *N. ilhabelae* (Gerlach, 1957), *N. lineata* Cobb, 1920, *N. nuda* Inglis, 1968, *N. omercooperi* Inglis, 1968 & *N. thorakista* (Schulz, 1935), is a kind of cephalic capsule developed because the first (1 & 2) cuticular annuli are broader than the others. This is also the case in *Nudora gourbaultae* sp. nov. The number of costae varies in the last group between 4 and 6 (*N. omercooperi*) to 18-20 (*N. armillata*).

The presence of a lateral row of costae (allowing the recognition of the juveniles and females) is an important character, that differentiates the new species from the related species *Monoposthia mirabilis* (which lives in the same sites as *Nudora gourbaultae* sp. nov.), but which lacks the lateral costae.

It is very probable that the gubernaculum has taken over at least partially the function of the spicule.

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