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MORPHOLOGICAL VARIABILITY IN WARM-TEMPERATE AND SUBTROPICAL POPULATIONS OF *MACRODASYS* (GASTROTRICHA: MACRODASYIDA: MACRODASYIDAE) WITH THE DESCRIPTION OF SEVEN NEW SPECIES

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Abstract.—Seven new species of *Macrodasys, M. ancocytalis, M. achradocytalis, M. deltocytalis, M. meristocytalis, M. dolichocytalis, M. blysocytalis* and *M. stenocytalis* (Gastrotricha: Macrodasyida: Macrodasyidae) are described from warm temperate and subtropical marine sediments along the Atlantic and Gulf coasts of Florida, U.S.A. Multivariate analyses of morphometric characters reveal that the shape and size of the reproductive organs are the most useful characters for discriminating among species. The numerically abundant species *M. achradocytalis* and *M. meristocytalis* displayed the widest geographic range. High morphological variability within *Macrodasys* populations at certain locations can be attributed to the presence of two or more species.

During previous investigations of the marine gastrotrich fauna of warm temperate and subtropical sandy sediments along the Atlantic and Gulf coasts of Florida, U.S.A (Evans 1992), several populations belonging to the genus *Macrodasys* were observed that exhibited differences in both internal and external morphology. Subsequently, I sampled nine locations in southern Florida (Fig. 1): Honeymoon Island (three locations), Crandon Park on Key Biscayne (two locations), Sombrero Beach on Vaca Key (one location), Bahia Honda Key (two locations), and Key West (one location). Variability of morphology of the forms within *Macrodasys* populations at each location was quantified and overall variability within populations was used to discriminate among forms, to identify critical taxonomic characters, and to assess the taxonomic status of each form. Particular attention was paid to the size and shape of the reproductive organs.

Members of the genus *Macrodasys* are simultaneous hermaphrodites with a reproductive system that consists of paired testes with vasa deferentia, a single ovary, a frontal organ which receives and stores allosperm, and a caudal organ which gathers autosperm and passes them to the partner during copulation. The frontal organ consists of an anterior seminal receptacle and a posterior spermatheca. The caudal organ comprises an anterior glandulomuscular structure and a posterior glandular sac ("antrum feminum" of Remane 1924). Ruppert (1978) provides a histological account of the functional anatomy of the reproductive system in two undescribed species of *Macrodasys*.

Materials and Methods

Littoral and sublittoral sediments were collected at each location in January, 1992 with a hand-held piston corer. The gastrotrichs were extracted by means of serial decantation with isosmotic $MgCl_2$ (see Evans & Hummon 1991). Specimens were located at 30× under a stereomicroscope, mounted on glass slides, and observed under Nomarski differential interference contrast op-

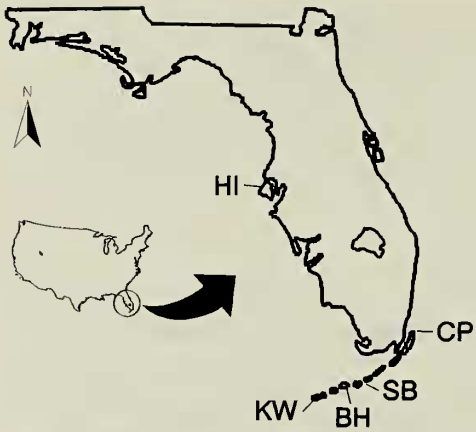

Fig. 1. Study locations in southern Florida. BH—Bahia Honda (two sites), CP—Crandon Park on Key Biscayne (two sites), HI—Honeymoon Island (three sites), KW—Key West (one site), and SB—Sombrero Beach on Vaca Key (one site). Littoral and sublittoral samples were taken at each site.

tics. During observation, high resolution Super-VHS video recordings were made of the living, narcotized animals. Recorded individuals were later measured using a video frame-grabber and a microcomputer-based measurement system. A minimum of five and a maximum of 40 specimens were measured for each form (putative species) according to their availability at the time of extraction. All measurements are reported in μm. Univariate statistics and canonical variates analysis were performed using the SAS-PC Statistical Analysis System. All type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). High resolution videotapes (Super-VHS format) of each type specimen are deposited in the Ohio University Invertebrate Museum, Athens, Ohio.

Statistical Analyses and Results

After observation and measurement, each specimen was preliminarily assigned to one of seven forms based on overall morphological similarity. Morphometric data were then submitted to analysis of variance and to canonical variates analysis. The mean and standard deviation of each metric and meristic character used in the analysis are presented in Fig. 2. All morphometric and meristic parameters were found to different significantly ($P < 0.01$) among forms. No individuals needed to be reassigned to another form based on the results of the canonical variates (CV) analysis.

Arraying individuals in two-dimensional canonical space (Fig. 3) results in seven tightly grouped, well-separated clusters. These morphologically coherent clusters can contain individuals from two or more geographic locations (depending on the number of locations at which a particular form was found), that is, individual forms are morphologically redundant regardless of their geographic population allegiances. The first two canonical variates (CV1, CV2) explained 91.8% of the total morphological variation among individuals ($R^2 > 0.6$). Character loadings based on standardized-canonical-variate scores are interpreted as follows: CV1—shape of the middle portion of the glandulomuscular structure of the caudal organ, CV2—relative lengths of the anterior and middle portions of the glandulomuscular structure and the presence of an auxiliary chamber on the seminal receptacle of the frontal organ. A 3rd canonical variate (not plotted) explained an additional 3.9% of the variation and is interpreted as the size and shape of the seminal receptacle. The seven forms are given species status and formally described below.

Taxonomy

Order Macrodasyida Rao & Clausen, 1970

Family Macrodasyidae Remane, 1924

Macrodasys Remane, 1924

Macrodasys ancocytalis, new species

Fig. 4

Holotype.—Adult specimen 650 μm in length, mounted on glass slide. Honeymoon Island, Florida, U.S.A., sand spit facing the

Measurement	Macrodasys						
	ancocytalis (n = 5)	achradocytalis (n = 40)	deltocytalis (n = 5)	meristocytalis (n = 40)	dolichocytalis (n = 5)	blysocytalis (n = 5)	stenocytalis (n = 5)
Total Length of Adult	621.4 ± 27.3	838.9 ± 86.1	669.9 ± 59.1	634.4 ± 75.6	690.2 ± 14.6	731.3 ± 75.2	669.6 ± 51.1
Head Width at Piston Pits	63.1 ± 9.2	73.5 ± 11.3	59.7 ± 6.4	58.4 ± 10.3	45.2 ± 6.0	54.4 ± 1.7	71.3 ± 7.2
Seminal Receptacle Length	62.3 ± 4.8	34.9 ± 3.4	23.7 ± 3.6	58.6 ± 7.4	64.9 ± 4.3	70.2 ± 9.6	64.4 ± 8.1
Seminal Receptacle Width	22.2 ± 0.9	24.5 ± 3.9	18.3 ± 2.7	21.8 ± 4.4	11.3 ± 1.4	32.6 ± 10.0	24.6 ± 2.7
SR Accessory Chamber Length	0	0	0	16.7 ± 3.1	0	28.2 ± 3.4	0
GMS Anterior Portion Length	83.5 ± 3.4	50.6 ± 8.4	38.4 ± 5.9	45.3 ± 11.4	61.8 ± 4.1	53.1 ± 17.5	55.4 ± 7.4
GMS Anterior Portion Width	19.1 ± 0.7	13.0 ± 2.1	11.9 ± 1.6	14.4 ± 3.1	17.4 ± 1.8	16.3 ± 2.6	14.9 ± 3.5
GMS Middle Portion Length	53.1 ± 0.6	98.3 ± 12.9	57.6 ± 4.4	58.0 ± 9.9	49.4 ± 8.7	69.8 ± 14.3	58.5 ± 11.8
GMS Middle Portion Width	30.6 ± 0.4	32.1 ± 3.7	21.6 ± 3.5	23.2 ± 4.7	19.8 ± 3.0	27.5 ± 6.8	27.6 ± 7.3
Anterior Adhesive Tubes F1	5 - 7	5 - 8	6 - 8	4 - 9	6 - 7	7 - 8	12 - 14
Anterior Adhesive Tubes F2	0	2 - 4	0	0	1 - 2	2 - 3	0
Anterior Ashesive Tubes F3	0	1 - 2	0	0	0	0	0
Ventral Adhesive Tube Rows	2	0	2	2	0	2	0
Dorsal Adhesive Tube Rows	0	2	0	0	0	0	0

Fig. 2. Metric and merisitic characters of seven species of *Macrodasys*. Metric characters are given as the mean ± standard deviation; meristic characters as the range. Abbreviations: GMS—glandulomuscular structure of caudal organ; SR—seminal receptacle of frontal organ; F1, F2, F3—Fields 1–3 of anterior adhesive tubes.

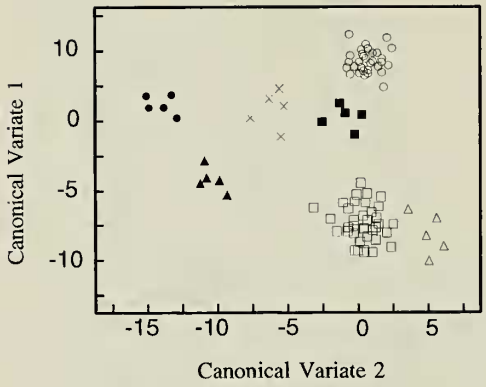

Fig. 3. Canonical variate (CV) plots of *Macrodasys* species, based on 14 characters. CV1 and CV2 are interpreted as the size and shape of the glandulomuscular structure of the caudal organ and the presence of an accessory chamber on the seminal receptacle of the frontal organ. Solid circles—*M. ancocytalis*, open circles—*M. achradocytalis*, solid squares—*M. deltocytalis*, open squares—*M. meristocytalis*, solid triangles—*M. dolichocytalis*, open triangles—*M. blysocytalis*, and X—*M. stenocytalis*.

Gulf of Mexico [28°05′N, 82°50′W]. USNM 168056.

Etymology.—*anco* (L.) meaning curved, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* meaning possession.

Diagnosis.—*Macrodasys* with trunk much longer than pharyngeal region. Lateral and ventral adhesive tubes present on trunk; dorsal tubes lacking. Anterior adhesive tubes ventral, a single row of from five to seven tubes on each side of body, near anterior margin of head. Frontal organ a small spermatheca and elongate seminal receptacle with small nozzle; accessory chamber absent. Glandulomuscular structure of caudal organ with anterior glandular portion longer than middle portion bearing circular musculature; posterior portion a small, curved "neck" with terminal pore; copulatory tube without branches. Glandular sac of caudal organ a rounded, triangular shape.

Description.—Elongate, strap-shaped body; adults 602–685 μm long, 49–65 μm wide. Caudum tapers into long, narrow "tail" (Fig. 4a). Dorsal and lateral body surfaces covered with long sensory bristles. Piston pits ("stempelgrube" of Remane 1924) on each side of head. Ventral surface entirely covered with locomotor cilia except small, bare area around female pore (Fig. 4b). Dorsal ciliary band present on head. Anterior adhesive tubes a ventral, single row, an arc of from five to seven tubes on each side of body, adjacent to mouth (Fig. 4c); most medial tube shortest, most lateral longest. About 16 lateral adhesive tubes on each side of trunk; an additional 10–12 tubes on each side of tail. Two ventral rows of adhesive tubes near lateral margins of trunk, about 16 per row. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction; lateral and ventral rows merge where trunk narrows into tail.

Mouth leads into buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U40 (U0, anterior-most tip; U100, posterior-most tip; in the terminology of Schoepfer-Sterrer 1969); pharyngeal pores (U24) small. Intestine narrows continuously from pharyngeal-intestinal junction to terminus; anus ventral.

Small, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to frontal organ (Fig. 4a). Frontal organ an anterior seminal receptacle and posterior spermatheca (Fig. 4d). Seminal receptacle with weak circular musculature and small, lightly cuticularized anterior pore (nozzle); length about three times width. Spermatheca hollow with few secretory droplets. Ovary adjacent to spermatheca; ova increase in size anteriorly. Ovum adjacent to nozzle of spermatheca receives sperm. Large caudal organ a spindle-shaped glandulomuscular structure and a glandular sac with opening to ventral surface (Fig. 4e); anterior tip of glandulomuscular structure adjacent to spermatheca.

Anterior portion of glandulomuscular structure longer than middle portion and sheathed in longitudinal muscles. Middle

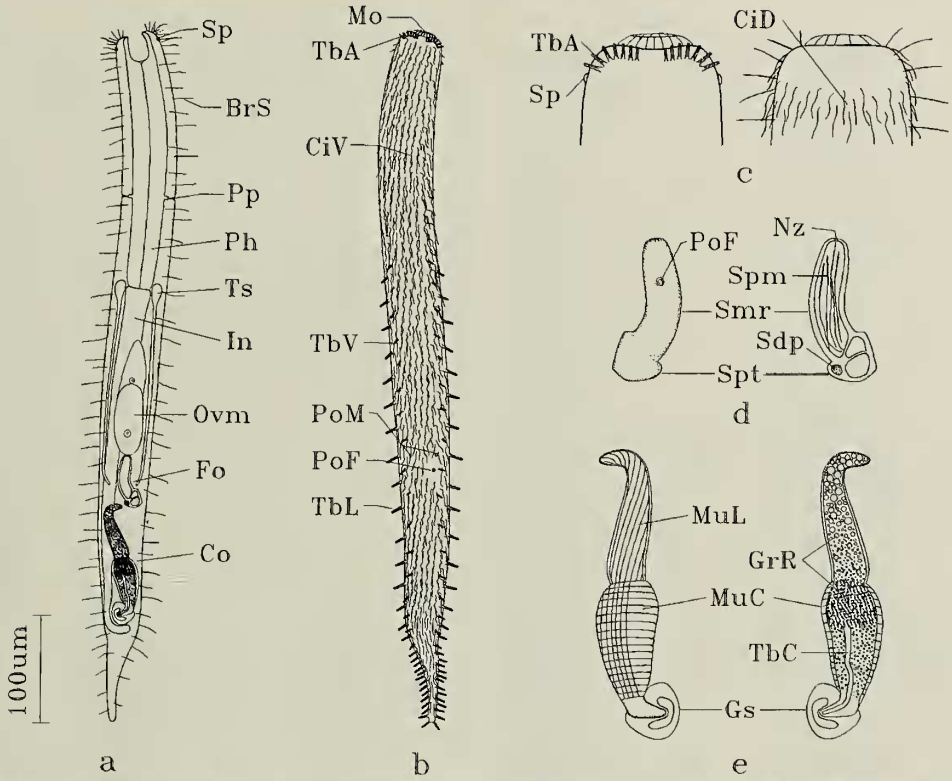

Fig. 4. *M. ancocytalis,* new species. Single row of anterior adhesive tubes. Ventral tubes present. Curved seminal receptacle of frontal organ lacks an auxiliary chamber. Anterior portion of glandulomuscular structure of caudal organ longer than middle portion. a) internal organs, b) ventral surface, c) ventral and dorsal head, d) frontal organ, and e) caudal organ. c–e not to scale. Abbreviations: BrS—sensory bristle, CiD—dorsal ciliary band, CiV—ventral locomotor cilia, Co—caudal organ, Eg—egg, Fo—frontal organ, GrR—refractile granules, Gs—glandular sac, MuC—circular muscles, MuL—longitudinal muscles, Nz—nozzle, Ov—ovum, Ph—pharynx, PoF—female reproductive pore, PoM—male reproductive pore, Pp—pharyngeal pore, PtP—piston pit, Sdp—secretory droplet, Smr—seminal receptacle, Spm—spermatozoa, SpT—spermatheca, TbA—anterior adhesive tube, TbD—dorsal adhesive tube, TbL—lateral adhesive tube, TbV—ventral adhesive tube, Ts—testis.

portion with longitudinal muscles on ventral side only, but entirely sheathed in robust circular muscles. Posterior portion of glandulomuscular structure an angled neck that extends into center of glandular sac. Glandulomuscular structure filled with refractile granules of various diameters; unbranched copulatory tube in middle portion of glandulomuscular structure leads to opening in neck. Glandular sac of caudal organ a rounded, triangular shape.

Distribution and habitat.—Uncommon species, found in littoral and sublittoral zones in coarse, poorly-sorted sediments with both siliceous and carbonate fractions. Honeymoon Island (two locations).

Macrodasys achradocytalis, new species
Fig. 5

Holotype.—Adult specimen 825 μm in length, mounted on glass slide. Bahia Honda Key, Florida, U.S.A., sandy beach facing the Atlantic Ocean [24°38′N, 81°35′W]. USNM 168055.

Etymology.—*achrado* (L.) meaning wild pear, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

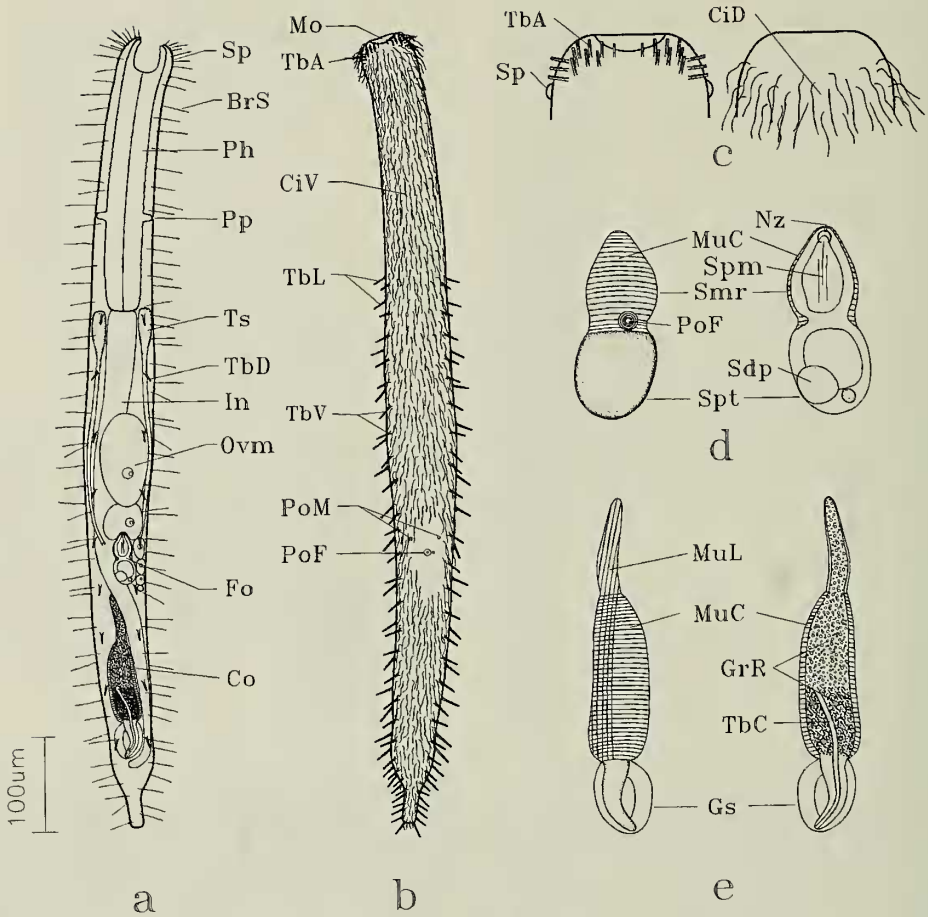

Fig. 5. *M. achradocytalis*, new species. Dorsal adhesive tubes in two rows of 10 tubes each. Anterior adhesive tubes in three fields. Seminal receptacle and spermatheca of frontal organ of similar size. Anterior portion of glandulomuscular structure of caudal organ much shorter than middle portion; neck long and narrow. Abbreviations and a–e as in Fig. 4; c–e not to scale.

Diagnosis.—*Macrodasys* with trunk much longer than pharyngeal region. Lateral and dorsal adhesive tubes present on trunk; ventral tubes lacking. Anterior adhesive tubes ventral in three fields on each side of body, near anterior margin of head. Anterior field a row of from five to eight tubes arranged in two distinct groups at 95° angle to each other; middle field a row with from two to four tubes; posterior-most field with one or two tubes. Frontal organ a rounded spermatheca and pear-shaped seminal receptacle; nearly equal in size. Seminal receptacle sheathed in circular muscles; nozzle large and cuticularized; accessory chamber absent. Anterior, glandular portion of glandulomuscular structure of caudal organ short and narrow, about one-half length of middle portion; neck long and slightly curved; copulatory tube without branches. Glandular sac of caudal organ oval.

Description.—Very long strap-shaped body; adults 661–1033 μm long and 54–97 μm wide. Caudum narrows abruptly into short tail (Fig. 5a). Dorsal and lateral body surfaces covered with long sensory bristles. Ventral surface entirely covered with locomotor cilia except large, bare area around

female pore (Fig. 5b). Sparse dorsal ciliary band on head. Anterior adhesive tubes ventral, in three fields on each side of body just posterior to mouth (Fig. 5c). Anterior field with row of seven tubes in two distinct groups at about 95° angle to each other; tubes increase in length from medial to lateral. Middle field a transverse row with from two to four tubes. Posterior-most field with one or two tubes. About 40 lateral adhesive tubes on each side of trunk; tubes longest where trunk narrows into tail. An additional five or six tubes on each side of tail. Two dorsal rows of about 10 small tubes each (Fig. 5a). Ventral adhesive tubes lacking. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction. Lateral tubes continue onto tail; dorsal tube rows end just anterior to tail.

Mouth leads into large buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U35; pharyngeal pores at U23. Intestine narrows toward caudal end of trunk; anus ventral.

Paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle. Spermatheca of frontal organ rounded with internal cavity and large secretory droplets. Seminal receptacle of frontal organ pear-shaped, anterior end with large, heavily cuticularized D-shaped nozzle; accessory chamber lacking. Seminal receptacle sheathed in circular muscles (Fig. 5d). Small tube leads from posterior ventral portion of seminal receptacle to ventral female pore. Spermatheca and seminal receptacle approximately the same size; secretory droplets often large. Ovary lies to right of frontal organ; ova increase in size anteriorly. Glandulomuscular structure of caudal organ with anterior portion short (one-third the length of middle portion) and narrow. Long, narrow neck of glandulomuscular structure extends to posterior end of glandular sac; copulatory tube unbranched. Refractile granules densest and smallest in posterior end of glandulomuscular structure (Fig. 5e). Glandular sac of frontal organ oval.

Distribution and habitat.—Common species, found in littoral and sublittoral zones in both coarse, poorly-sorted carbonate sediments and medium-fine siliceous sediments. Abundant where found. Crandon Park (two locations), Bahia Honda (two locations), and Sombrero Beach.

Macrodasys deltocytalis, new species
Fig. 6

Holotype.—Adult specimen 670 μm in length, mounted on glass slide. Crandon Park, Florida, U.S.A., small, sandy beach facing harbor on Biscayne Bay [25°44′N, 80°10′W]. USNM 168058.

Etymology.—*delto* (L.) meaning in the shape of a triangle, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with pharynx and trunk of about equal length. Lateral and ventral adhesive tubes present on trunk; dorsal tubes lacking. Anterior adhesive tubes ventral, in one row of from six to eight tubes on each side of body, near anterior margin of head. Tubes arranged in arc with shortest tubes medially and longest tubes laterally. Spermatheca of frontal organ simple, round; seminal receptacle triangular-shaped, twice as long as diameter of spermatheca and without visible circular musculature; accessory chamber absent. Anterior portion of glandulomuscular structure of caudal organ wide and about two-thirds length of middle portion; neck strongly curved; copulatory tube without branches. Glandular sac of caudal organ small.

Description.—Strap-shaped body; adults 602–685 μm long, 49–65 μm wide. Caudum tapers quickly into medium-length tail (Fig. 6a). Dorsal and lateral body surfaces sparsely covered with long sensory bristles. Ventral surface entirely covered with locomotor cilia except small, bare area around female

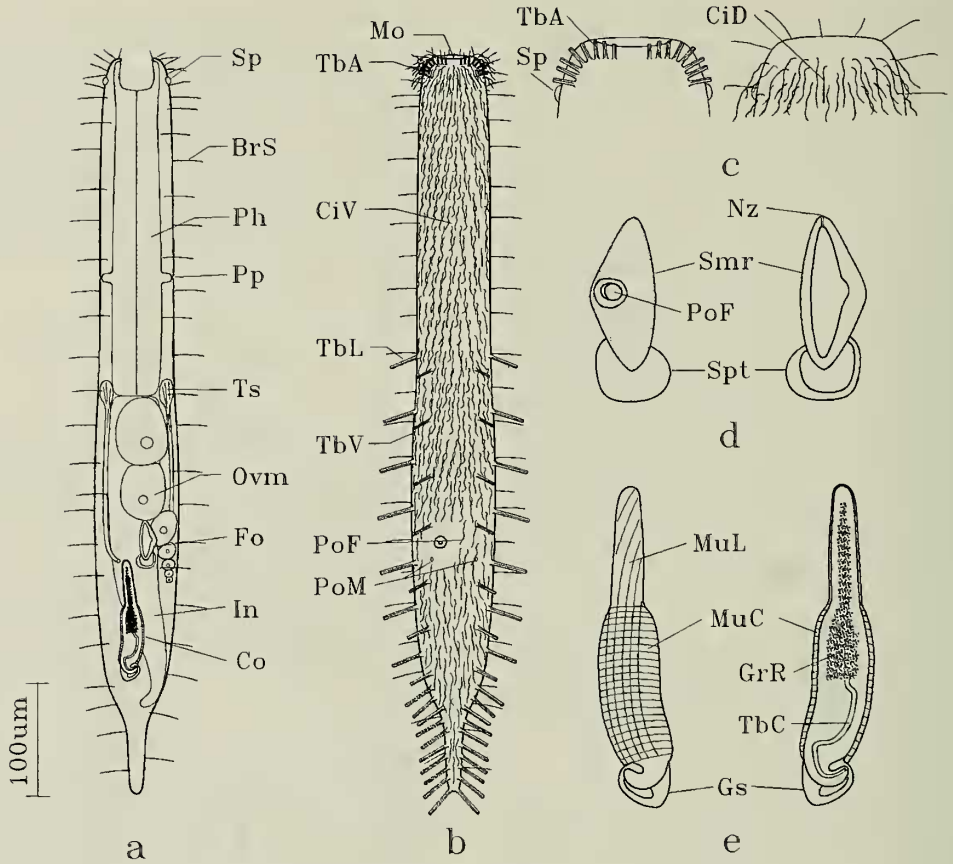

Fig. 6. *M. deltocytalis,* new species. Pharyngeal region and trunk equal in length. Anterior adhesive tubes in a single row of eight tubes. Ventral adhesive tubes present. Seminal receptacle of frontal organ triangular in shape. Abbreviations and a–e as in Fig. 4; c–e not to scale.

pore (Fig. 6b). Sparse dorsal ciliary band on head near anterior margin. Anterior adhesive tubes a single ventral row of from six to eight tubes on each side of body near anterior margin of head and arranged in an arc with tubes increasing in length from medial to lateral (Fig. 6c). About 10 lateral adhesive tubes on each side of trunk; additional seven or eight tubes on each side of tail. Lateral tubes longest in mid-trunk region. Two ventral rows of about seven tubes each. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction. Lateral and ventral rows converge where trunk narrows into tail.

Mouth leads into shallow buccal cavity, which opens into long pharynx. Pharyngeal-intestinal junction at U50; pharyngeal pores at U30. Intestine narrows at caudal end of trunk; anus ventral.

Small, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to posterior edge of spermatheca. Spermatheca of frontal organ rounded, with large internal cavity; secretory droplets not observed. Seminal receptacle of frontal organ triangular-shaped with small nozzle at anterior apex; thick-walled tubular chamber leads to ventral female pore from lateral apex. Ventral pore surround by epidermal sculpturing. Right wall of seminal recepta-

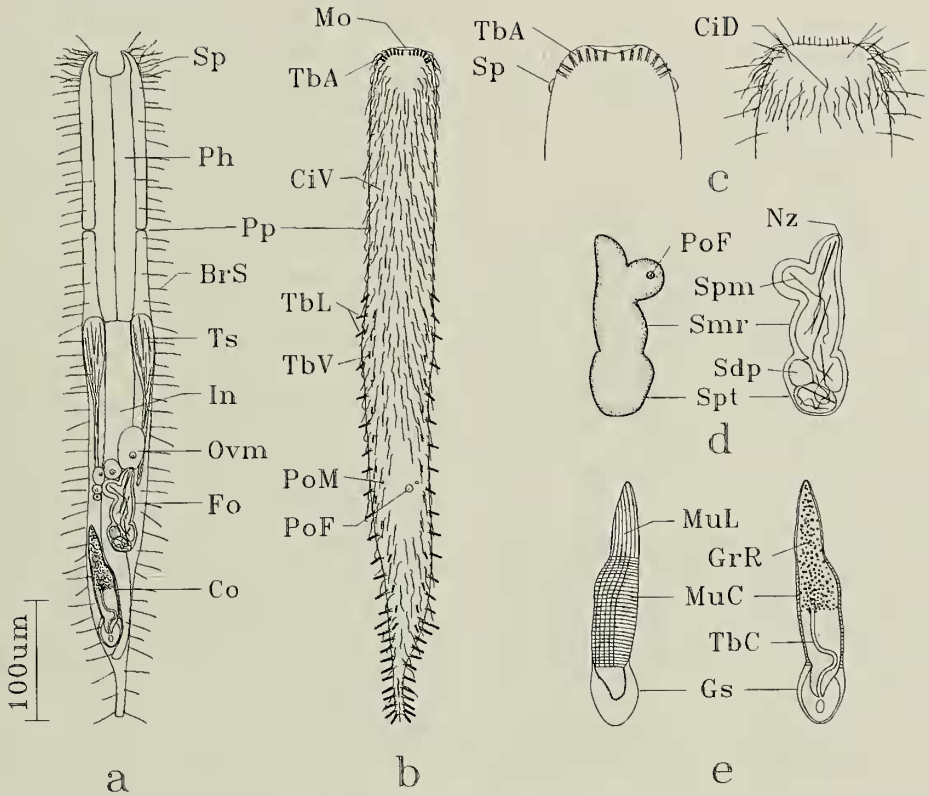

Fig. 7. *M. meristocytalis,* new species. Ventral adhesive tubes present. Seminal receptacle of frontal organ with a small accessory chamber containing female pore. Testes large. Anterior portion of glandulomuscular structure of caudal organ about one-half as long as middle portion. Abbreviations and a–e as in Fig. 4; c–e not to scale.

cle thickened; circular muscles not evident. Accessory chamber lacking. Seminal receptacle approximately 2.5 times as long as diameter of spermatheca. Ovary lies posterior and right of frontal organ; ova increase in size anteriorly. Glandulomuscular structure of caudal organ with anterior portion broad and about two-thirds as long as middle portion (Fig. 6e). Short, severely curved neck of glandulomuscular structure extends to left margin of glandular sac; copulatory tube unbranched. Refractile granules present from anterior end of copulatory tube to anterior tip of glandulomuscular structure. Glandular sac of caudal organ small.

Distribution and habitat.—Uncommon species, found only in littoral zone of small beach facing harbor on Biscayne Bay. Well-sorted, medium-fine siliceous sediments. Crandon Park (one location).

Macrodasys meristocytalis, new species
Fig. 7

Holotype.—Adult specimen 670 μm in length, mounted on glass slide. Key West, Florida, U.S.A., small sandy beach facing Atlantic Ocean [24°35′N, 81°50′W]. USNM 168060.

Etymology.—*meristo* (L.) meaning divided, after the division of the seminal receptacle into two chambers; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk slightly longer than pharyngeal region. Lateral and

ventral adhesive tubes present on trunk; dorsal tubes lacking. Anterior adhesive tubes ventral, a single row of from four to nine tubes on each side of body, near anterior margin of head. Testes very large. Frontal organ a simple, round spermatheca and elongate seminal receptacle. Seminal receptacle 2.5 times as long as diameter of spermatheca and without visible circular musculature; accessory chamber present. Anterior portion of glandulomuscular structure of caudal organ broad and short, about two-thirds length of middle portion; neck very short; copulatory tube unbranched. Glandular sac of caudal organ oval.

Description.—Strap-shaped body; adults 495–797 μm long, 38–89 μm wide. Caudum tapers gradually into narrow tail (Fig. 6a). Dorsal and lateral body surfaces covered with numerous sensory bristles. Ventral surface entirely covered with locomotor cilia except a V-shaped, bare area posterior to anterior series of adhesive tubes and a large, bare area surrounding female pore (Fig. 7b). Sparse dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral, a single row of from four to nine tubes on each side of body near anterior margin of head, arranged in an arc with tubes increasing in length from medial to lateral (Fig. 7c). About 20 lateral adhesive tubes on each side of trunk; an additional eight or nine tubes on each side of tail. Lateral tubes longest where trunk narrows into tail. Two ventral rows of about 13 small tubes each. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction. Lateral and ventral rows converge where trunk narrows into tail.

Mouth leads into shallow buccal cavity, which opens into long pharynx. Pharyngeal-intestinal junction at U41; well-developed pharyngeal pores at U26. Intestine narrows at caudal end of trunk; anus ventral.

Very large, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle of frontal organ. Spermatheca of frontal organ rounded with dual internal cavities; secretory droplets present. Seminal receptacle of frontal organ a rounded cone, with bulbous accessory chamber on right side; small nozzle present at anterior apex (Fig. 7d). Thin-walled, cylindrical tube leads from accessory chamber to simple ventral female pore. Seminal receptacle approximately 2.5 as long as the diameter of spermatheca; circular muscles not visible. Ovary lies posterior to and left of frontal organ; ova increase in size anteriorly with largest ovum in front of seminal receptacle. Glandulomuscular structure of caudal organ with broad anterior portion that tapers to rounded point anteriorly, about three-quarters as long as middle portion. Stubby, slightly-curved neck of glandulomuscular structure extends to center of glandular sac; refractile granules sparse; copulatory tube unbranched. Glandular sac of caudal organ oval.

Distribution and habitat.—Common species, found in littoral and sublittoral zones in coarse, poorly-sorted carbonate sediments and in medium-fine, siliceous sediments. Abundant where found. Honeymoon Island (one location), Crandon Park (two locations), Bahia Honda (one location), and Key West.

Macrodasys dolichocytalis, new species
Fig. 8

Holotype.—Adult specimen 690 μm in length, mounted on glass slide. Honeymoon Island, Florida, U.S.A., beach facing the Gulf of Mexico near causeway [28°05′N, 82°50′W]. USNM 168059.

Etymology.—*dolicho* (L.) meaning elongate, after the shape of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk longer than pharyngeal region. Lateral adhesive tubes present on trunk; ventral and dorsal tubes lacking. Anterior adhesive tubes ven-

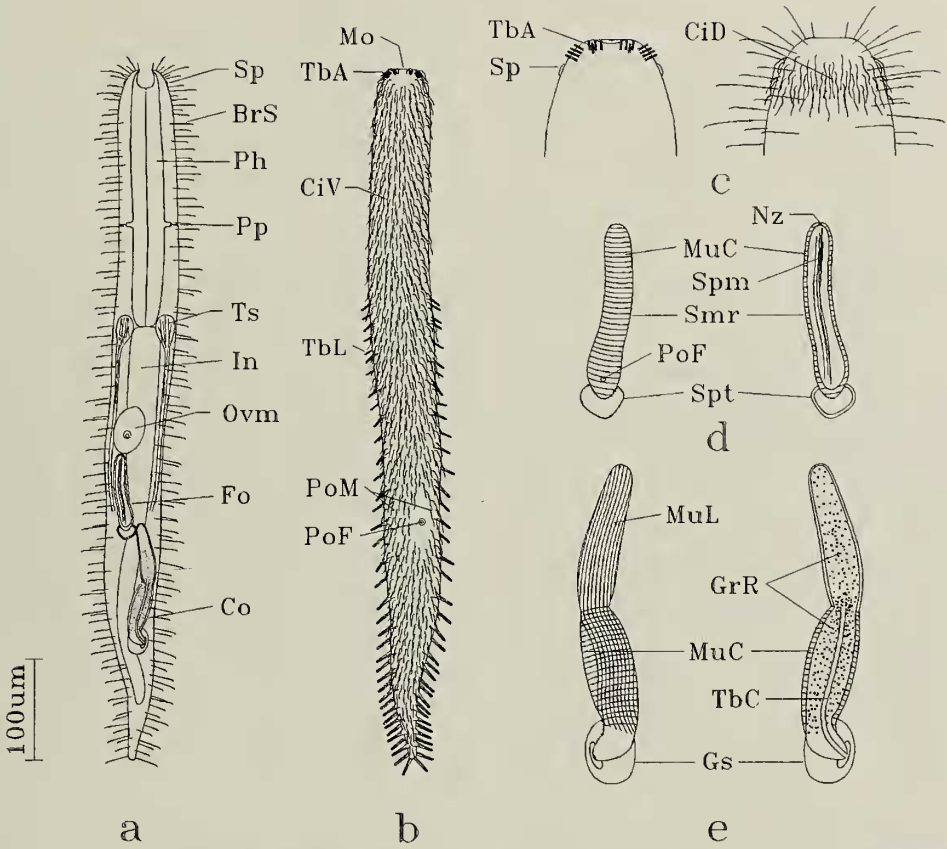

Fig. 8. *M. dolichocytalis,* new species. Lateral adhesive tubes abundant, especially in tail region. Anterior adhesive tubes in two fields. Seminal receptacle of frontal organ about six times as long as wide. Sperm with very long tails. Anterior portion of glandulomuscular structure of caudal organ slightly longer than middle portion. Abbreviations and a–e as in Fig. 4; c–e not to scale.

tral, in two fields on each side of body, near anterior margin of head. Anterior field a row of six or seven tubes of equal size in two distinct groups of three or four tubes each, at about 130° angle to each other. Second field with one or two tubes. Seminal receptacle of frontal organ long and narrow, about six times as long as wide, with strong circular musculature; accessory chamber lacking. Spermatheca of frontal organ small. Anterior portion of glandulomuscular structure of caudal organ nearly as wide as, and slightly longer than, middle portion; neck wide; copulatory tube without branches. Glandular sac of caudal organ ovoid.

Description.—Strap-shaped body; adults 680–701 μm long, 41–49 μm wide. Caudum tapers gradually into wide tail. Dorsal and lateral body surfaces densely covered with long sensory bristles (Fig. 8a).Ventral surface entirely covered with locomotor cilia except small, bare area posterior to anterior series of adhesive tubes and bare, diamond-shaped area surrounding female pore (Fig. 8b). Dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral in two fields, on each side of body, near anterior margin of head (Fig. 8c). Anterior field a row of six or seven tubes of equal size in two distinct groups of three or four each, at about 130° angle to each other. Second field with one or two tubes. No anterior

tubes reach level of sensory pits. About 26 lateral adhesive tubes on each side of trunk; an additional 10 tubes on each side of tail. Lateral tubes slightly longer near caudum. Adhesive tubes on trunk begin just anterior to pharyngeal-intestinal junction.

Mouth leads into small buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U35; pharyngeal pores at U23. Intestine narrows in mid-trunk region; anus ventral.

Round, paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle of frontal organ. Spermatheca of frontal organ small and irregular in shape, without secretory droplets. Seminal receptacle long and narrow, six times longer than wide with rounded apex; very small nozzle present at apex (Fig. 8d). Thin-walled tube leads from posterior end of seminal receptacle to simple ventral female pore. Seminal receptacle approximately five times as long as the diameter of spermatheca; circular muscle bands present. Ovary not observed, large ovum in front of seminal receptacle. Glandulomuscular structure of caudal organ with anterior portion long and broad with broadly rounded apex, about same length as middle portion; refractile granules sparse; copulatory tube unbranched. Stubby, curved neck of glandulomuscular structure extends to left side of glandular sac of caudal organ. Glandular sac ovoid.

Distribution and habitat.—Uncommon species, found only in sublittoral zone of small beach facing Gulf of Mexico. Coarse, poorly-sorted siliceous/carbonate mixed sediments. Honeymoon Island (one location).

Macrodasys blysocytalis, new species
Fig. 9

Holotype.—Adult specimen 780 μm in length, mounted on glass slide. Honeymoon Island, Florida, U.S.A., inside of sand spit beach facing St. Joseph Sound [28°05′N, 82°50′W]. USNM 168057.

Etymology.—*blyso* (L.) meaning bubble, after the bubble-like accessory chamber on the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk much longer than pharyngeal region. Lateral and ventral adhesive tubes present; dorsal tubes lacking. Anterior adhesive tubes ventral, in two fields on each side of body, near anterior margin of head. Anterior field a row of seven or eight tubes of equal size in two distinct groups of three or four tubes each, at about 100° angle to each other. Second field a row of two or three tubes. Additional, single lateral adhesive tube on each side of head separate from anterior series. Frontal organ a large, cone-shaped seminal receptacle with large, ovoid dorsal accessory chamber and a thick-walled spermatheca, about same size as seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ broad with rounded tip, about half as long as middle portion; neck short; copulatory tube T-shaped. Glandular sac of caudal organ small.

Description.—Strap-shaped body; adults 678–784 μm long and 53–56 μm wide. Caudum tapers gradually into indistinct tail (Fig. 9a). Dorsal and lateral body surfaces covered with sensory bristles. Ventral surface entirely covered with locomotor cilia except small, bare area surrounding female pore (Fig. 9b). Sparse dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral, in two fields on each side of body, near anterior margin of head (Fig. 9c). Anterior field a row of seven or eight tubes in two distinct groups of three or four tube each, at about 100° angle to each other; tubes in medial group one-half as long as tubes in lateral group. Posterior field a row of two or three tubes about 1.5 times as long as tubes in anterior field. Additional, single ventrolateral adhesive tube on each side of head separate from usual

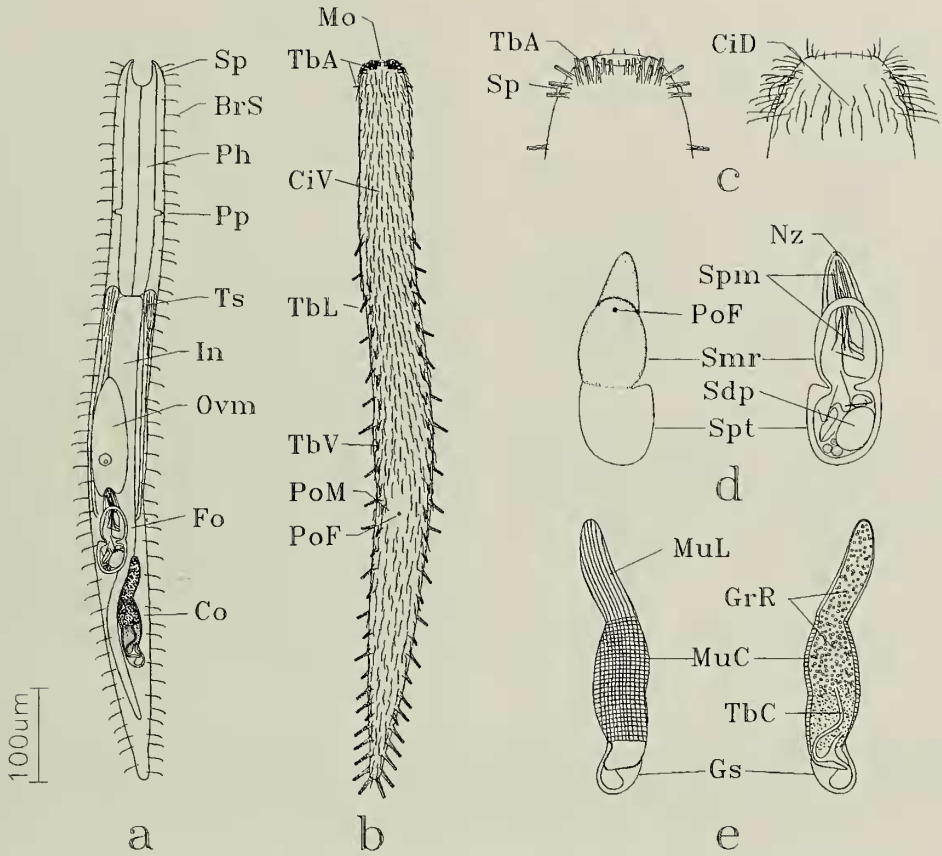

Fig. 9. *M. blysocytalis,* new species. Caudum tapers gradually into indistinct tail. Anterior adhesive tubes in three fields; additional pair of tubes laterally in head region. Seminal receptacle of frontal organ with accessory chamber in the form of a large, ventral blister. Copulatory tube of glandulomuscular structure of caudal organ branched. Abbreviations and a–e as in Fig. 4; c–e not to scale.

anterior series. About 15 lateral adhesive tubes on each side of trunk; additional six or seven tubes on each side of tail. Aside from single pair of tubes near anterior series, lateral tubes begin nearly at level of pharyngeal pores and are of uniform size. Two ventral rows of adhesive tubes begin posterior to second pair of lateral tubes and are much smaller than lateral tubes; about 10 ventral tubes per row. Lateral and ventral rows begin to converge on posterior third of trunk; ventral rows stop where tail begins.

Anterior mouth leads into buccal cavity, which opens into pharynx. Pharyngeal-intestinal junction at U30; pharyngeal pores at U21. Intestine narrows abruptly in mid-trunk region; anus ventral.

Elongate, paired lateral testes at pharyngeal-intestinal junction taper gradually into vasa deferentia; male pores separate and ventral, adjacent to anterior end of seminal receptacle of frontal organ. Spermatheca of frontal organ small and irregular in shape, with thick wall and large secretory droplets. Seminal receptacle cone-shaped with large, ovoid dorsal accessory chamber, about same size as spermatheca (Fig. 9d). Small nozzle present in anterior end of seminal receptacle; circular muscles not evident. Female pore exits from anterior end of accessory

chamber of seminal receptacle. Ovary not observed; large ovum lies in front of seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ wide with rounded apex, about half as long as middle portion. Copulatory tube T-shaped, branching as it enters middle portion of glandulomuscular structure (Fig. 9e); refractile granules larger anteriorly. Stubby, curved neck of glandulomuscular structure extends to left side of glandular sac of caudal organ.

Distribution and habitat.—Uncommon species, found only in littoral zone on inside of sand spit facing St. Joseph Sound. Medium-fine, well-sorted siliceous sediments. Honeymoon Island (one location).

Macrodasys stenocytalis, new species
Fig. 10

Holotype.—Adult specimen 670 μm in length, mounted on glass slide. Sombrero Beach, Vaca Key, Florida, U.S.A., small beach facing Atlantic Ocean [24°41′N, 81°05′W]. USNM 168061.

Etymology.—*steno* (L.) meaning narrow or constricted, after the constriction of the seminal receptacle; *cyto* (L.) meaning chamber or receptacle; *alis* (L.) meaning possession.

Diagnosis.—*Macrodasys* with trunk about same length as pharyngeal region. Lateral adhesive tubes present; ventral and dorsal tubes lacking. Anterior adhesive tubes ventral, in single row of from 12 to 14 tubes on each side of body, near anterior margin of head. Tubes arranged in arc with shortest medial and longest lateral. Frontal organ a seminal receptacle with muscularized bulb anterior to narrow constriction and an ovoid spermatheca about one-half as long as seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ broad, both with narrow extension to tip, slightly more than one-half as long as middle portion; copulatory tube without branches; refractile granules sparse. Glandular sac of caudal organ small.

Description.—Broad, strap-shaped body; adults 661–680 μm long, 67–74 μm wide. Caudum tapers abruptly into short tail (Fig. 10a). Dorsal and lateral body surfaces covered with long sensory bristles. Ventral surface entirely covered with locomotor cilia except small, bare area surrounding female pore (Fig 10b). Sparse dorsal ciliary band on head at level of sensory pits. Anterior adhesive tubes ventral, in single row of from 12 to 14 tubes on each side of body, near anterior margin of head (Fig. 10c). Medial tubes shortest, lateral tubes longest. About 24 lateral adhesive tubes on each side of trunk; an additional six to eight tubes on each side of tail. Lateral tubes begin just anterior to pharyngeal-intestinal junction and are longest and most numerous where trunk constricts to form tail.

Mouth leads into buccal cavity, which opens into the pharynx. Pharyngeal-intestinal junction at U45; pharyngeal pores at U30. Intestine gradually narrows toward tail; anus ventral.

Paired lateral testes at pharyngeal-intestinal junction taper into vasa deferentia; male pores separate and ventral, adjacent to seminal receptacle of frontal organ. Spermatheca of frontal organ large and ovoid, with various-size secretory droplets. Seminal receptacle with ovoid posterior section which narrows before forming a bulbous, muscularized, anterior portion; small nozzle present (Fig. 10d). Seminal receptacle about twice as long as spermatheca. Female pore exits from posterior portion of seminal receptacle. Ovary not observed; large ovum lies in front of seminal receptacle. Anterior portion of glandulomuscular structure of caudal organ broad, but with narrow tip; slightly more than one-half as long as middle portion (Fig. 10e). Middle portion broad at midsection, narrow at ends; copulatory tube straight; refractile granules present. Short, curved neck of glandulomuscular structure extends to left side of glandular

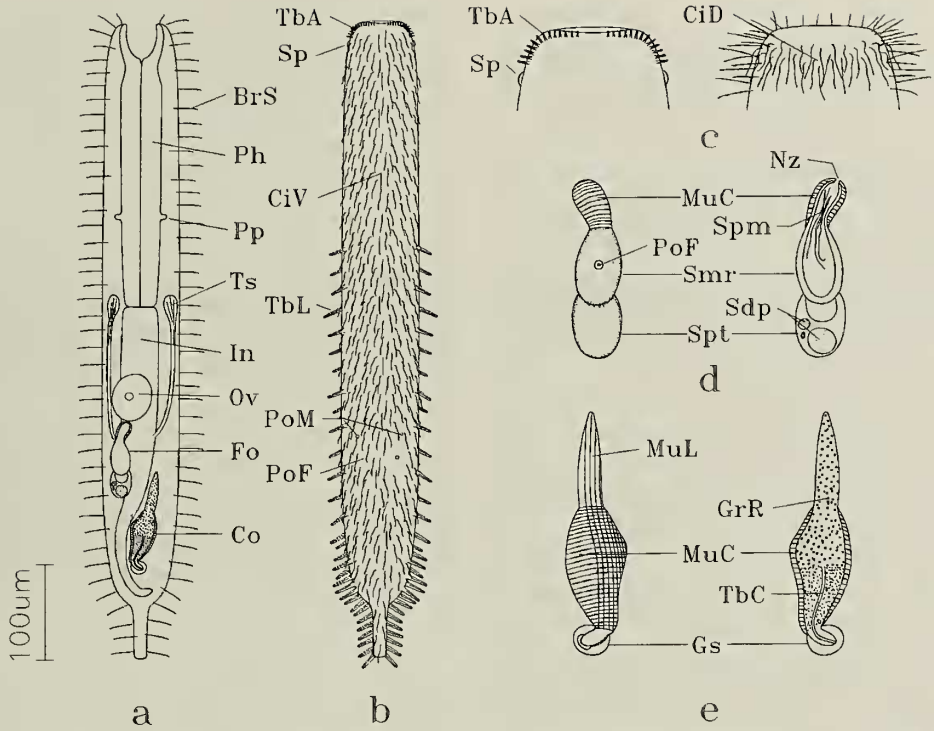

Fig. 10. *M. stenocytalis,* new species. Numerous small anterior adhesive tubes in single row. Seminal receptacle of frontal organ constricted in the middle; portion anterior to constriction sheathed in circular muscles. Glandular sac of caudal organ very small. Abbreviations and a–e as in Fig. 4; c–e not to scale.

sac of caudal organ. Glandular sac very small.

Distribution and habitat.—Uncommon species, found only in sublittoral zone on small beach facing the Atlantic Ocean. Coarse, poorly-sorted carbonate sediments. Sombrero Beach.

Discussion

Comparing the species described above to previously described species on the basis of reproductive morphology is difficult because descriptions of the reproductive system have been either omitted or described in insufficient detail by previous workers (e.g., Boaden 1963, Ganapati & Rao 1967, Roszczak 1939, Thane-Fenchel 1970). Where details of the reproductive system are given (e.g., Remane 1936, Schmidt 1974, Valbonesi & Luporini 1984, Wieser 1957) they do not match any of the species described herein; however, *M. meristocytalis* does closely resemble the *Macrodasys* sp. II of Ruppert 1978, fig. 1c, p. 210 from Florida. The reproductive morphologies of the seven Florida species described here are unique and provide an excellent basis for discriminating among species. Schoepfer-Sterrer (1974) found this to be the case with the only other genus, *Urodasys,* in the family Macrodasyidae.

It is also possible to make correct species assignments, at least in south Florida populations of *Macrodasys,* on the basis of external features such as length, the number of rows of lateral adhesive tubes, and the arrangement of the anterior tubes, when these features are used in combination. However, adhesive tubes, especially of the anterior, dorsal, and ventral series can be difficult to see without differential interfer-

ence contrast optics. The number of tubes in each series is hard to determine and varies with the age of the individual, making them an unreliable character (Luporini et al. 1973). Conversely, the reproductive organs, once formed, are stable in size and shape, large, and easily observed in adult specimens, even with transmitted-light microscopy. They are often visible even when the specimen otherwise is in poor condition and would be the preferred characters for identifying species in this genus.

What might appear to be a considerable amount of morphological variability in *Macrodasys* populations at particular geographic locations is, in the Florida case, largely caused by species that are superficially similar and whose ecological distributions overlap. For example, the Crandon Park inside-location had three species occurring together in the littoral zone that contributed to the overall variability of the *Macrodasys* population as a whole. Morphometric analyses based on reproductive characters can help to resolve such variability into species-specific components.

The two most abundant species (*M. achradocytalis* and *M. meristocytalis*) had much wider geographic distributions than the rarer species. Each of the two occurred at five locations, in both littoral and sublittoral zones, and in a wide variety of sediment types. When found in the same beach, these two species exhibited non-overlapping horizontal distributions in steep, tidal beaches, but were mixed in narrow, atidal beaches. Less abundant species were found only at one, or at most two, sampling locations and were always restricted to either the littoral or sublittoral zone. Vertical overlap of species within beaches and seasonal changes in geographic and ecological distributions were not investigated.

The large number of species found in a limited (on a global scale) geographical area in this and similar studies (Schmidt 1974, Valbonesi & Luporini 1984), suggests that *Macrodasys* is a very speciose genus. This requires that claims of global distributions for members of this genus, particularly the frequently reported *M. caudatus*, be supported by detailed morphological analyses on local and regional bases.

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