

**FIVE NEW SPECIES OF *URODASY*
AND REMARKS ON THE TERMINOLOGY
OF THE GENITAL ORGANS
IN MACRODASYIDAE (GASTROTRICHA)**

by

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Résumé

Description de cinq nouvelles espèces d'*Urodasy* et terminologie du système génital chez les Macrodasysidae (Gastrotricha).

Cinq nouvelles espèces (et deux autres de position incertaine) sont décrites des côtes de Floride, de Caroline du Nord, des Bermudes et de la Méditerranée. Les nouvelles espèces diffèrent des espèces connues par la possession d'un stylet cuticulaire et d'un testicule impair. Des diagnoses ainsi qu'une clé systématique sont présentées. Une nouvelle interprétation du système génital est suggérée.

INTRODUCTION

In continuation of a series of publications (Schoepfer-Sterrer, 1969; Ruppert, 1970) dealing with new forms of marine Gastrotricha from North Atlantic coasts, the present paper concentrates on the genus *Urodasy*. Three species of this genus have been described so far: *U. mirabilis* (Remane, 1926) from the North Sea, the cosmopolitan *U. viviparus* (Wilke, 1954), known from the Mediterranean, the Caribbean (my own material) and the Indian Ocean (Gerlach, 1961), and *U. elongatus*, described by Renaud-Mornant (1969) from Tuamotu.

In spite of high similarity in general appearance, the three species differ markedly in their reproductive system. Whereas *U. elongatus* is known to have both ovaries and testes, *U. viviparus* is lacking male organs. *U. mirabilis*, long believed to lack female organs, was recently found to have ovaries (Teuchert, 1968; Schmidt & Teuchert, 1969).

The discovery of five new species of *Urodasy*, described in the following as *U. cornustylis*, *U. spirostylis*, *U. nodostylis*, *U. calicostylis* and *U. remostylis* further emphasizes the taxonomic importance of

the reproductive system in this genus. Besides the well developed male and female organs, those 5 species also share the possession of very significant cuticularized stylets. This feature, rather unusual in Gastrotricha (but see Boaden, 1965, *Platydasys styliferus* and Claparède, 1867, *Hemidasys agaso*) made it appropriate to reconsider the classical interpretation of the reproductive organs in the family Macro-dasyidae. A new interpretation is suggested on page 252. Wherever the classical terminology is used, it is put in inverted commas ("penis", "bursa"), whereas the new terminology is used without (Fig. 7 A, B).

Methods of extraction, preparation and description are those outlined in previous papers (Sterrer, 1968; Rieger & Sterrer, 1968; Riedl, 1969). This applies especially to the use of units to characterize the relative position of organs; it takes the length of the animal (excluding the tail) as 100 units (U 0-U 100), U 0 being the anterior tip of the animal. The type material is deposited at the Department of Living Invertebrates at the Museum of Natural History, New York.

As all the new species are very similar with regard to external and most internal features, a description of the general morphology will precede the more detailed individual species descriptions.

I wish to express my thanks to Professor Tor Karling (Museum of Natural History, Stockholm) and to my husband for valuable discussion and advice.

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GENERAL MORPHOLOGY

External features and behaviour

The body length of adults, excluding the tail, ranges from 300-650 μm and can vary, within the same species, by over 200 μm . The maximum width of the body is about 90 μm . The anterior end, about 40 μm wide, is blunt, and no head region is delimited. The ribbon-shaped body broadens gradually and reaches its maximum width at about U 65, then tapers again towards the posterior end. The slender (10 μm wide) tail is less than half or maximally twice as long as the body. Its length can vary considerably within one species, possibly due to mechanical damage. The general appearance of the transparent body is rather soft and fragile, the skin usually wrinkled (Figs. 1A, 2A, 3A, 4A; Pl. IA, IIA, IIIA).

Locomotion is extremely slow. The animal, attached with its tail end, cautiously stretches to full tail length, but retracts again when hitting an obstacle. When the way is clear the adhesive papillae of the tail end let go and the animal glides slowly, its tail dragging behind. The adhesive ability of especially the end of the tail is very high.

Ciliation and sensory organs

The ventral ciliation consists of long single cilia (10-15 μm) which completely cover the surface under the pharynx. Behind the end of the pharynx there are two lateral fields of cilia which end at the base of the tail. Dorsally, bundles of cilia occur on either side of the head and are connected by a narrow transverse row of cilia.

Tactile cilia of 20-40 μm length are concentrated laterally all around the body circumference and, more scarcely, scattered over the rest of the body surface, including the tail. The tips of most of these otherwise rather stiff cilia are sharply bent posteriorly. On the head sensory cilia are arranged in a mostly regular pattern, with 4 pairs on either side, one cilium being dorsal, the other ventral (Figs 2B, 3B, 4B).

Piston pits were lacking completely in three species. Their presence could be ascertained in *U. spirostylis* and *U. nodostylis* (Figs 2B, 3B). However, there is a possibility that in those species which do not show piston pits, they might be reduced below perceptibility with light microscopical techniques. This is underlined also by the fact that even within one species, piston pits could not be ascertained in all individuals.

Adhesive tubules

The number of tubules not only varies considerably within one species, but in some instances even differs on both sides of one specimen. Different stages of development may account for part of this observation, technical difficulties of analysis for another. It must be concluded, however, that the number and arrangement of tubules is rather variable. For better comparison, the tubules will be dealt with in groups along the regions of the body, i.e. head, pharynx, trunk and tail region. Their position on the body surface will be referred to separately (lateral, dorsal, ventral). The species descriptions contain a code based on maximal number of tubules, and assume these were identical on both sides of one individual. Due to the high variability of the taillength tubules of that region are not included in the code. Tubules on the head and tail region are generally half as long as the ones along the bodyside.

TABLE I

Maximum and minimum (in brackets) numbers of pairs of adhesive tubules and occurrence of piston pits in the Genus *Urodasyd*.

	<i>U. elongatus</i>	<i>U. mirabilis</i>	<i>U. spirostylis</i>	<i>U. nodostylis</i>	<i>U. cornustylis</i>	<i>U. calicostylis</i>	<i>U. viviparus</i>			
							Naples Maldives	Bermuda	Florida	Panama
head region	4	6	8 (6)	8 (6)	7 (3)	10 (7)	3	6	5 (4)	6 (4)
pharynx	10	0	4 (3)	7 (5)	6 (2)	3 (1)	2	4	4	4
trunk region	10	18	13 (4)	10 (5)	13 (5)	8 (7)	4	3	4	7 (4)
piston pits	—	—	+	+	+	—	+	+	+	+

Dorsal glands

Dorsolaterally a paired row of refractile, granular glands was present in all five species. The average number of glands is around 20, the maximum around 30 pairs. Their diameter varies from 5 to 10 μm .

Digestive tract

The terminal mouth opening is surrounded by a circle of about 16 cuticularized ridges connected by a membrane. They form a ring-shaped shield which covers both the interior (in the form of tiny cuticular plates) and exterior surface of the mouth opening (Figs 1C, 3B). Their function may be to protect the head, or to serve as reinforced insertions for the pharynx musculature. The pharyngeal pores are situated at about U 35. The ratio of pharynx length to body length (pharynx-body index) is about 0,3-0,4, and can reach 0,6 in *U. spirostylis*. The pharynx walls regularly contain a large number of refractile inclusions of about 1 μm diameter. The short intestine ends without an anus, taking up approximately one third of the trunk (U 40 to U 60). In a few specimens, a well developed lumen was present, frequently containing diatoms. The median part of the body behind the gut is filled with strongly vacuolized tissue in which part of the reproductive organs are embedded.

Protonephridia

A pair of protonephridia situated just anterior to the pharyngeal pores was observed in only one specimen of *U. spirostylis* (Fig. 2E).

As this feature is extremely delicate, however, it may very well have been overlooked in the other species.

Reproductive system

I. Female organs

The paired ovaries are situated dorsolaterally. The smallest oocytes are found at about U 75 and ripen rostrally. Single mature eggs of up to 70 μm diameter occupy almost the whole width of the body, overlapping the gut laterally. An organ, interpreted as a bursa copulatrix, was found in four species (the fifth is known in only one specimen) at U 70-80. Usually round or pear-shaped, it is made up of a thin membrane, and in some species provided with a cuticularized structure and openings (Fig. 6). In two species (*U. cornustylis*, *U. spirostylis*) these bursae regularly contained actively moving sperm. According to shape, appendage and openings, 3 types of bursae can be distinguished.

1) The simplest bursa (*U. calicostylis*, Fig. 4A) consists of only an elongated, constricted bladder. In none of the three specimens found, this bursa contained sperm.

2) A bursa with a narrow anterior portion containing a delicate

bursa mouthpiece, is characteristic of *U. cornustylis* (Fig. 1D, E). In addition, the bursa in this species seems to open to the ventral body surface.

3) In two further species (*U. spirostylis*, *U. nodostylis*) the bursa is provided with a cuticular appendix that can best be interpreted as a vagina mouthpiece. In *U. spirostylis* this mouthpiece connects the bursa with a distinct pore on the dorsal body surface (Fig. 2C, D; Pl. IIB, C, D). In *U. nodostylis*, a characteristic bursa was not found; however, all specimens contained a cuticularized canal (vagina mouthpiece) leading from a dorsal pore ventro-rostrally toward the mature egg (Fig. 3C, E).

II. Male organs

Contrary to the diagnosis of the previously described species of *Urodasys*, all the new forms had only one testis, situated on the left side of the body. In mature specimens, it extends from just behind the pharyngeal pores (U 35) to about the rostral end of the ovaries (U 50-60). It is usually filled with 2-4 bundles of tightly packed parallel sperm, a formation which is particularly conspicuous in *U. cornustylis* and *U. spirostylis* (Figs 1A, 2A). In none of the species *vasa deferentia* could be traced.

The sperm, in all species, is characterized by a spiralized part and, apart from *U. nodostylis* (Fig. 3D), an arrow-shaped head. Basically, the same type of sperm occurs in *U. remostylis* and *U. spirostylis* (Figs 3H; 2F) (where the head is separated from the spiralized part by a straight middlepiece) and in *U. cornu-* and *calico-**stylis* (Figs 1B; 4D) (where the head joins right to the spiralized part).

The male apparatus (Figs 1F; 2G-K; 3C, F, G ; 4C, E; Pl. IB-D; IIF, G; III C, E; IV A, C, D) typically consists of two elongated muscular bulbs (situated between about U 85 and U 95) of which the left one contains glandular material (gland bulb), the right one a cuticular stylet (stylet bulb). The two bulbs, almost parallel, consist of several layers of circular and longitudinal muscles. The lumina of the two bulbs communicate frontally through a delicate canal. Caudally, the stylet bulb opens into a rather spacious cavity near the ventral body surface (at U 95). Strangely enough, it seemed as if the posterior part of the glandular bulb would also open into the same cavity. In only a few specimens, a pore connecting the cavity to the ventral bodysurface could be distinguished with certainty. A pair of large glands, filled with refractile granula, extends frontally and laterally of the male apparatus. They open into the canal connecting the two bulbs but seem to discharge their secretion mainly into the lumen of the gland bulb.

In all of the five new species (as well as the two uncertain ones), the right muscular bulb contained a cuticularized stylet of 33-72 μm length (Fig. 5A-G). Its constant and specific shape provides an excellent character for species differentiation. All stylets resemble each other in that they consist of a proximal, funnel-shaped part and a narrower distal part which is either straight, curved or spiralized, and pointing medioventrally.

SPECIES DESCRIPTIONS***URODASYSS CORNUSTYUS* NOV. SPEC.**

Figs 1, 5C; Pl. I.

General data

Material: 14 adult specimens
 Holotype: AMNH 766
 Paratypes: AMNH 767

Type locality: Florida, one mile off Big Pine Key, water depth 3 m, fine coral-line sand from the vicinity of a small patch reef, collected December 29, 1968 (13 specimens).

Further locality: Beaufort, North Carolina, sample taken on "Eastward" cruise Station No. 10999, lat. 34°45'0 N, long. 75°45'0W, on November 25, 1968 with a Pierce box dredge, depth: 41 m, substratum: clean coarse sand with shell particles (1 specimen).

Species name: from Latin "cornu" - horn, referring to the shape of the stylet.

Body measurements:

Body length varies from 300-525 μm , tail length from 45-750 μm . Width of pharynx region 30-50 μm ; maximum body width at about U 65 up to 100 μm (if a ripe egg is present).

Adhesive tubules :

(a) Head region: up to 7 pairs of rather irregularly scattered tubules on the ventral body surface; (b) pharynx region: up to 6 pairs of tubules, of which one pair is situated ventrally, two are laterally and three are dorsally; (c) gut region: up to 13 pairs, of which 4 are situated ventrally, 3 laterally and 6 dorsally; (d) tail region: in 1 specimen with a 550 μm long tail, 21 tubules were encountered on one side of the tail, 18 on the other; a single terminal tubule may be present or missing.

Tubule code :

Head region 7 pairs; pharynx region 6 pairs; trunk region 13 pairs.

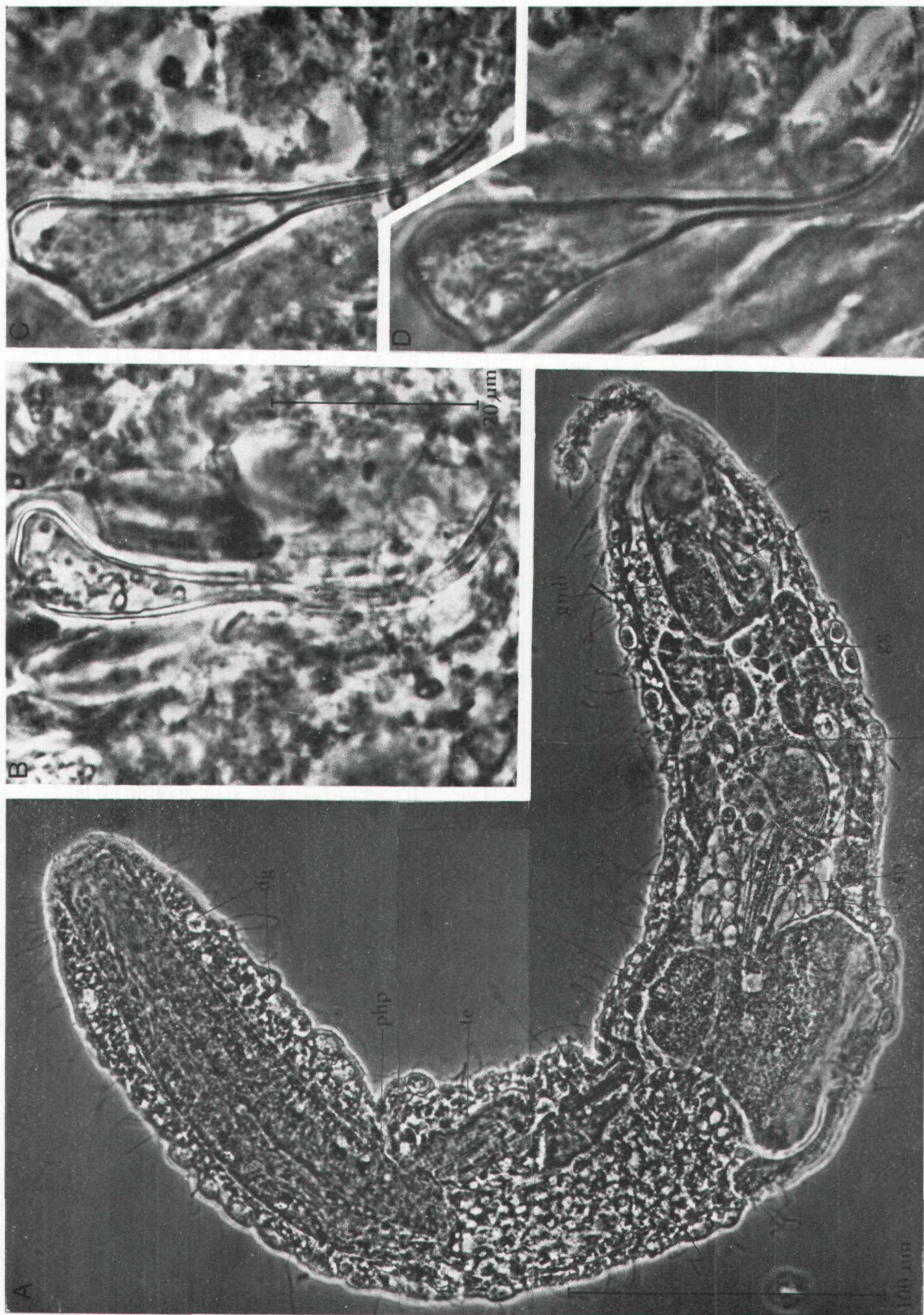
Piston pits:

In none of the 14 specimens.

Pharynx - body index: 0,3-0,4.

Female reproductive system.

The bursa (Fig. 1, D, E) situated dorsomedially at U 63-U 75, is usually pear-shaped and surrounded by a thin membrane. It measures 35-84 μm in length (average 70 μm), and 28-54 μm in width (average 40 μm). Its pointed rostral part approaches the dorsal body surface and may, in the case where a ripe median egg is present, protrude into it. The bursa of one specimen contained a structure that may represent a bursa mouth piece. It consisted of a cone-like

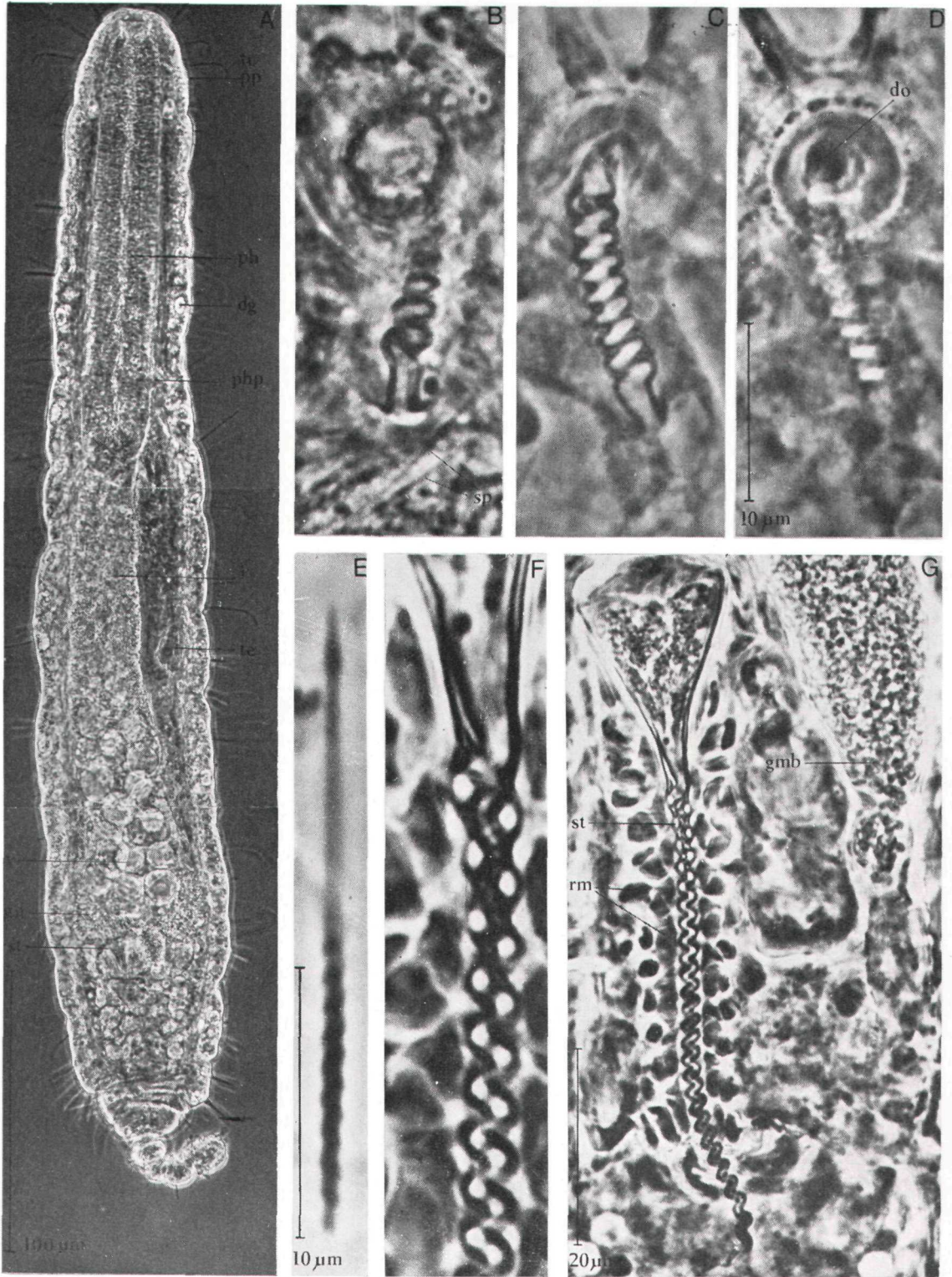


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PLATE I

Urodasya cornustylis nov. spec.

A : ventral view ; B - D : different types of stilet ; B : North Carolina specimen.
 (B, C, D in the same scale.)



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PLATE II

Urodasys spirostylis nov. spec.

A : ventral view; B-D : vagina mouth piece, in ventral (B) ; median (C) and dorsal (D) focus; E : sperm ; F : stylet, transition from funnel-shaped part to spiralized part ; G : stylet apparatus.

(B - D and E, F in the same scale.)

Abbreviations p. 254.

cap over the rostral end of the bursa, with a series of faintly cuticularized rings surrounding a narrow, 3 μm long canal on its anterior end. During squeeze preparation of this specimen, sperm actually penetrated into the cone-like bursa cap and finally ended up with their heads sticking in the mouth piece. In 9 of the 14 specimens observed the bursa contained sperm. Whereas some of these sperm form a ball in the caudal part of the bursa, most of them are arranged

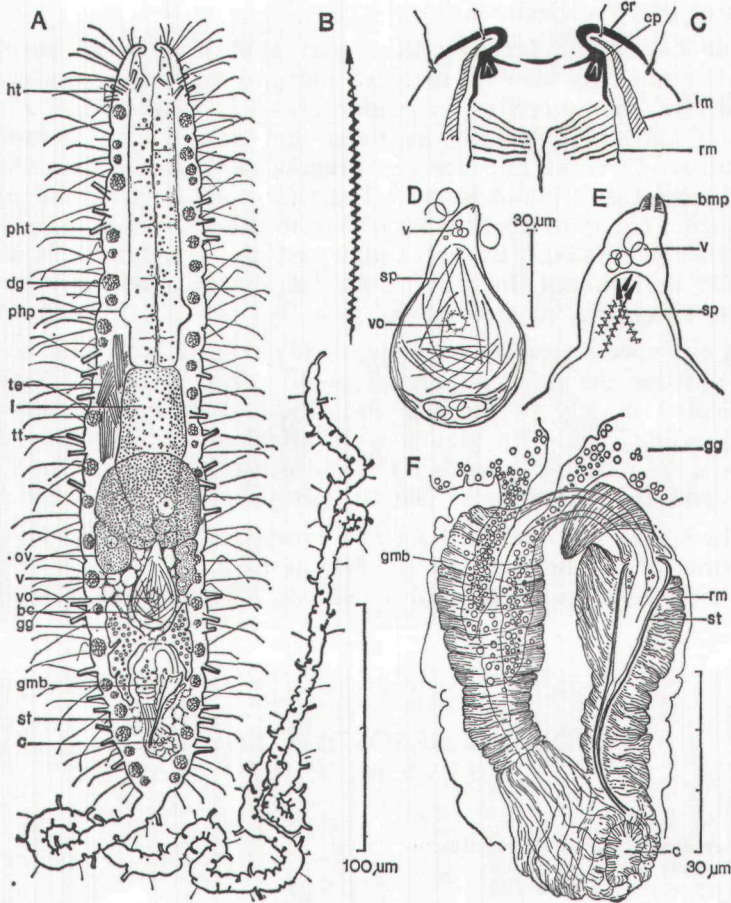


FIG. 1

Urodasys cornustylis nov. spec.

A : dorsal view ; B : sperm ; C : anterior end ; D : bursa copulatrix ;
E : bursa copulatrix, anterior portion enlarged ; F : stylet apparatus.
(B, C, E, F in same scale.)

so that their arrow-shaped heads point toward the rostral end of the bursa. The latter sperm usually perform a vigorous rotation around their longitudinal axis. In one specimen the empty bursa was situated much closer to the stylet apparatus than usual. The bursa, in this specimen, definitely opened to the ventral body surface through a round pore, thus confirming an uncertain observation made on several other specimens.

Male reproductive system.

The stylet (Figs 1F, 5C; Pl. IB-D) is 43-50 μm long and consists of a funnel-shaped proximal part (19-22 μm long and 7-9 μm wide) and a tube-shaped distal part. The funnel is asymmetrical insofar as its wide opening is in an oblique angle to the stylet axis. The distal part is curved, the end pointing toward the right bodyside. In the North Carolina specimen (Pl. IB), the proximal part of the stylet was slightly smaller and the distal part 2 μm wider than the stylets of Florida specimens.

The two bulbs forming the stylet apparatus in *U. cornustylis* are surrounded by an extremely strong and distinctive musculature. Rostrally, a characteristic triangular muscle ascends from a ventral direction and then dorsally overlaps the canal which connects the two bulbs. Circular muscles are predominant in the proximal part of both stylet and gland bulbs. Together with longitudinal muscles they form a cavity at about U 95 which, in this species only, is densely and entirely ciliated. In its caudal part the stylet bulb is situated ventrally underneath the gland bulb. A ventral opening was visible in some specimens at about U 95.

In one specimen only, a single, empty muscle bulb was developed at the position the stylet apparatus would normally take. 55 μm long, it consisted mainly of circular muscles and opened distally at its slightly wider part. No glands were attached to this bulb, and the specimen also lacked a testis. On the other hand, it showed a ripe ovary, and the bursa contained 9 active sperms (Table 2A).

The sperm is 47-52 μm long and consists of a spiralized part and an arrow-shaped head which is 3-4 μm long. The spiralized part consists of 22-27 turns around a delicate straight axis (Fig. 1B).

URODASYS SPIROSTYLIS NOV. SPEC.

(Figs 2, 5E; Pl. II).

Material: 8 adult specimens
 Holotype: AMNH 762
 Paratypes: AMNH 763

Type locality: Florida, one mile off Big Pine Key, water depth 3 m, fine coral-line sand from the vicinity of a small patch reef, collected December 29, 1968.

Species name: refers to spiralized stylet.

Body measurements:

Body length varies from 450 to 530 μm , tail length from 65 μm to 290 μm , body width at pharynx region is 40-50 μm , maximal width at about U 65 is 80-90 μm .

Adhesive tubules:

(a) Head region: in 3 specimens a semicircular row of 6 ventral tubules on each side of the head, in 2 specimens 7 tubules on one side and 8 or 6 on the other; (b) pharynx region: 3 tubules on either

side (2 ventral, 1 lateral), or 3 or 4 on one side and 2 on the other; (c) trunk region: maximum 13 pairs of tubules (minimum 4). In a specimen with 8 pairs of tubules, 6 were ventral, 2 lateral. From U 85 to U 90 (stylet level) rather constantly a group of 4 tubules was encountered on either body side; (d) tail region: number of tubules depending on length of tail, with either a single terminal one or none.

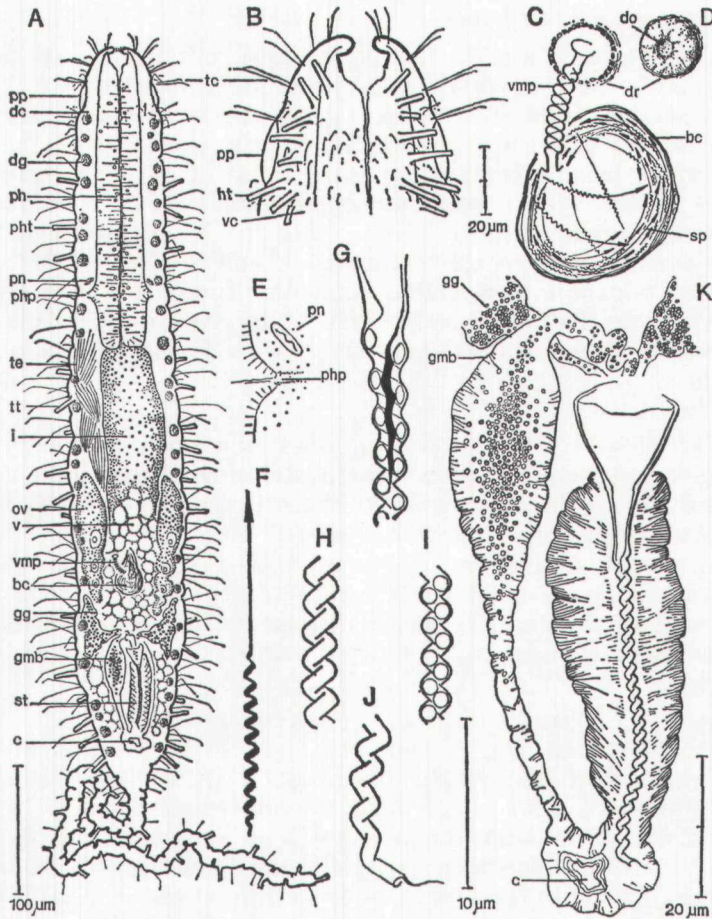


FIG. 2

Urodasys spirostylis nov. spec.

A : dorsal view ; B : anterior end ; C : bursa copulatrix ; D : dorsal rosette of vagina mouth piece ; E : protonephridium ; G - J : different views of the stylet ; K : stylet apparatus.

(E, C, D, K and G - J in the same scale.)

Tubule code:

Head region 8 pairs; pharynx region 4 pairs; trunk region 13 pairs.

Piston pits:

Very clear in one specimen. It was $23\ \mu\text{m}$ long, the groove was $10\ \mu\text{m}$ deep (Fig. 2B).

Protonephridia:

In one specimen, a beating ciliary flame of 6 μm length was situated just in front of the pharyngeal pori (Fig. 2E). In the other specimens protonephridia could not be distinguished.

Pharynx - body index: 0,4-0,6.

Female reproductive system.

The bursa is a bladder- to pear-shaped organ situated dorsally, approximately at U 65 to U 75, between the 2 ovaries (Fig. 2C). It is 30-49 μm long and about 24 μm wide. In most specimens it was filled with very active sperm. The bursa is connected with the dorsal body surface by a spiralized cuticular canal of 15-17 μm length and 2,5-3 μm width. This vagina mouthpiece consists of 6 to 11 turns. The straight proximal part, leading into the bladder, is 2-3 μm long and provided with a delicate "turned over" collar. The equally straight distal part widens into a shallow cuticular funnel of 5 μm diameter, which opens to the dorsal body surface. In one specimen this funnel was covered by a rosette-shaped body, with 5 delicate knoblike thickenings on its edge (Figs 2C, D; Pl. IIB-D).

Male reproductive system.

The stylet consists of a proximal funnel-shaped and a distal spiralized part. The funnel is 20-24 μm long, its rostral opening is 13 μm wide. Distally it proceeds into a most distinctive spiral (of 22-25 turns), 42-50 μm long and 2 μm wide. The first few turns of the spiral enclose a solid central core (representing a continuation of one wall of the funnel) which disappears in the following turns. The caudal end of the spiral is sharply pointed, its tip directed towards the right bodyside (Figs 2G, J, K; 5E; Pl. II F, G).

The stylet is surrounded by an approximately 10 μm thick muscular sheath which extends from the base of the funnel caudally to almost the end of the spiral. It consists of three layers of circular muscle fibres (Pl. IIG) which form a wide spiral around the stylet. In the distal part, longitudinal as well as muscles from the gland bulb form a rather spacious cavity (15 μm diameter) which, in some specimens, opened to the ventral body surface at about U 95. Different stages of stylet and bursa development could be encountered (Table IIB); in one specimen without testis but with ovaries, the vagina mouth piece was a delicate unspiralized membrane and the stylet apparatus was either developing or being reduced. The stylet funnel, in this specimen, was 18 μm , the spiral 35 μm long, with 13 turns. In another specimen, only a 5 μm long base of the stylet funnel was present, whereas the spiral was developed in its normal length.

The sperm, with an overall length of 19-21,5 μm , consists of three parts: an arrow-shaped head of 2 μm length, a straight middle piece of 10-11 μm , and a spiralized tail of 9-10,5 μm length and 10-11 turns (Fig. 2F; Pl. IIE).

URODASYS NODOSTYLIS NOV. SPEC.

(Figs 3A-F, 5A; Pl. III).

General data

Material: 11 adult specimens
Holotype: AMNH 764
Paratype: AMNH 765

Type locality: Bermuda, Three Hills Shoals, a big sand area between the reefs. Water depth: 15 m; substratum very fine, clean coralline sand.

Further locality: Bermuda, Harrington Sound, off Trunk Island. Water depth: 3-4 m; substratum: fine muddy sand with high detritus content. Samples from both localities collected with hand dredge, spring 1972.

Species name: from Latin "nodus" - knob, referring to the shape of the stylet.

Body measurements:

Body length varies from 390-650 μm , tail length from 90-810 μm (can thus be twice as long as the body), width of the head and pharynx region: 33-44 μm , maximal body width at about U 65: 50-90 μm .

Adhesive tubules:

Up to 12 μm long.

(a) Head region: maximum 8 pairs (minimum 6 pairs) of ventral tubules, which are mostly arranged in two semicircular rows on either side of the head; (b) pharynx region: up to 7 pairs; 4 dorsally, 3 ventrally; (c) trunk region: up to 10 pairs; 6 dorsally, 4 ventrally; (d) tail region: a 530 μm long tail had 17 tubules on one side and 15 on the other. In most specimens a single terminal tubule was encountered.

Tubule code:

Head region 8 pairs; pharynx region 7 pairs; trunk region 10 pairs.

Piston pits:

Very distinct in more than half of the specimens observed, with the piston being 15 μm long and the groove 3 μm deep.

Pharynx - body index: 0,4.

Female reproductive system.

In all specimens, an extremely delicate cuticularized structure was found dorsomedially at U 65-U 70 in the vacuolized part of the trunk. It consists of a 12 μm wide funnel situated under the dorsal body surface (or the ripe egg, Fig. 3C) and a distal canal, 8 μm long and 1 μm wide. The latter extends caudally and opens to the dorsal body surface in a distinct 5 μm wide, oval pore. The edge of the pore is irregularly crenated. None of the specimens was found to have a proper bursa; due to its dorsal pore, however, the funnel-shaped organ is interpreted as a vagina mouth piece.

Male reproductive system.

The stylet (Figs 3C, F; 5A; Pl. IIIC) is 40-47 μm long (one specimen had an exceptionally long stylet of 60 μm). It is characterized by

a 3-5 μm long and 7-9 μm wide knob-like proximal part (in one specimen 8 μm long, 11 μm wide) which is separated from the distal part by a narrow neck of 5 μm width. The distal part is a proximally 7 μm (9 μm) wide cone which then tapers to 2-3 μm . Terminally the stylet bends to the left at a 90° angle, forming an approximately 7 μm long shovel-like appendage. Another bifurcated appendage origi-

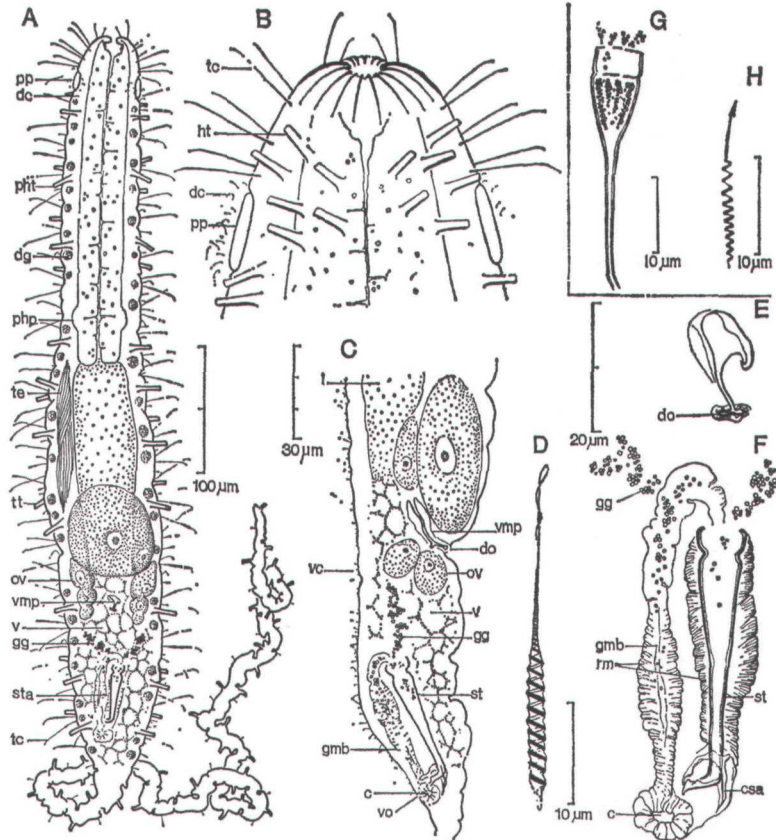


FIG. 3

Urodasys nodostylis nov. spec.

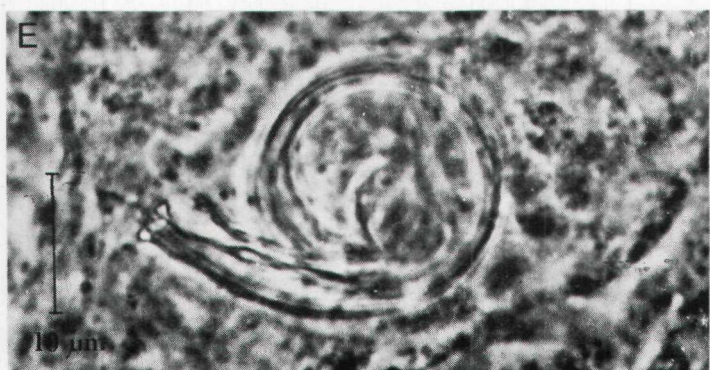
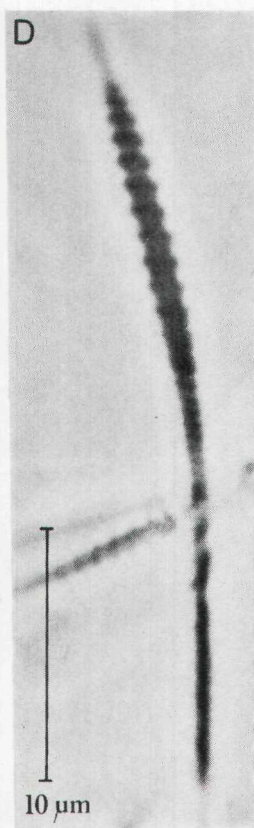
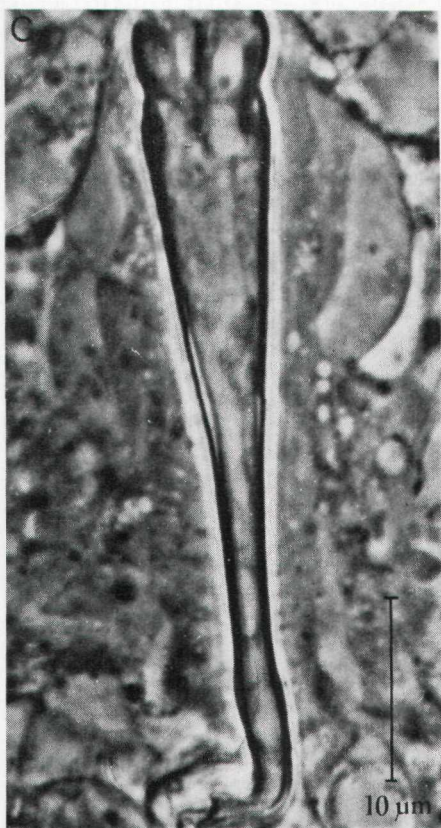
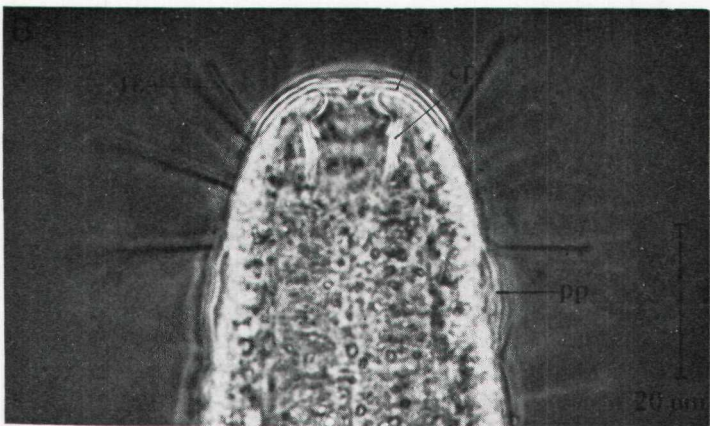
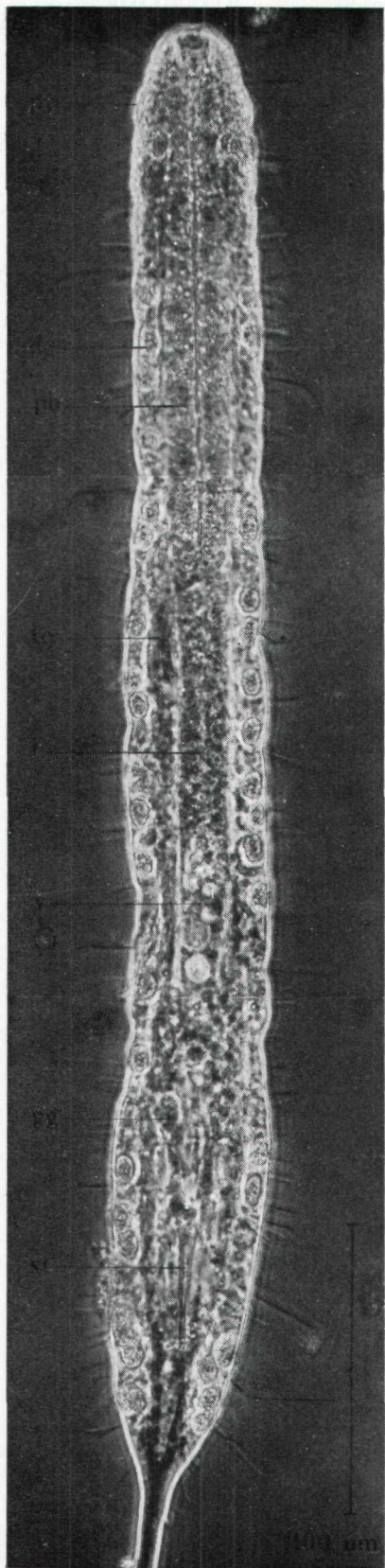
A : dorsal view ; B : anterior end ; C : lateral view of posterior end ; D : sperm ; E : vagina mouth piece ; F : stylet apparatus.

U. remostylis

A : stylet ; G : sperm.
(B, E, F in the same scale.)

nates ventrally on the distal part of the cone. Its left branch bends concavely towards the tip of the shovel and is provided with a tiny ridge, whereas its right branch, about 12 μm long, is slightly curved and points caudally.

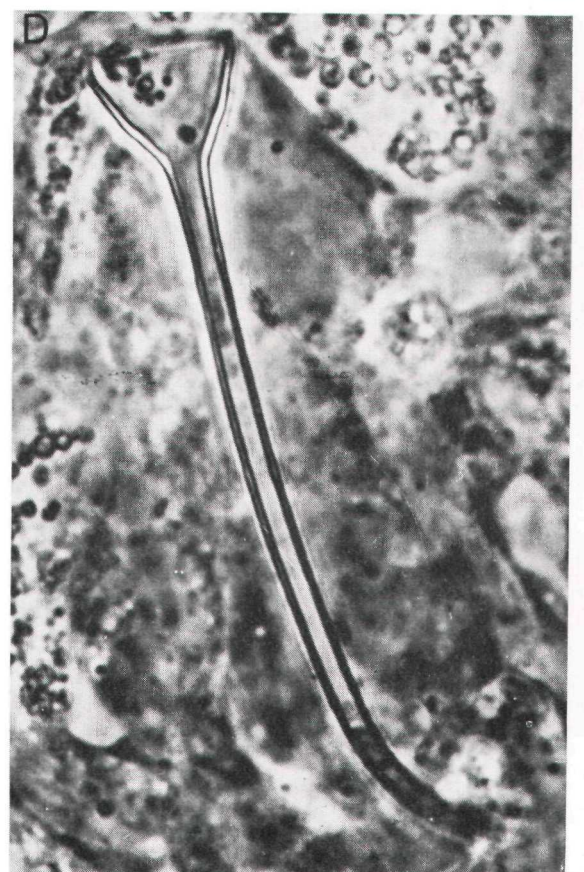
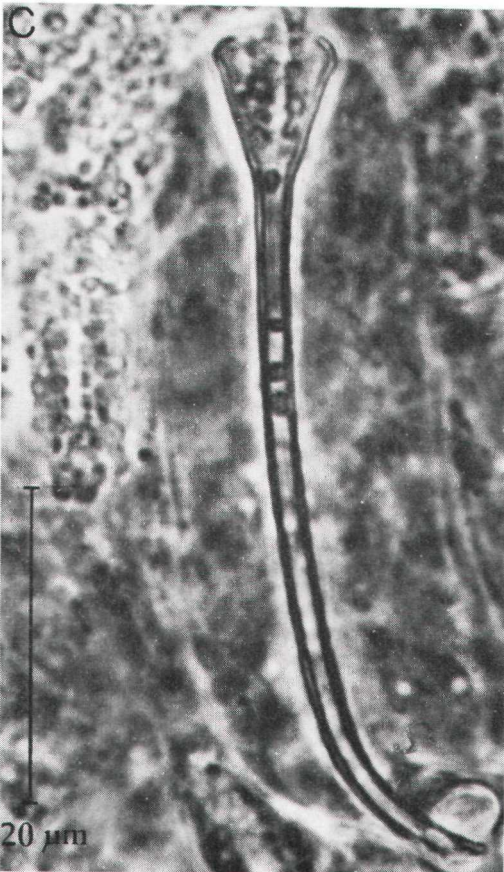
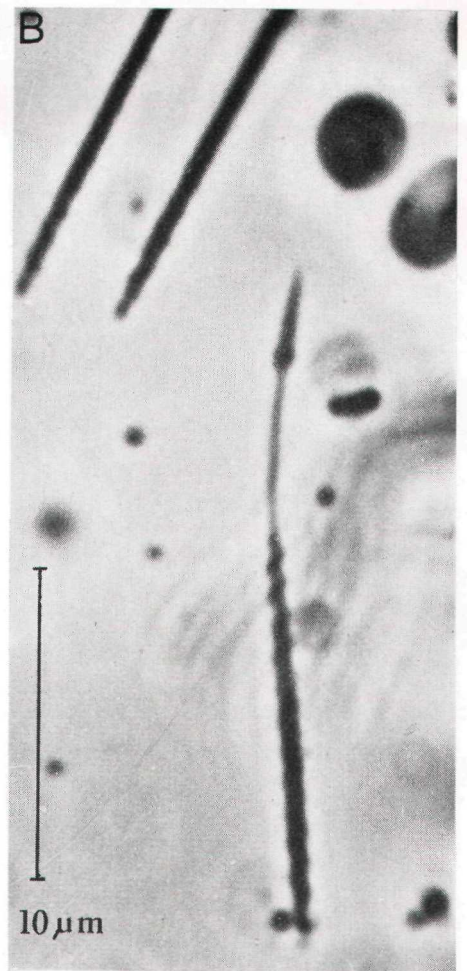
The muscle sheets surrounding the stylet and gland bulb are poorly developed in most specimens. The same is true for the paired



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PLATE III

A : *U. nodostylis*, dorsal view ; B : *U. nodostylis*, anterior end ; C : *U. nodostylis*, stylet ; D : *U. nodostylis*, sperm ; E : *U. sp. II*, stylet.



gland attached to the stylet apparatus; only few granula were found both in the glands themselves and in the gland bulb.

The sperm is up to 35 μm long, consisting of a spiralized and an unspiralized part (Fig. 3D; Pl. IIID). The first (15 μm long) part of the spiral shows up to 12 wide turns, followed by an 8 μm long densely spiralized part with approximately 14 turns. The tail end is twisted back on itself like a whip on its handle.

***URODASYS CALICOSTYLIS* NOV. SPEC.**

(Figs 4; 5D; Pl. IVC, D).

General data

Material: 3 adult specimens
Holotype: AMNH 760
Paratype: AMNH 761

Type locality: Beaufort, North Carolina, sample taken on "Eastward" cruise Station No. 11035, with Pierce Box Dredge, latitude 34°58,2 N, longitude 76°26,3 W. Water depth: 8 fathoms.

Species name: from Latin "calix" - cup, referring to the shape of the stylet.

Body measurements :

Body length 300-450 μm , tail length 150-550 μm , width of head and pharynx region 35-50 μm , maximal body width (at approximately U60) 55 μm .

Adhesive tubules :

(a) Head region: 6 μm long, minimum 5 ventral tubules on one side of the head, 7 on the other; maximum 10 tubules on one side, 9 on the other; arranged in a semicircular row; (b) pharynx region: 3 pairs; (c) trunk region: up to 8 tubules on one side, 6 on the other. Tubule length on pharynx and trunk region is 10 μm ; (d) tail region: 4 μm long; number depending on length of tail.

Tubule code:

Head region 10 pairs; pharynx region 3 pairs; trunk region 8 pairs.

Piston pits:

Absent.

Body - pharynx index: 0,3.

Female reproductive system.

At U 64-U 72 an elongated constricted bladder was found in all three specimens. Although it did not contain any spermatozoa, but

PLATE IV

A : *U. remostylis*, stylet ; B : *U. remostylis*, sperm ; C : *U. calicostylis*, stylet ; D : *U. calicostylis*, stylet.

(A - B and C-D in the same scale.)

granular and rather indistinct filiform material, its position and recurrence suggest a bursa. No openings to the body surface could be observed.

Male reproductive system.

The stylet (Figs 4C, E; 5D; Pl. IVC, D) measures 52-58 μm in length. Its proximal part has the shape of a shallow, 8-12 μm long and up to 6-9 μm wide cup, whereas the subsequent tube is 2 μm wide and on its distal end slightly bent towards the right side of the body. Differences in the proximal part consist in the walls of the cup being

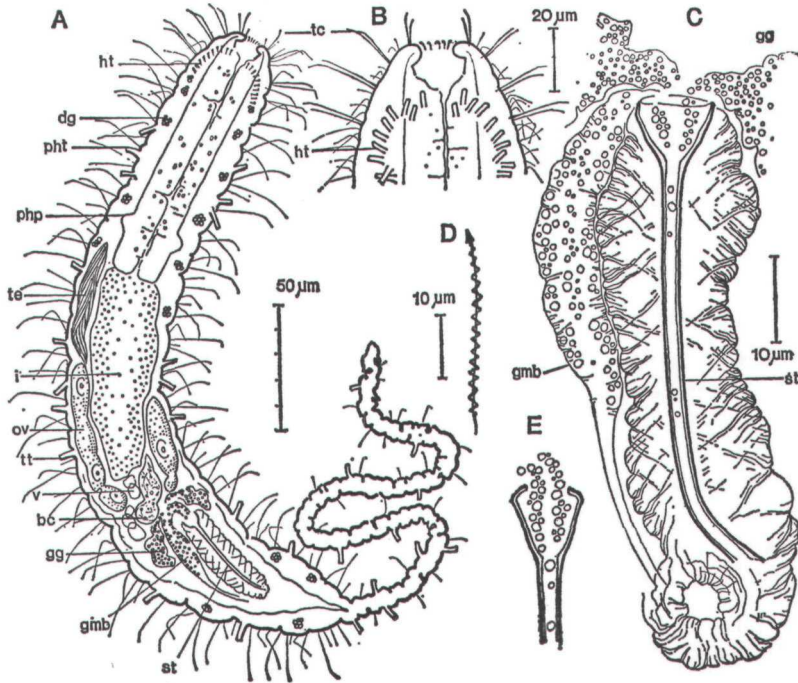


FIG. 4
Urodasya calicostylis nov. spec.

A : dorsal view ; B : anterior end ; C : stylet apparatus ; D : sperm ;
E : variation of the funnel-shaped stylet part.
(C, E in the same scale.)

more curved in two specimens, and rather straight in one specimen (Fig. 4E). A very distinct muscle sheath of 15 μm diameter, consisting of parallel fibres surrounds the stylet in a wide spiral. Distally, the fibres are arranged rather diffusely, forming a cavity into which both the stylet and the gland bulb seem to discharge. An opening to the body surface could not be verified.

The sperm (Fig. 4D) is 35 μm long. It consists of a 2 μm long arrow-shaped head, and a spiralized part made up of a straight axis and 15 turns of a membrane.

URODASYS REMOSTYLIS NOV. SPEC.
(Figs 3G, H; Pl. IV A, B).

General data

Material: one adult specimen.
Type locality: Florida, Lower Matecumbe Key. Water depth: 0,5 m, substratum: fine, muddy sand, collected December 1968.
Species name: from Latin "remus" - paddle, referring to the shape of the stylet.

Body measurements :

Body length: 350 μm , tail length: 243 μm , width of the head: 37 μm , maximal width (at about U 80): 52 μm .

Adhesive tubules:

Data are incomplete; 6 pairs of tubules in the head region were encountered, only 2 in the pharynx and 4 pairs in the trunk region. The actual number is probably higher.

Piston pits:

Absent.

Body - pharynx index: 0,3.

Female reproductive system.

Not developed in this specimen.

Male reproductive system.

The unpaired testis, situated on the left side of the animal and extending from U 43-U 57 consisted of two separated bundles of parallelly oriented sperm.

The stylet is 33 μm long, with a proximal funnel part 12 μm long and 7 μm wide. A shallow circular constriction, 3 μm behind the opening, divides the funnel into an anterior and posterior part, the latter containing 4 bundles of granular gland material. The distal tube-shaped part of the stylet is rather straight and only slightly bent to the left on its very end. It is a little longer than the proximal funnel-shaped stylet part (Fig. 3G; Pl. IV A).

The sperm is 16-18 μm and consists of a 3 μm long arrow-shaped head, a short straight middle part, and a spiralized part of 10-13 μm length (12 turns) (Fig. 3H; Pl. IV B).

INCERTAE SPECIES

Two further species of *Urodasys*, although characterized by rather distinctive stylets, are not sufficiently known to warrant a species description. For the sake of completeness of the data on this genus, however, a brief description is given in the following.

Species I (Fig. 5F) was found off Beaufort, North Carolina, in a **sample** taken on "Eastward" cruise Station No. 10999, latitude 34°45'0N, longitude 75°45'0 W, on november 25th, 1968 with a Pierce Box dredge. Water depth: 41 m.

Its body is 370 μm long, the tail 300 μm , the body shape is of the general *Urodasys* type. The stylet embedded in a thick muscular bulb is a narrow, roughly S-shaped tube (83 μm long, 2 μm wide). The slightly wider (5 μm) proximal part is accompanied partly by a delicate, 1 μm wide second tube. The distal half of the stylet is less curved than the proximal part and presumably leading to a ventral opening in the body surface.

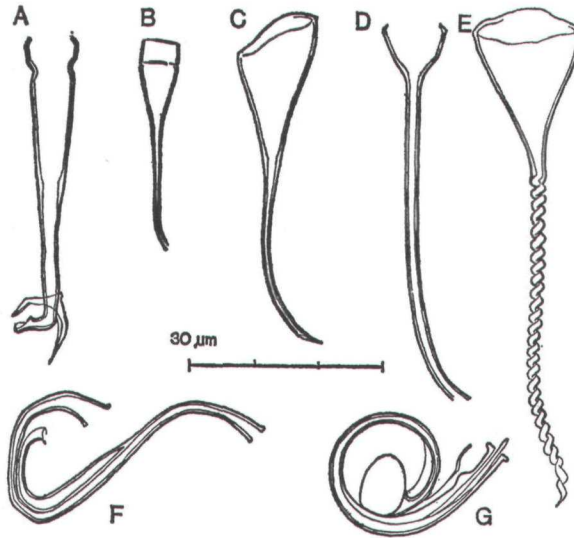


FIG. 5

Cuticular stylets of the genus *Urodasys*

A : *U. nodostylis* ; B : *U. remostylis* ; C : *U. cornustylis* ; D : *U. calicostylis* ; E : *U. spirostylis* ; F : *U. sp. I* ; G : *U. sp. II*.

Species II (Fig. 5G; PI. III E) was found at Banyuls-sur-Mer, France, October 1966, at "Le Racou" (South of the Biological Station). Water depth: 4 m. Substratum: fine sand with ripple marks.

Its body is 473 μm long, the tail 585 μm long, its body shape again corresponded to the general *Urodasys* type. The stylet, a rather complex structure, is roughly bugle-shaped, with the proximal part forming a circle and ending in a wide rostral opening (11 μm diameter). The actual length of the cuticularized stylet tube is 82 μm , its average width 4 μm . Ridges accompanying the proximal and distal stylet part were difficult to resolve in every detail.

DIAGNOSES

A) The genus *Urodasys* Remane 1926.

Macrodasyidæ with a tail less than half as long or up to twice as long as the body. Head undelimited and ending bluntly. Body and tail with a fair number of tubules. Pharyngeal pores situated close to the end of the pharynx. Without anus ; with paired ovaries ; testes paired, unpaired, or lacking.

Mostly protandric hermaphrodites ; some viviparous. Several species with cuticularized structures in reproductive system. Piston pits present or lacking.

B) The species of *Urodasys*: (The number of tubules is mentioned for completeness and easier comparison within the genus, but does not necessarily have species significance).

U. mirabilis Remane 1926: Long (up to 800µm) *Urodasys* with paired testes, left one bigger than right one. Ciliation covers entire ventral body surface. Piston pits absent. With 4-6 pairs of tubules in head region, none in pharynx, and up to 18 pairs in trunk region.

U. viviparus Wilke 1954: Viviparous *Urodasys*, up to 400 µm long, without testes. Head smaller than rest of body, with piston pits on transition to wider body part. Ovaries ripening caudally. Ventral ciliation complete under pharynx, and in a pair of strips under trunk. 3 (6 pairs) of tubules in head region, 2 (4) in pharynx and 4 (7) in trunk region.

U. elongatus Renaud-Mornant 1969: Small (up to 350 µm) *Urodasys* with paired testes. Piston pits absent. Ventral ciliation in a pair of strips under pharynx region. 4 pairs of tubules in head region, 10 in pharynx and 10 in trunk region. Tubules on tail are twice as long as on body.

U. cornnstylis nov. spec: Up to 525 µm long *Urodasys* with unpaired testis, ovaries ripening rostrally. Ventral ciliation complete under pharynx, and in a pair of strips under trunk. Male stylet (average length 47 µm) slightly curved, horn-shaped, with an oblique funnel-shaped proximal part merging continuously into a tube-shaped distal part. Without piston pits. Sperm consists of spiralized part and arrow-shaped head. Up to 7 pairs of tubules in head region, 6 in pharynx and 13 in trunk region.

U. remostylis nov. spec: Small (350 µm long) *Urodasys* with unpaired testis. Male stylet (33 µm long) paddle-shaped, with a deep proximal part and a distal tube-shaped part only slightly longer than proximal part. Without piston pits. Sperm consisting of a spiralized and unspiralized part and an arrow-shaped head.

U. calicostylis nov. spec: Small (up to 450 μm long) *Urodasys*, with unpaired testis; ovaries ripening rostrally. Ventral ciliation complete under pharynx, and in a pair of strips under trunk. Male stylet (average length 55 μm) with a cup-shaped proximal part and a tube-shaped distal part about 5 times as long as the proximal part. Without piston pits. Sperm consisting of a spiralized part and an arrow-shaped head. With up to 10 pairs of tubules in the head region, 3 in the pharynx and 8 in the trunk region.

U. nodostylis nov. spec.: Up to 650 μm long *Urodasys* with unpaired testis; ovaries ripening rostrally. Ventral ciliation complete under pharynx, and in a pair of strips under trunk. With a cuticularized funnel-like dorsal vagina mouthpiece. Male stylet (average length 45 μm) with a knob-like proximal part delimited from the equally wide distal part by a constriction. With piston pits. Sperm consisting of a wide and densely spiralized part and an unspiralized tail whose end is twisted backwards. With up to 8 pairs of tubules in the head region, 7 in the pharynx and 10 in the trunk region.

U. spirostylis nov. spec.: Up to 530 μm long *Urodasys* with unpaired testis; ovaries ripening rostrally. Ventral ciliation complete under pharynx, and in a pair of strips under trunk. Male stylet (average length 68 μm) consisting of a wide funnel-shaped part and a narrow spiralized tube (average 22 turns). With a spiralized dorsal vagina mouth piece (average 9 turns). With piston pits. Sperm consisting of a spiralized and unspiralized part, and an arrow-shaped head. With up to 6 pairs of tubules in head region, 4 in the pharynx and 13 in the trunk region.

key

1. No testes present. Ovaries ripening caudally. Head narrower than rest of body. Piston pits present. Viviparous. *U. viviparus* Wilke 1954
- Testes present 2
2. Testes paired, piston pits absent 3
- Testis unpaired, cuticularized structure in reproductive system present .. 4
3. With adhesive tubules along pharynx region. Tubules on tail twice as long as on body *U. elongatus* Renaud-Mornant 1969
- Without adhesive tubules on pharynx region. Left testis bigger than right one *U. mirabilis* Remane 1926
4. With a spiralized stylet in the posterior part of the body and a spiralized vagina mouth piece. Piston pits present *U. spirostylis* nov. spec.
- With an unspiralized stylet 5
5. With a cuticularized funnel-like curved vagina mouth piece. Stylet with knob-like proximal part delimited from the equally wide distal part by a constriction. Piston pits present *U. nodostylis* nov. spec.
- Usually without a cuticularized vagina mouth piece, male stylet of different shape. Piston pits absent 6
6. Funnel-shaped proximal part of stylet in form of a shallow cup and more or less delimited from tube-shaped distal part, which is about 5 times as long as proximal part *U. calicostylis* nov. spec.
- Funnel-shaped proximal part of stylet merging continuously into tube-shaped distal part 7
7. Proximal part of stylet a deep cup. Distal tube-shaped part rather straight and only slightly longer than proximal part *U. remostylis* nov. spec.
- Proximal part of stylet with oblique opening, distal part slightly curved *U. cornustylis* nov. spec.

DISCUSSION

External features figure prominently as diagnostic characters in previously described species of *Urodasys*. With every new geographic region explored, however (Ruppert, 1970, p. 121) we realize that the available data do not allow to distinguish between within—population variability and geographic variability. This applies to body size and proportions, and is especially true for the number and arrangement of tubules. Until more extensive statistical data are available, therefore, the number of tubules given in Table I should only be used as accessory species characteristics. This does not apply to the absence of tubules in the pharynx region reported for *U. mirabilis*, nor for *U. elongatus*, where the tubules are twice as long in the tail region as on the rest of the body.

In view of this lack of diagnostic reliability of external features, it is only fortunate that the new species possess cuticularized structures suitable for morphometric comparison. Within Gastrotricha a male stylet has been reported so far from two species of the family Thaumastodermatidae, namely *Hemidasys agaso* Claparède 1867 and *Platydasys styliferus* Boaden 1965. For *Macrodasys affinis*, Remane 1936 (Fig. 129b) describes a short cone-shaped cuticular tube ("Kutikularrohr") situated at the caudal end of the gland-muscle bulb ("Bursa"). With regard to position and structure, the gland-muscle bulb in *Macrodasys* may be considered homologous to the whole stylet apparatus in *Urodasys*. Whereas the posterior, muscular and cone-bearing portion of the bulb in *Macrodasys affinis* is directly comparable with the stylet-bulb of *Urodasys*, the gland-bulb in *Urodasys* might have developed by a complete retroflexion of the anterior glandular portion of this organ in *Macrodasys*. Such a situation seems to be anticipated in the curling of the glandular portion in *Macrodasys africanus* Remane 1950.

With regard to the low occurrence of penis stylets in Gastrotricha and the rather simple structure of the few existing ones, it seems logical to assume that, within the genus *Urodasys*, stylets have developed from a simple to a more complicated form, rather than being a series of reductions. Within the more or less straight stylets, a shape similar to that of *U. cornustylis* (including *U. remostylis* and *U. calicostylis*) could have led to the slightly more complicated, such as of *U. nodostylis* and the spiralized one of *U. spirostylis* on one side, and the curved stylets on the other. The latter comprise the uncertain species *U. sp.I* and *U. sp.II*. Apart from the fact that they are both curved, however, they do seem rather different as far as can be concluded from the sparse material available.

All the new stylet-bearing species are characterized by the possession of only the left testis. This clearly distinguishes them from *U. elongatus* Renaud-Mornant 1969 (paired testes), *U. mirabilis* Remane 1926 (paired but right testis smaller than left) and *U. viviparus* Wilke 1954 (no testes). In agreement with the assumption that the

paired symmetrical situation is more primitive than the unpaired assymetrical one, the evolution within the genus *Urodasys* could have proceeded as shown in Fig. 7C.

All we know of the female system is the presence of mature eggs in *U. elongatus* (probably paired ovaries, see Renaud-Mornant, 1969, p. 388) and in *U. mirabilis* (see Teuchert, 1968, and Schmidt & Teuchert, 1969, p. 10). *U. viviparus* is known to have paired ovaries, with eggs maturing caudally and joining in an uterus carrying the embryo (see Wilke, 1954). In contrast, the four new species of which the female system is known are all characterized by paired, dorsal ovaries, with the eggs maturing rostrally, often with one large ripe egg in front of the ovaries. The need to accommodate a large embryo

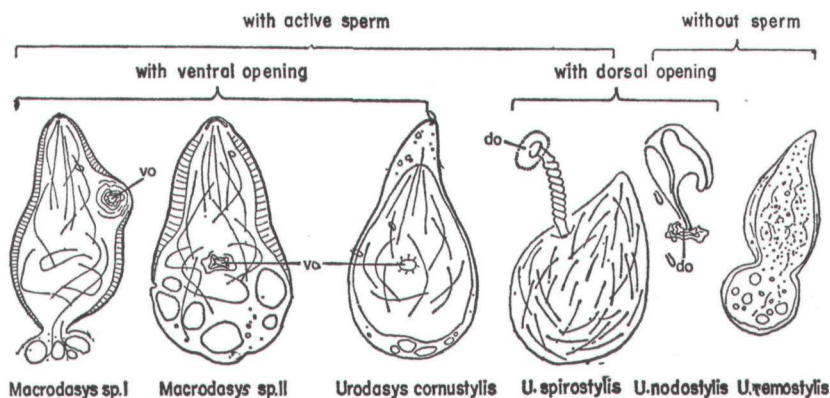


FIG. 6

Different types of bursa copulatrix within the genera *Macrodasys* and *Urodasys*.

in the uterus within restricted space may, in *U. viviparus*, account for this otherwise striking reversal of the ovaries.

High heterogeneity is also displayed by the bursa, especially with regard to its openings. A synopsis of bursal structures is given in Fig. 6. In both *U. spirostylis* and *U. nodostylis*, a dorsal opening is accompanied by a cuticular vagina mouth piece. Whereas this leads into a well developed bursa in the former species, a bursa is lacking in the latter. In contrast, though less documented, *U. cornustylis* seemed to have a simple opening to the ventral bodysurface. This situation is also found in *Macrodasys* (Fig. 7B). Since neither an opening nor sperm were found in a bladder-shaped structure of *U. calicostylis*, its homology as a bursa was concluded only from its relative position.

The striking resemblance in stylet and vagina mouthpiece in *U. spirostylis* suggests its functional interpretation as a key-lock system. This would imply that, during copulation, the stylet is inserted into the mouthpiece in a corkscrew-like manner, with 9-11 turns. Although the presence of a spiralized musculature further supports this interpretation, it seems rather unlikely that the precision required to insert a 'key' into such a delicate, rigid 'lock' is actually achieved. It is more likely to assume that this opening, although originally a vagina, has lost its function due to overcomplication.

The stylet would then simply enter the bursa via the body surface. Since the function of the stylet as an organ for sperm transfer is rather doubtful, however, the above hypothesis carries little weight (p. 251).

The high plasticity with regard to the position of the female opening and the direction of egg maturation, within the genus *Urodasyd*, is surprising—considering that such differences, in other groups, often distinguish families or orders. One has to remember, however, that the hindgut, in *Urodasyd*, is highly vacuolized and rather represents parenchyma than a compact organ. Vertical movement of the organs, therefore, may be facilitated. The contrasting position of the ovaries in *Macrodasys* (ventrally to a compact gut) and *Urodasyd* (dorsally, above the 'gut parenchyma') may be due to the same factor.

THE BURSA - PENIS PROBLEM IN MACRODASYIDAE

The new findings of cuticularized structures in the genital system of *Urodasyd* make it necessary to re-examine the previously used terminology (Fig. 7A, B). This applies especially to the penis (defined as the organ which, in the partner acting as male, transfers the sperm) and the bursa (defined as the organ which, in the animal acting as

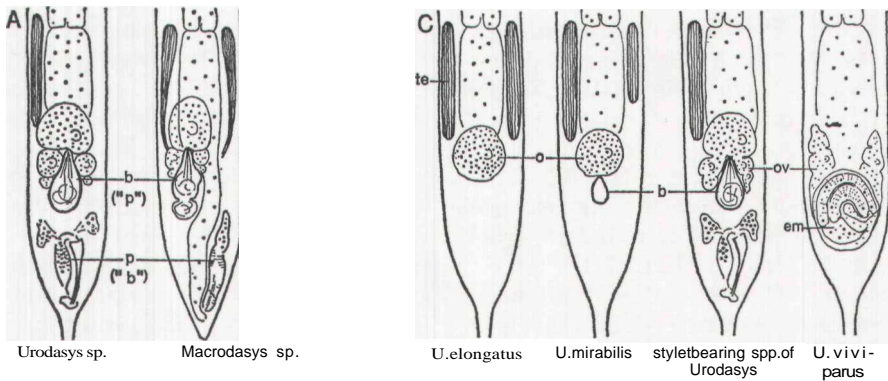


FIG. 7

A : scheme for a new terminology of genital organs, versus the classic terminology (in brackets), dorsal view ; B : lateral view ; C : types of genital organs within the genus *Urodasyd*, showing gradual reduction of testes.

female, stores the partner's sperm). The following discussion will be restricted to the family Macrodasysidæ, and concentrates on the most closely related genera *Macrodasys* and *Urodasyd*, with an occasional glimpse on other forms of particular interest.

In the description of the first representative of the family Macrodasysidæ, *Macrodasys buddenbrocki*, Remane (1924) describes the testes as "gradually and imperceptibly" tapering into the vasa deferentia, which open at about the last quarter of the body into a bladder

("vesicula seminalis"), situated ventrally to the intestine. In a later paper Remane (1926, p. 646) states: "Die Art der Einmuendung konnte ich allerdings noch nicht mit der wuenschenswerten Genauigkeit feststellen". In a further paper (1936, p. 135), he reiterates that the vasa deferentia do not actually join the "penis" but that they end close to the anterior tip of the "penis", immediately under the ventral body surface. He notes that the "penis pouch" is filled with mobile sperm, which often have their heads oriented towards the opening of the "penis". ("Eine Einmuendung der Vasa deferentia liegt nicht im inneren Teil der Penistasche, sondern dicht neben der Penismuendung, auf Schnitten lassen sich die Vasa dicht vor diese Stelle verfolgen, sie sind hier ganz der Ventralflaeche genaehert. Die Penistasche ist mit beweglichen Spermien erfuellt, oft sind dabei alle Koepfe der Penisoeffnung zugekehrt"). He further reports that in *Macrodasys*, the posterior part of this organ opened in a pore to the ventral body surface. If my interpretation of Remane is correct, i.e. if "penis opening" refers to the anterior tip of the "penis" and not to the ventral pore, then it agrees with my own observations on *Macrodasys* spp. I and II given in Fig. 6. Remane, however, reports (1926, p. 646) that he "could not figure out at all how the penis should be everted and retracted".

In agreement with the above interpretation of the anterior organ in *M. buddenbrocki* as a "penis", Remane describes a posterior thick walled muscular pouch provided with a ventral opening next to the anus as a "bursa copulatrix".

The above terminology and interpretation was accepted for all of the 12 species of *Macrodasys* described since. As a consequence, relatively little additional data on the reproductive system were added, most of them only in the form of drawings. This applies especially to the question of whether or not the vasa join directly with the "penis". In two species, *M. remanei* (Boaden, 1963, Fig. 8) and *M. hexadactylus* (Chandrasekhara Rao, 1970), drawings show a direct connection; however, those species differ from all others insofar as their "penis" is situated in front of the ovary and thus not directly comparable to that of the other species where it is posterior to the ovary. *M. cephalatus* (Remane, 1927, Fig. 2) also shows a connection between vasa deferentia and "penis" (but see Remane, 1936, as quoted above). In the remaining 9 species, the vasa deferentia either end in about the first third of the trunk (e.g. *M. neapolitanus* Papi 1957), or they point towards the "penis" without actually entering it. The figure given by Wieser (1957, p. 375, Fig. 1) exactly reflects the situation met with in specimens of *Macrodasys* sp. found on the North Carolina and Bermuda coasts: both vasa deferentia come very close to the anterior tip of the "penis", the left one sometimes even seems to enter it, but more careful analysis invariably reveals that the posterior-most bundle of sperm is situated as close as 1 μm above the ventral body surface, whereas the anterior tip of the "penis" (where the heads of the sperms are pointing to) is at least 10 μm above it. It is therefore suggested here that both vasa deferentia open to the ventral surface in two separate pores and that the organ formerly considered as the "penis" is rather a bursa. Since this new interpretation is not actually based on observation of function

but rather on accumulated morphological evidence, it may be advisable to sort the material into arguments for and against.

The strongest argument in favour of the classical interpretation is that vasa deferentia, although never actually entering the "penis", mostly end in its close proximity. In no case have they been observed to extend further caudally, to the proximity of the "bursa". The function of this organ becomes very enigmatic. A point of minor consequence is Remane's observation (1936, Fig. 143) that, in a histological cross section, tissue identified as "penis" actually protruded from the "male" opening in *Macrodasys cephalatus*. Muscular contraction during histological fixation may very well cause tissue to be extruded from any body opening, without this being an indicator of a natural function.

The following arguments are in favour of interpreting the "penis" as a bursa.

1) The position of the organ, immediately behind the ripe egg, with its anterior tip actually indenting the egg, is classical for a bursa. Among others, an organ in identical position in *Paradasys cambriensis* (Lepidodasyidae) has been called a receptaculum seminis (Boaden, 1963).

2) The position and direction of the sperm within the organ (i.e. bundled, with their heads towards the anterior tip) again is typical for sperm in a bursa (Boaden, 1963 ; Wilke, 1954).

3) A cuticularized structure in the form of a nozzle, often found on the anterior tip of this organ (*Macrodasys africanus* Remane, 1950, *M. caudatus* Schrom, 1966; Wilke, 1954, *M. cunctatus* Wieser, 1957 and *Urodasys cornustylis*) is a common structure in sperm-storing organs of lower worms (e.g. many Turbellaria, Gnathostomulida). It is believed that its function is to release the sperm one by one to the mature egg.

4) The cuticular structure connecting a dorsal body opening with this organ (*U. spirostylis*, *U. nodostylis*) can definitely not be related to any male function. If it functions in copulation at all (see Disc, p. 247, then it must be considered a vagina mouthpiece.

In addition to these points that rather clearly define the "penis" as a bursa, the following arguments contradict the classical interpretation of the organ formerly called "bursa".

1) A cuticular stylet of the type found in the new *Urodasys* species is, in lower worms, often associated with male organs but never with a bursa (e.g. Turbellaria, Gnathostomulida, Nematoda). The same is true for the glands accompanying the stylet apparatus.

2) The fact that the "bursa" is remote from the mature eggs and no connective canal is present has already puzzled Remane (1936, p. 124). Since oviposition is effected by rupture of the body wall next to the mature egg (Teuchert, 1968) the effectiveness of such a remote bursa for fertilization must be doubted.

3) Remane (1936, p. 124) states that "the bursa not infrequently contains sperm" ; however, his observation has never been confirmed since. In my own material of 62 specimens of *Macrodasys* and *Urodasys*, none of the "bursae" ever contained sperm.

Whereas the above points strongly oppose an interpretation of this organ as a "bursa", its function as a penis remains doubtful. An alternative would be its function as a stimulating or glandular organ probably in connection with copulation. A still different explanation is that this organ has lost its function altogether. In her study on the turbellarian *Gyatrix hermaphroditus*, Reuter (1961) found that a certain race of this species, in spite of having become parthenogenetic, retained its complex male stylet apparatus.

As Macrodasypoidea are considered protandric hermaphrodites (Remane, 1926), observations on specimens of different sexual maturity further support our new interpretation (Table II) :

TABLE II
Correlation between body length and maturity of genital organs

A. - *Urodasys cornustylis*

Body length in μm	280	300	350	350	390	405	420	430	432	465	510	525
ovary												
bursa												
testis	—										—	
stylet length in μm		47,5	47,5	47	48	50	43	48	47	48		50

B. - *Urodasys spirostylis*

Body length in μm	440	450	480	480	490	530
ovary	—	+		+	+	+
bursa	v	•	•		O	•
testis	+	+		4.	4.	4.
stylet length in μm	66	66	72	69	64	64

— absent - + present - • full bursa present - O empty bursa present - v only vagina mouth piece present.

1) Teuchert (1968, p. 349) noticed that male animals, ready for copulation, show their posterior ends curled up. Two specimens of *Macrodasys* sp., found in this position and subsequently squeezed, revealed fully developed testes and penis ("bursa"), but no ovary and an empty bursa ("penis"). Similarly, one specimen of *Urodasys cornustylis* had a well developed testis and stylet apparatus, but an empty bursa and no ovary. Several more specimens were found to have a well developed testis and stylet apparatus, a full bursa, but no ovaries. As animals may receive and store sperm before an ovary has matured, however, this latter observation does not necessarily contradict our hypothesis.

2) Another specimen of *U. cornustylis*, in female phase, showed a ripe ovary, a filled bursa, but no testis, the stylet apparatus consisting of only a small empty muscle bulb.

In conclusion, it seems reasonably safe to assume that, in *Urodasys*, the organ formerly called "penis" is in fact a bursa copulatrix. The same is suggested for *Macrodasys*, although the deviation of two species (*M. hexadactylus*, *M. remanei*) from the generalized pattern of genital organs necessitates re-examination. We can further conclude that the organ previously called a "bursa" is not a bursa, but part of the male genital system both in *Macrodasys* and *Urodasys*. Whether it does act as a penis, or a stimulating or glandular organ, or has lost its function in reproduction altogether, cannot be decided.

Summary

Five new species (plus two uncertain ones) of the genus *Urodasys* are described from the coasts of Florida, North Carolina, Bermuda and the Mediterranean. The new species differ from the previously known species by the possession of a cuticularized stylet and an unpaired testis. Diagnoses as well as a key to all the known species of *Urodasys* are given. A new interpretation of the genital organs is suggested.

Zusammenfassung

Fünf neue Arten (und zwei unsichere Arten) der Gattung *Urodasys* werden von den Küsten Floridas, Nord Carolinas, Bermudas und des Mittelmeers beschrieben. Von den bisher bekannten Arten unterscheiden sich die neuen Arten durch den Besitz eines kutikularisierten Stiletts und eines unpaaren Hodens. Diagnosen so wie ein Bestimmungsschlüssel aller bekannten *Urodasysarten* werden gegeben. Eine neue Interpretation der Genitalorgane wird vorgeschlagen.

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Abbreviations used in figures

bc	: bursa copulatrix	o	: ripe egg
bmp	: bursa mouth piece	ov	: ovary
c	: cavity of male apparatus	ph	: pharynx
cp	: cuticular plates of mouth opening	php	: pharyngeal pores
cr	: cuticular ridges of mouth opening	pht	: adhesive tubules belonging to the pharynx region
csa	: cuticular stylet appendix	pn	: protonephridia
dc	: dorsal ciliation	pp	: piston pits
dg	: dorsal glands	rm	: circular muscles
dö	: dorsal opening	sp	: sperms
dr	: dorsal rosette of vagina mouth piece	st	: stylet
em	: embryo	sta	: stylet apparatus
gg	: glands belonging to the male genital system	tc	: tactile cilia
gmb	: gland muscle bulb	te	: testis
ht	: adhesive tubules belonging to the head region	tt	: adhesive tubules belonging to the trunk region
i	: intestine	v	: vacuoles
lm	: longitudinal muscles	vc	: ventral ciliation
		vmp	: vagina mouth piece
		vo	: ventral opening