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A Monograph of the Genus *Macrostomum* O. Schmidt 1848.

Part III.

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(With 35 Text-Figures.)

Eingeg. 30. Juni 1939.

Description of Species and Varieties.

Macrostomum appendiculatum (O. FABR.).

1826 *Planaria appendiculata*, O. FABRICIUS in: Danske Selsk. Afh. 2, 17 t. 1 lit. B f. 1, 2. — 1843 *Macrostoma hystrix* + *M. appendiculatum*, A. ÖRSTED in: Naturh. Tidsskr. 4, 465. — 1844 *Macrostoma hystrix* + *M. appendiculatum*, A. ÖRSTED, Plattwürmer, pp. 72, 73 t. 2 f. 28, 29, 34, 72, 73. — 1848 *Macrostomum hystrix*, O. SCHMIDT, Rhabd. Strudelw. süss. Wass. p. 54 t. 5 f. 15. — 1850 *Turbella appendiculata* + *Turbella hystrix*, DIESING, Syst. Helm. 1, 224. — 1851 *Macrostomum hystrix*, M. SCHULTZE, Turbell. p. 56 t. 1 f. 15; t. 5 f. 3 (Abb.). — 1851 *Macrostoma hystrix*, R. S. MAITLAND in: Lugduni-Bataavorum pp. 183—190. — 1877 *Macrostoma hystrix*, A. O. GRIMM in: »Trudi« der St. Petersburger Ges. d. Naturforscher 8, 114. St. Petersburg (russisch). — 1879 *Macrostomum hystrix*, HALLEZ in: Trav. Wimereaux 2, 8, 63, 67 t. 1 f. 12; t. 6 f. 3; t. 11 f. 36, 37. — 1879 *Macrostomum hystrix*, G. DUPLESSIS in: Bull. Soc. Vaudoise Sci. Nat. sér. V, 16, 157—160. Lausanne. — 1882 *Macrostoma hystrix*, L. GRAFF, Monogr. Turbell. 1, 240 t. 4 f. 1—3 (Abb.). — 1884 *Macrostomum hystrix*, G. DUPLESSIS-GOURET in: Arch. Zool. exp. gén. 2, sér. 2, 36—67, Tab. II, Paris. — 1884 *Macrostoma hystrix*, W. SILLIMAN in: Z. wiss. Zool. 41, 49. — 1885 *Macrostoma hystrix*, M. BRAUN in: Arch. Dorpat. Ges. Naturk. ser. 2, 10, 137. — 1885 *Macrostoma hystrix*, P. STEPANOW in: Arb. (Truidi) Naturf. Ges. b. d. Universität Charkow 19, 28 (russisch). — 1887 *Macrostoma hystrix*, P. STEPANOW in: Bull. Soc. Natural. Moscou 62 (2 partie) 189. Moscou. — 1890 *Macrostoma hystrix*, L. VAILLANT in: Lombriciens, Hirudiniens, Bdello-morphes, Térétulariens et Planariens 3 (2) 621—656, Tab. XXVIII und XXIX. Paris. — 1892 *Macrostoma hystrix* + *Macrostoma ventriflavum*, PEREYASLAWZEWA in: Zap. Novoross. Obshe. 17 (3) 178, 244 t. 2 f. 16; t. 16 f. 150. — 1893 *Macrostoma erinaceum*, C. GIRARD in: Ann. Sci. Nat. ser. 7, 15, 214. — 1900 *Macrostoma hystrix*, P. BUTSCHINSKY in: Zool. Anz. 23, 495. — 1900 *Macrostoma hystrix*, A. SELIGO in: Untersuchungen in den Stuhmer Seen pp. 44—49. Danzig. — 1902 *Macrostoma hystrix*, DORNER in: Schr. phys.-ökon. Ges. Königsb. 43, 14. — 1904 *Macrostoma hystrix*, MARKOW in: Trudi Kharkov Univ. 39, 22 t. 1 f. 3. — 1905 *Macrostoma hystrix*, LUTHER in: Festschr. Palmén, 1 (5) 4, 48 f. 2; t. 1 f. 2, 4—8, 10, 17—19, 27; t. 2

f. 1, 7, 8, 10; t. 3 f. 1—8; t. 4 f. 1—7, 16—22, 28, 31—35 (Anat. Histol.). — 1905 *Macrostomum appendiculatum*, L. GRAFF in: Z. wiss. Zool. 83, 80 t. 2 f. 1. — 1909 *Macrostomum appendiculatum*, L. GRAFF in: Brauer, Süsw. 19, 76 f. 155, 156. — 1909 *Macrostomum appendiculatum*, C. E. STRINGER in: Zool. Anz. 34, 257. — 1910 SEKERA, E., p. 1. — 1911 SEKERA, E., p. ?. — 1911 GRAFF, L., p. 30. — 1912 HOFSTEN, N. v., pp. 561, 563, 577, 606, 676, 677. — 1913 GRAFF, L., p. 49. — 1915 FULINSKI, B., pp. 159—175. — 1915 MEIXNER, J., p. 469. — 1917 HOFSTEN, N. v., pp. 698, 721, 722, 723, 727, 729, 733, 734. — 1917 BEKLEMISCHEFF, W., p. 349. — 1918 LUTHER, A., p. 48. — 1918 HIGLEY, R., pp. 39, 42. — 1919 NASSONOV, N., p. 70. — 1923 NASSONOV, N., pp. 72, 75, 330, 342, 343, 344, 347. — 1924 NASSONOV, N., p. 331. — 1925 NASSONOV, N., p. 60. — 1926 GIEYSZTOR, M., p. 623. — 1926 STEINBÖCK, O., pp. 430, 434, 438. — 1926 THIENEMANN, A., p. 183. — 1927 BEKLEMISCHEFF, W., p. 177. — 1929 CARTER, J. S., p. 431. — 1930 GIEYSZTOR, M., p. 308. — 1931 GIEYSZTOR, M., p. 131. — 1932 STEINBÖCK, O., pp. 304, 337. — 1932 FULINSKI, B., and E. SZYNAL, pp. 192, 206. — 1933 REISINGER, E., p. 240. — 1935 BEAUCHAMP, P., p. 148. — 1937 FERGUSON, F. F., p. 30.

Macrostomum appendiculatum (O. FABR.), (*M. hystrix* OE., *M. ventriflavum* PEREYASLAWZEWA, *M. erinaceum* GIRARD) is found in many types of fresh, brackish and salt water the world over. The American representative is an animal which moves sluggishly upon the sub-strate. It is quite gregarious.

This animal, whose extended body has a blunt anterior end and a spatulate posterior end, measures according to SCHULTZE (1851, p. 57) 1 mm. in length and .25 mm. in width (Fig. 1). FERGUSON (1937, p. 57) gives the average length of ten sexually mature specimens as 1.25 mm. The animal is colorless with the exception of that color imparted by the enteric contents. GRAFF (1913, p. 46) depicts three types of rhabdites: (1) Very small ones, 5 μ long possessing stumped ends. They are found in groups of from two to ten and usually project from the epidermis over the entire body surface; (2) larger ones with spindle shape, pointed on both ends, arranged in groups of two and three, 10 μ long, and very numerous in tail region; (3) small ones, one end pointed, one end blunt, 4.5 μ to 9 μ long, and located anteriorly around the mouth and in "Stäbchenstrassen". These latter are undoubtedly rhammiten. The rhabdoids in the American form may be divided only into rhabdites and rhammiten, there being only one type of rhabdite.

SCHULTZE (1851) and GRAFF (1913) describe a two-fold epidermal ciliation consisting of cilia and sensory hairs. FERGUSON (1937, p. 30) notes a three-fold ciliation consisting of cilia, sensory hairs and spines, for the American animal.

The "brain" is well drawn in GRAFF (1882, Taf. IV, Fig. 2). Ganglion cells are discretely represented in either bulbar ganglion.

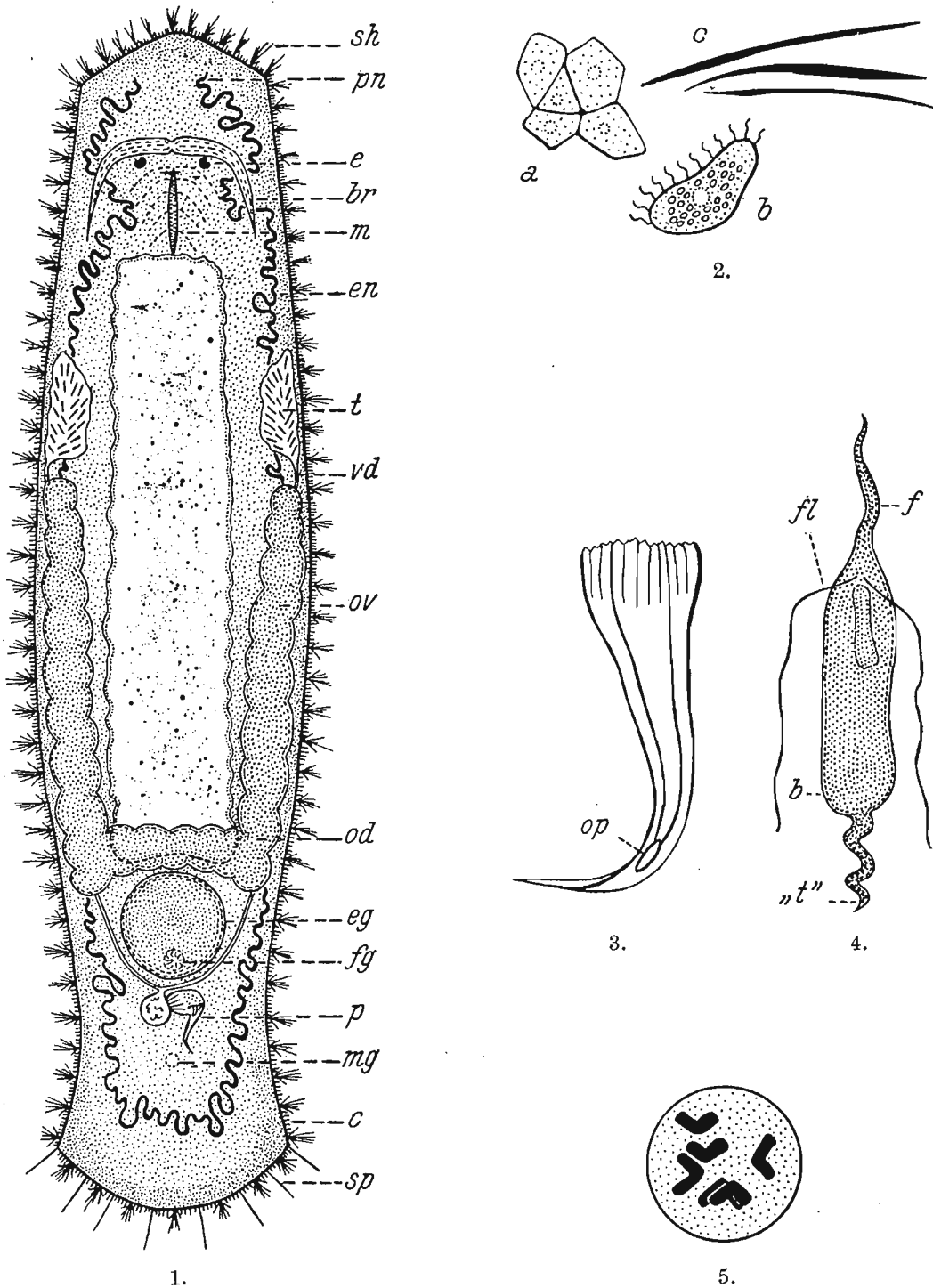


Fig. 1. *M. appendiculatum* O. Fabr. Dorsal view of gross anatomy. $\times 100 \times$.
 Fig. 2. *M. appendiculatum* O. Fabr. a) Epidermal cells; b) enteric cell; c) muscle fibers of tait. $350 \times$.
 Fig. 3. *M. appendiculatum* O. Fabr. Penis-stilette. $660 \times$.
 Fig. 4. *M. appendiculatum* O. Fabr. Mature sperm cell. $2000 \times$.
 Fig. 5. *M. appendiculatum* O. Fabr. Chromosomes. $2000 \times$.

There is an unusually wide commissure between the halves of the "brain". The bean-shaped eyes are not embedded in "brain" tissue in the American form as they are in the European form. The lens in the European form is smaller than in the American form.

The first fifth of the body contains the mouth, which forms a very constantly shaped longitudinal ventral split. The pharynx is relatively large and is well supplied with gland cells which empty at the mouth. The enteron's epithelium (Fig. 2) is provided with a dense coat of fine flagella. Temporary diverticula are often seen in the enteron's wall.

The protonephridial system is composed of two longitudinal main branches which extend laterally from one end of the body to the other. The convoluted tubules, as shown in BRONN (1908, p. 2152), composing this system empty to the exterior close behind the mouth in short transverse branches from the main lateral tubule. FERGUSON (1937, p. 29) shows that the main lateral lines unite in the posterior just behind the point of the penis-stilette.

There is a distinctive set of glands around the female gonopore. It is located at the beginning of the last body fourth, while the male gonopore is somewhat further from it than it is from the posterior end and lacks accessory glands.

The compact testes are laterally located in the second fourth of the body and may extend one-third of the body length. The vasa deferentia unite before entering the false vesicula seminalis. The ellipsoidal vesicula seminalis tapers to enter into a narrow ciliated canal which is connected to the distal vesicula granulorum. The latter is lined with a sausage-shaped secretory mass whose granules are very fine. It bears a colorless, pliable penis-stilette. The sharply pointed stilette is generally bent at right angles. GRAFF (1913, p. 50) remarks that the thickness of the point and of the widened proximal portion of the stilette varies. FERGUSON (1937, p. 30) notes that "measurements taken on the stilette (Fig. 7) show these average figures; length 59.8 micra, width of base 19.5 micra, length of somewhat elliptical opening 8 micra. The shape of the penis-stilette (Fig. 7) agrees with the illustrations of BRONN (1908, Taf. XVII, Fig. 13, 14), in that the funnel-shaped stilette gradually narrows from a widened, crenated base and terminates in a distal right angle bend. The opening is located in the convexity of the curve, subterminal to the pointed tip of the stilette." GIEYSZTOR (1931, p. 131) studied *M. appendiculatum* and noted that the forms taken at Albufera had stilettes whose terminations were strongly rebent. GRAFF (1882, Taf. VI, Fig. 6) shows the sperm cells in European forms to be very delicate elongate threads without cellular differentiation, while FERGUSON (1937, Text-Fig. 8) displays them as spindle-shaped structures

which measure 50 micra in length. They have two long flagella ("Nebengeißeln") as shown in (Fig. 4) from FERGUSON (1937, Text-Fig. 8, *fl*). GRAFF (1913, p. 50) remarks that the sperm cells when mature (.1 mm. long), are filamentous with a thickened middle region and a very fine tail.

The female reproductive system has roundish, compact ovaries, which are located dorsal to the testes. The mature eggs may possess a bright golden shell. In the American form very small worms may have eggs in the genital atrium. The eggs are yellow-brown when deposited.

A meiotic mitosis at metaphase, as taken from testes tissue, presents three pairs of chromosomes (Fig. 5). There is a large pair and two smaller pairs; all have median constrictions.

Paratype: U. S. N. M. No. 20449.

Species Diagnosis.

Macrostomum appendiculatum (O. FABRICIUS): Body has blunt anterior end, spatulate posterior end; length up to 1.25 mm.; triple variation in rhabdites and epidermal ciliation; pharynx relatively large; excretory system has posterior commissure and empties posterior to mouth; penis-stilette funnel-shaped, bent to right in sharpened termination, opening in convexity of curve, subterminal to the pointed tip, length 59.8 micra, sperm cells spindle-shaped, thickened middle portion with two lateral flagella, chromosomes in three pairs, one large pair, two smaller pairs.

Macrostomum appendiculatum var. *sillimani* mihi (*M. sensitivum* SILLIMAN).

1884 *Macrostoma sensitivum*, W. S. SILLIMAN in: Z. wiss. Zool. 41, 49 t. 3 f. 17, 18. — 1893 *Macrostoma sensitivum*, C. GIRARD in: Ann. Sci. Nat. ser. 7, 15, 215. — 1911 *Macrostomum sensitivum*, L. GRAFF in: Z. wiss. Zool. 99, 30 t. 2 f. 28—30. — 1905 LUTHER, A., pp. 28—30. — 1908 GRAFF, L., in: BRONN, H. G., p. 2152. — 1913 GRAFF, L. v., pp. 51, 52 f. 55. — 1918 HIGLEY, R., pp. 39, 42. — 1929 NASSONOV, N., pp. 423, 424. — 1929 CARTER, J. S., p. 431. — 1933 BRESSLAU, E., in: KÜKENTHAL and KRUMBACH.

Macrostomum appendiculatum var. *sillimani* mihi inhabits the fresh waters of Monroe County, New York, and the brackish waters of Falmouth, Massachusetts¹.

The body of this form is broadest in the middle, while the anterior end is blunt. With the exclusion of the golden-brown enteron, the body is grayish-white in color. This animal measures up to 1.5 mm. in length.

Rhabdites occur singly or in packets of two and three over

¹ This new variety is named in honor of Dr. W. A. SILLIMAN, who first studied it in Monroe County, New York, in 1884.

the external body surface. "Rhabditenstrassen" which originate in glandular cells near the "brain" empty their contents at the foremost tip of the body. Sensory hairs which are developed over the body surface are particularly long at the anterior end, measuring up to 30μ .

The "brain" (Fig. 6) in this species is unusual in that it does not possess the usual median constriction so common to *Macrostomum*. The small eyes are dorsally situated with respect to the "brain".

The mouth (Fig. 6, *m*) is ventrally located in the first body fifth. This opening is limited by longitudinal lips which are gran-

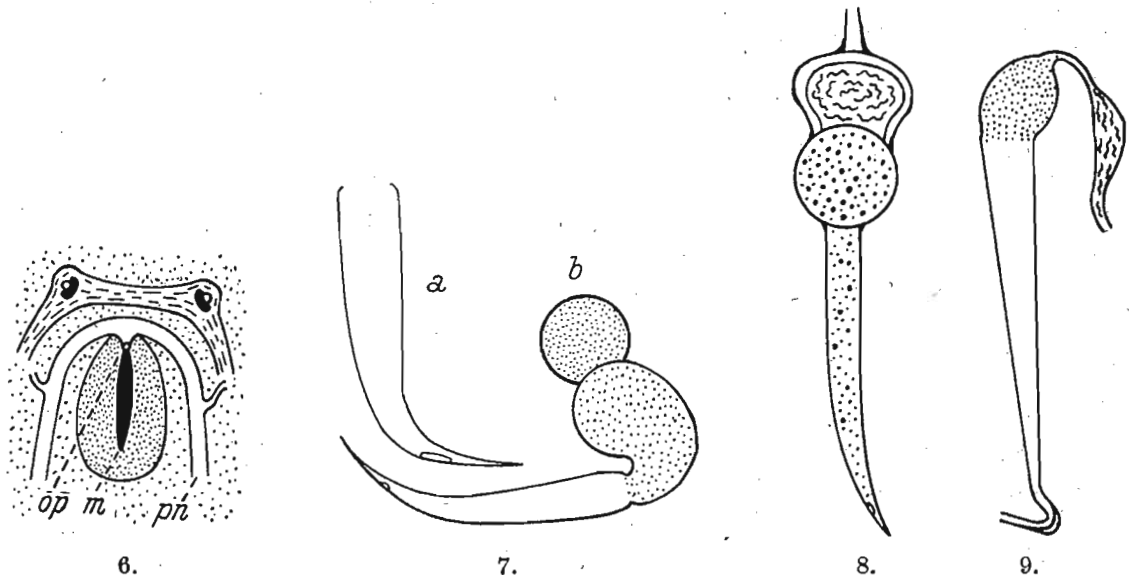


Fig. 6. *M. appendiculatum* var. *sillimani*. Opening of protonephridia (after Silliman 1884, Taf. III, Fig. 17). $\times ?$

Fig. 7. a) *M. appendiculatum* O. Fabr. Penis-stilette (after Graff 1882, Taf. IV, Fig. 9). $\times ?$.

b) *M. appendiculatum* var. *sillimani* mihi. Penis-stilette (after Graff 1911, Taf. II, Fig. 29). $\times ?$.

Fig. 8. *M. appendiculatum* var. *sillimani* mihi. Penis-stilette (after Silliman 1884, Taf. III, Fig. 18). $\times ?$.

Fig. 9. *M. beauchampi* mihi. Penis-stilette (after Beauchamp 1935, p. 4). $\times ?$.

ulated. The flagellated enteron is provided with regularly shaped lateral diverticula.

The excretory system is composed of lateral protonephridia which join in the anterior end (Fig. 6, *pn*) between the "brain" and the mouth, into which the cross commissure communicates.

The male reproductive system is partially described; the muscular globoid vesicula seminalis (Fig. 7b) communicates with the larger vesicula granulorum, which ostensibly contains many granular lobes which terminate in the region of the penis-stilette's origin. The penis-stilette (Fig. 8) is almost straight in its main axis and is terminally bent in an angle of approximately 25° . The small external opening is sub-terminal, being located upon

the convexity of the curve. The female reproductive system is not described in the literature.

Taxonomically, *M. appendiculatum* var. *sillimani* mihi differs from *M. appendiculatum* (O. FABR.) in that the variety does not possess the peculiar morphology of the "brain" and eyes (Fig. 1, *br*, *e*), the protonephridial system, or the "Haftpapillen" of the species. There is, however, a great similarity in the morphology of the penis-stilettes as shown in (Fig. 7, *a*, *b*), and in the stumped anterior ends of these two *Macrostomum*.

The above morphological description of *M. appendiculatum* var. *sillimani* mihi is based upon SILLIMAN (1884).

Variety Diagnosis.

Macrostomum appendiculatum var. *sillimani* new variety: Body widest at middle, anteriorly truncated, grayish-white, antero-lateral "Rhabditenstrassen" present, anterior sensory hairs unusually long ($30\ \mu$), brain lacks median constriction, excretory system empties into anterior mouth division from protonephridial commissure, granular material in sausage-shaped lobes in vesicula granulorum, penis-stilette is elongate funnel with terminal point bent at angle of 25° , opening subterminal, body length up to 1.5 mm.

Macrostomum beauchampi mihi (*M. viride* var. *elgonense* BEAUCHAMP)².

1935 *Macrostomum viride* var. *elgonense*, P. DE BEAUCHAMP in: Mission Scientifique de l'Omo. Tome III Zoologie Fasc. 23 Feb. P. Lechevalier and Sons. Paris 1935.

Macrostomum beauchampi mihi has been collected from several stations near Mt. Elgon in Uganda, Africa.

This African form resembles *M. appendiculatum* O. FABR. in shape. The epidermis is supplied by groups of rhabdites. The pharynx is stated to occupy one-fifth of the body, which measures up to 2 mm. The posterior region is spatulate.

Although most anatomical features were poorly described in this species, the penis-stilette is well described and figured. Remarking upon this unusually long stilette (Fig. 9), BEAUCHAMP (1935, p. 148) remarks: "Le tube pénien atteint une longueur de .55 mm. chez les grands, donc plus du quart de la longueur totale, sa partie moyenne est droite et régulièrement atténuée, l'extrémité mince se courbe à angle droit ou plutôt avec une légère torsion hélicoïdale et présente du côté convexe une petite crête de renforcement. Elle s'ouvre par un orifice terminal, mais taillé en biseau." The muscular elongate vesicula seminalis is joined by

² The animal described by BEAUCHAMP as *M. viride* var. *elgonense* BEAUCHAMP is renamed *M. beauchampi* mihi in this work.

a very narrow ductus ejaculatorius to the bulbar vesicula granulorum.

Taxonomically, this African form occupies the position of a new species, since it in no wise resembles *M. viride* BENEDEN, and since the literature does not include a description comparable to that given above for the penis-stilette. Further work upon this unusual form is most desirable.

Species Diagnosis.

Macrostomum beauchampi new species: Body shape resembles that of *M. appendiculatum* (O. FABR.), pharynx long, posterior spatulate, vesicula seminalis elongate, ductus ejaculatorius slender, vesicula granulorum bulbar, penis-stilette (550 μ long) is long funnel with straight walls and helicoidal distal termination, opening terminal at oblique truncation, body length up to 2 mm.

Macrostomum beaufortensis FERGUSON.

1937 *Macrostomum beaufortensis* FERGUSON, F. F. FERGUSON in: Zool. Anz. **120** (1937) 1, 12. H. 9/10.

The figures to the text of the above reference and the species diagnosis are included here for purposes of comparative study.

Species Diagnosis.

Macrostomum beaufortensis FERGUSON: Body slender, extremities rounded, posterior sensory hairs and "Haftpapillen", enteron dorsal to sex apparatus, vesicles in lateral main stems of excretory system, vesicular areas and zoochlorellae in parenchyma, vesicula granulorum greatly reduced, stilette a widened and greatly curved funnel with undulating basal rim, chromosomes very small, body length up to 1.4 mm.

Paratype: U. S. N. M. No. 20429, 20430, 20450 and 20451.

Macrostomum boreale RIEDEL (*M. anocela* RIEDEL).

1932 *Macrostomum boreale*, G. RIEDEL in: Vidensk. Meddel. Dansk. naturh. Foren. **94**, 33—107 t. 1 f. 1; t. 2, 8, 10, 15, 16, 27. — 1932 STEINBÖCK, O., pp. 304, 335. — 1934 REISINGER, E., p. 246.

Macrostomum boreale RIEDEL is a marine form found living in the waters of the Insel Disco in Greenland.

The body is elongate, measuring about 1 mm. and has blunt extremities. A spatulate tail is present, to a degree as shown by RIEDEL (1932, Text-Fig. 27). There is no color and there are neither eyes nor ciliated pits in this form. "Rhabditenstrassen" are located at the anterior end of the animal.

The epithelium, as depicted in RIEDEL (1932, Taf.-Fig. 1 a, ep), is made up of cylindrical cells which measure up to 8 μ in height. The cilia (z) measure about 1.5 μ in length. A row of basal bodies and a basal membrane are integral parts of this tissue.

This animal's body is richly supplied with glandular tissue. In RIEDEL (1932, Taf.-Figs. 3, 12) a developmental series in the production of rhabdites may be followed. These adenal rhabdoid

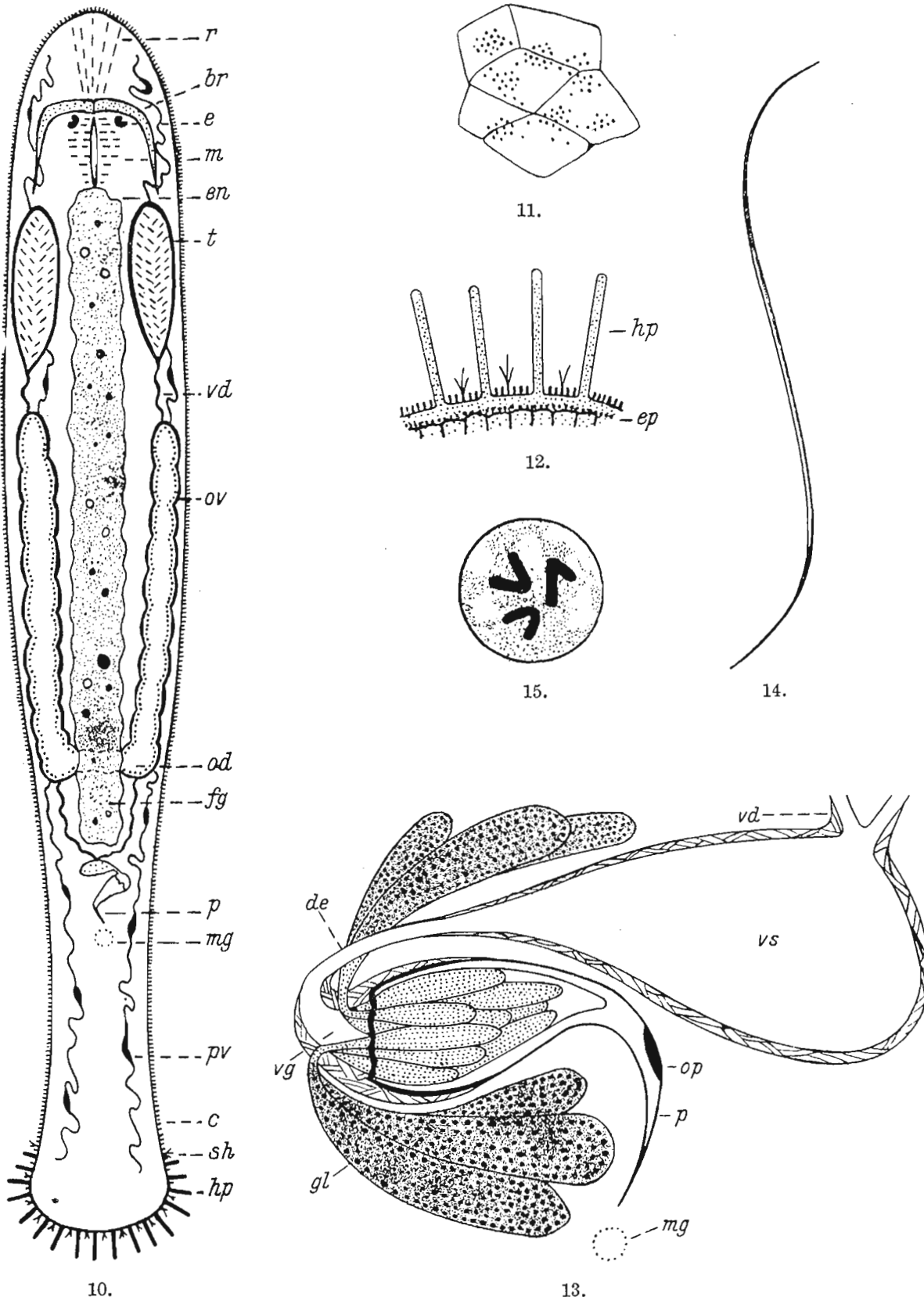


Fig. 10—15. *M. beaufortensis* Ferguson.
 Fig. 10. Dorsal view of gross anatomy. 100 ×. — Fig. 11. Epidermal pigmentation. 250 ×. —
 Fig. 12. Epidermal "Haftpapillen". 1000 ×. — Fig. 13. Male sex apparatus. 1500 ×. — Fig. 14. Ma-
 ture sperm-cell. 1500 ×. — Fig. 15. Meiotic chromosomes. 6000 ×.

cells send their product from the place of origin, antero-dorsal to the "brain" close under the epidermis, to the anterior margin of the body. These gland cells measure about $10\ \mu$ in length. The gland cells are constituted of a gray homogeneous plasma containing a spheroidal nucleus.

The body musculature is well developed as shown by the dorso-ventral fibers in RIEDEL (1932, Taf.-Fig. *dvf*). These fibers are concentrated in the tail and head region, and are about $2\ \mu$ thick. The pharynx simplex does not possess circular muscle-fibers nor an epithelio-basal-membrane.

The lengthened slit-like mouth communicates with the pharynx, which is slightly bowed out. There is a gradual transition between the pharyngeal epithelium and the parenchyma, in which the gland cells of the pharynx become less frequent among the surrounding parenchymal cells. At the middle level of the pharynx the gland cells which limit this structure are arranged in rosettes.

The digestive system is regular in its morphology. The digestive epithelium is composed of cells which are $90\ \mu$ high. Ostensibly there is a tendency here toward a syncitial development.

The "brain" presents the usual features for *Macrostomum*. The ganglia which compose the "brain" are $67\ \mu$ in diameter. These structures divide the glands of the "Rhabditenstrassen" into two groups—a larger dorsal one and a smaller ventral one.

The vesicula seminalis is oval in shape and is strongly developed. A muscular mantle houses this organ, which measures $46\ \mu$ by $20\ \mu$. There are no cell limits to the epithelial homogeneous plasmatic layer as shown in (Fig. 16). Externally the vesicula granulorum is encased by a set of longitudinal muscle-fibers. Many external circular muscles are in evidence.

The vesicula granulorum has three openings—one for the reception of the sperm cells, and two laterally located ones for the granular material. A set of sphincter muscles care for the opening and closing of the vesicula granulorum at its first portal. There are no cilia in the vesicula granulorum. The proximal epithelium in the granulorum is composed of cells low in stature while the cells of the distal epithelium are distinctly larger. In this distal region there are cells whose large size seems to suggest the inference that they were instrumental in the development of the penis-stilette. A set of strong accessory muscles is connected to both the granulorum and the tunic of the penis-stilette (Fig. 16).

The penis-stilette (Fig. 17) is $120\ \mu$ long. The genital canal

which serves the penis-stilette is composed of a ciliated epithelium near the male gonopore.

The antero-laterally located ovaries are deeply lobed (Fig. 18) resembling those of *M. orthrostylum* BRAUN in MEIXNER (1915, p. 473, Taf. 1, Fig. 7, 8) and those of *M. viride* BENEDEN in LUTHER (1905, p. 42). More or less indented ovarian radiations from the "Sammelgang" are present. The ovaries open directly into the oviduct.

The ovocytes are arranged close together in the individual lobes of the ovaries, with many canaliculi between them. Numerous

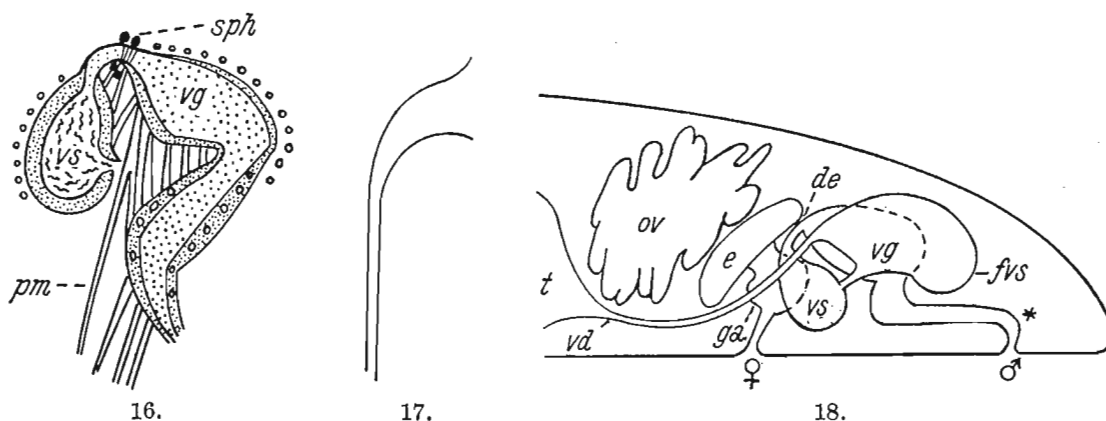


Fig. 16. *M. boreale* Riedel. Musculature of male sex apparatus (after Riedel 1932, Taf. III, Fig. 8). ? ×.

Fig. 17. *M. boreale* Riedel. Penis-stilette (after Riedel 1932, Fig. 16). × ?.

Fig. 18. *M. boreale* Riedel. Sex apparatus (after Riedel 1932, p. 61). × ?.

shell droplets are found between the ovocytes and the "Sammelgang". The eggs in the oviduct are non-spheroidal in shape, measuring 130μ by 48μ . The anterior epithelium of the genital atrium is nucleated and measures from 8 to 10μ in height. Ciliation in the distal part of the genital atrium is sparse. Numerous sperm cells are to be found implanted in the fore-wall of the genital atrium. This description has been taken from those references cited at the first of the paper.

Species Diagnosis.

Macrostomum boreale RIEDEL: Body elongate, colorless, eyes lacking, "Rhabditenstrassen" present, non-ciliated vesicula granulorum, penis-stilette is a slender basally widened funnel with proximal right angle bend, external opening is terminal at an oblique angle, body length up to 1 mm.

Macrostomum bulbostylum mihi.

M. bulbostylum mihi lives in fresh water ponds, springs, small streams and lakes. So far, it has not been found in the high mountain country of eastern America by the author. However, it has been found abundantly in the foothill country of the Blue Ridge and Smoky Mountains in Virginia and Ten-

nessee. *M. bulbostylum* has been described in Europe under the mistaken name of *M. tuba* VON GRAFF by these authors: GIEYSZTOR (1931, p. 305) found it at the University of Varsovie and gave two drawings (Figs. 20, 21) upon the stilette, and it was studied by BEKLEMISCHEV (1927, p. 202), who also gave a drawing of the stilette termination (Fig. 19). This form has a peculiar inter-generic relationship, for usually when it is found in great abundance there are practically no other rhabdocoeles present in the collection. In a newly formed lake in western Virginia (Giles County), this form abounded to the utter exclusion of other rhabdocoeles for an entire summer.

This animal, more so than in any other studied by the author, effects a gregarious and an almost sessile habit. It very rarely moves except when disturbed or in search of food. The author has observed cannibalism in this species among hungry animals.

The body is barge-shaped (Fig. 22) with a blunt anterior end, and a rounded semi-spatulate posterior region. It is practically colorless with the exception of that color furnished by the contents of the enteron. The average length of specimens taken in Tennessee was 2.5 mm.

Adenal rhabdites are present in groups of from two to ten over the body surface. The largest of these structures (Fig. 23) are about 17μ in length. The dorsal body surface is thickly set with groups of rhabdites, while in comparison there are only one-fourth as many rhabdites ventrally. There is an exceptionally large number of rhabdites just antero-subterminal.

In the Virginia form the rhabdites are very much more numerous at the anterior than at the posterior end of the body. They appear to be more numerous in the first dorsal body sixth than elsewhere. There are definitely more of them located laterally. The rhabdites emerge at a pore through the epidermis grouped in a pyramidal manner in which only one or two actually project (Fig. 22).

Rhammiten are present (Fig. 23) as adenal products in gland cells around the mouth.

Epidermal sensory hair-tufts are uniformly dispersed over the dorsal body surface. These short tufts are about 9μ long. There are no spines. Cilia are just as numerous ventrally as dorsally and measure about 4μ . Distinct basal bodies are present. The pattern of the ciliary action is shown in (Fig. 24).

The nervous system has been depicted in (Fig. 25) as having a "brain" with two ganglia, a very short median commissure, a circum-pharyngeal ring and lateral ganglionic extensions which serve the posterior body. In this latter region they grow noticeably thicker.

A detailed description has been given of the eye in KEPNER and STIFF (1932). They are small and black and are located dorso-posterior to the "brain" proper. For an accurate description of the anatomy of the eye in *M. bulbostylum mihi*, I quote KEPNER and STIFF (1932, p. 223): "HESSE (1897)

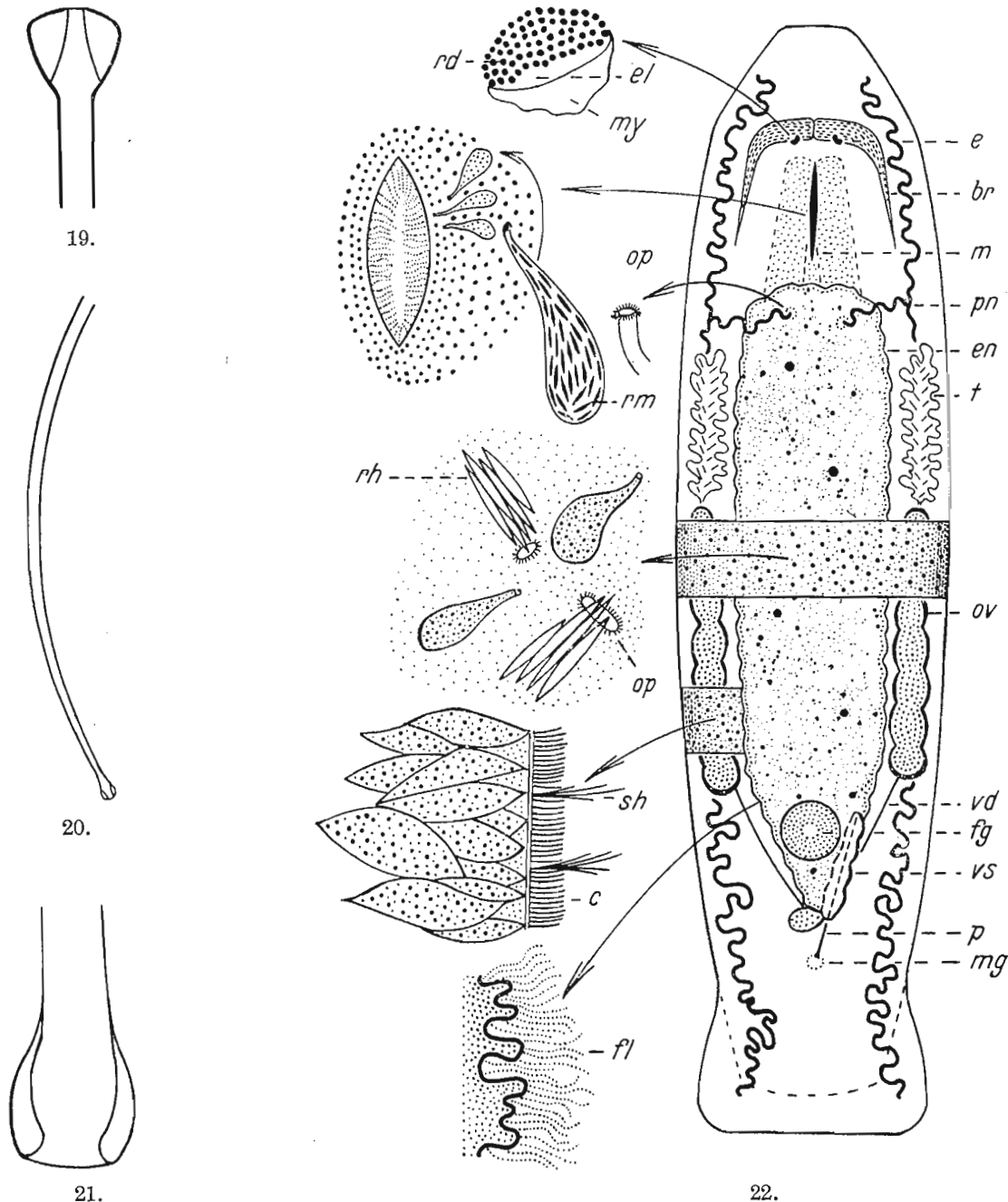


Fig. 19. *M. bulbostylum mihi*. Penis-stilette (*M. tuba* of Beklemischeff 1927, Taf. I, Fig. 6). ? ×.
 Fig. 20. *M. bulbostylum mihi* (*M. tuba* of Gieysztor 1931, p. 210, Fig. 2). Penis-stilette. ? ×.
 Fig. 21. *M. bulbostylum mihi* (*M. tuba* of Gieysztor 1931, p. 210, Fig. 3). Terminus of penis-stilette. ? ×.
 Fig. 22. *M. bulbostylum mihi*. Dorsal view of gross anatomy. ca. 50 ×. Detail of eye, 380 ×. Ventral view of mouth, 80 ×. Mucous glands and rhabdites piercing epidermis, 1330 ×. Ciliation, 850 ×. Enteric flagella, 850 ×. Penis-stilette, 350 ×. Terminus of penis-stilette, 1330 ×.

described a rhabdome-like region of the retinula that lay within the pigment cup of the triclad eye. KEPNER and TALIAFERRO (1916) discovered that at the base of the rhabdome of *Prorhynchus* (*Geocentrophora*?) *applanatus* there is a refractive, lens-shaped, middle region, thus recognizing three regions of the retinula of the turbellarian eye. JÄNICHEN (1896), as TALIAFERRO (1920, p. 61)

indicated, was probably the first to describe the middle region in the retinula of the turbellarian eye as a definite structure. It was left, however, for KEPNER and FOSHEE (1917) to name these three regions as rhabdome, ellipsoid, and myoid, and to indicate a striking analogy, in this manner, existing between the retinula of the vertebrate and that of the rhabdocoele. KEPNER and LAWRENCE extended this analogy when they discovered that the retinula of the rhabdocoele *Polycystis goettei* BRESSLAU presented rhabdome, ellipsoid, and myoid. The American investigators, therefore, were inclined to consider

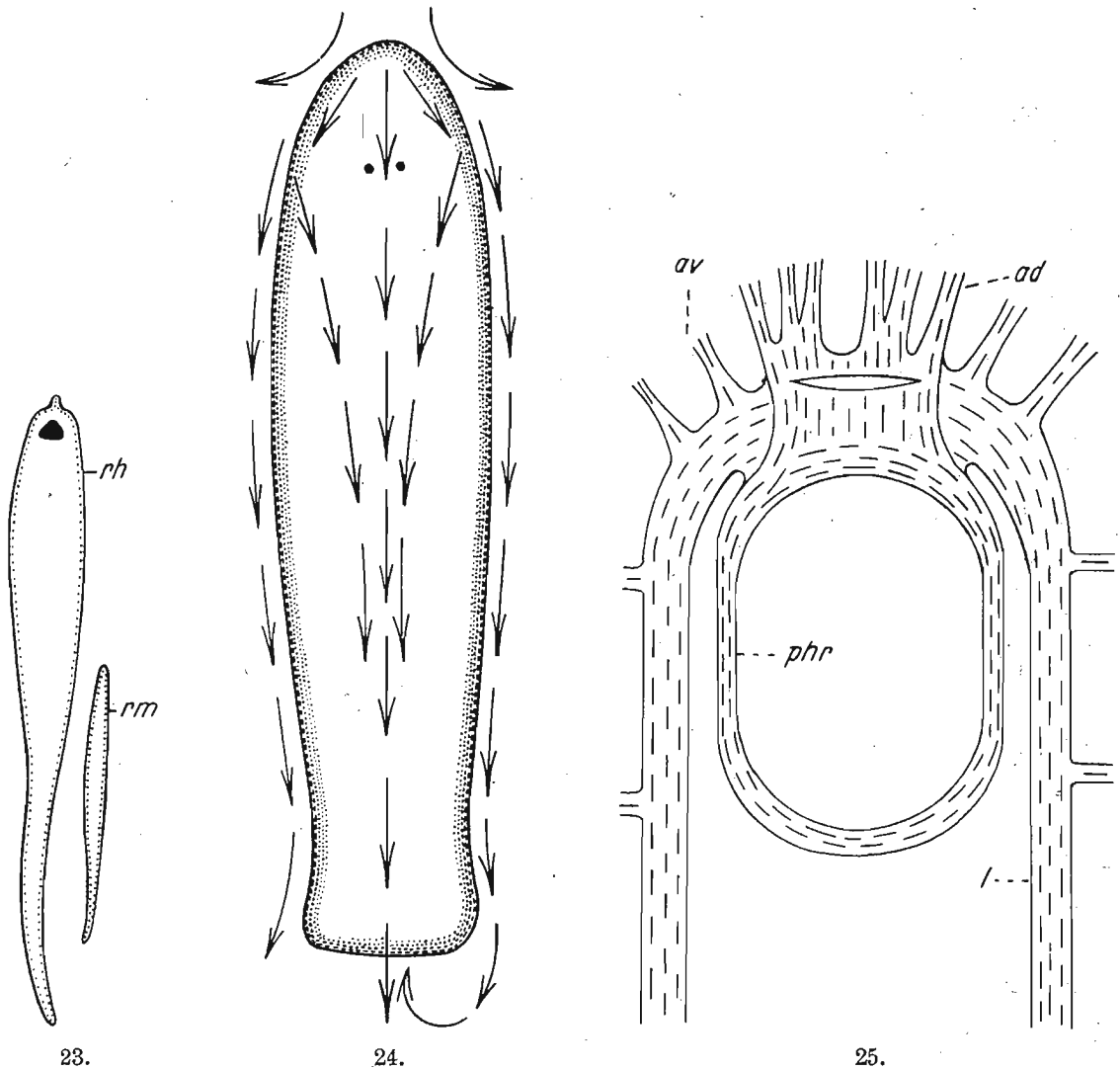


Fig. 23. *M. bulbostylum mihi*. Detail of rhabditic elements. 4000 ×.

Fig. 24. *M. bulbostylum mihi*. Drawing showing direction of ciliary currents. 30 ×.

Fig. 25. *M. bulbostylum mihi*. Detail of anterior nervous-system. 135 ×.

that the turbellarian retinula presented a striking analogy with that of the vertebrate retinula. The appearance, however, of STEINBÖCK'S excellent 'Monographie der Prorhynchidae (Turbellaria)' (1927) somewhat weakened the convictions of some of us concerning the presence of the three regions of the turbellarian retinula. STEINBÖCK was unable, for example, to find an ellipsoid in the retinula of the European *Geocentrophora appplanata*. BARRETT (1929), therefore made a second study of the eye of the American *Geocentrophora appplanata* and was able to demonstrate the ellipsoid.

The study of *Macrostylum tuba* (*M. bulbostylum mihi*) has revealed an interesting feature in this connection, for when ex-

amed under a 4 mm. or waterimmersion objective a lens-shaped, highly refractive, colorless body may be seen projecting beyond the mouth of the simple pigment cup of the eye. This refractive object (Fig. 3, *el*) resembled the refractive ellipsoid that KEPNER and THALIAFERRO (1916) found in a living, greatly compressed *Prorhynchus* (*Geocentrophora*) *applanatus*. A straw-colored (by transmitted light) region (Fig. 3, *r*) practically filled the lumen of the pigment cup of the living specimen. The living animal, therefore, showed a pigment cup (Fig. 3, *pc*), a straw-colored structure lying within the lumen of the cup, and a refractive lens-like body projecting from the mouth of the pigment cup. The fixed material showed that there was but a single retinula associated with each pigment cup, and that this retinula was very clearly differentiated into rhabdome, ellipsoid, and myoid (Fig. 4, *r, el, my*)."

M. bulbostylum mihi probably has the largest mouth in the genus. It is quite long and highly distensible and is located ventrally, equidistant between the eyes and the enteron. The pharynx, quite narrow in retraction, is capable of great enlargement. A limiting group of gland cell openings is found around the mouth as shown in (Fig. 22).

The enteron in contraction is distinctly wedge-shaped. There are many temporary diverticula. This entire structure which extends dorsal to the genital atrium and almost to the vesicula seminalis is clothed with a covering of fine, long, non-synchronized flagella. With its amazing propensity for extension this organ may engulf objects as large as the entire animal (Fig. 31).

The glands of this species present an interesting study. They furnish adenal rhabdoids, mucus, enzymes and granular material for the vesicula granulorum. Adenal rhammiten are excreted at the borders of the mouth as seen in the ventral view in (Fig. 22). Mucous gland cells (Fig. 22) are found over the body surface, in number equalling the groups of rhabdites. Enzymatic gland cells (Fig. 29) pour their contents into the enteron. Granular material for the vesicula granulorum is elaborated in loose groups of follicular cells which connect to the vesicula granulorum at the ductus ejaculatorius. Both the granular material in the gland-cell and in the vesicula granulorum are eosinophilic (Fig. 26).

Each lateral main branch of the excretory system sends a short off-shoot meso-dorsally to open to the exterior just behind the mouth and about 160 μ anterior to the anterior tips of the testes. This examination may be facilitated by keeping the animal in

a strong eosin solution for six hours. The opening is oval and ciliated (Fig. 22). Flame cells are observable at the terminations of the fine end branches.

The testes are located in the first body half, occupying a lateral position equidistant from the enteron and body wall. They

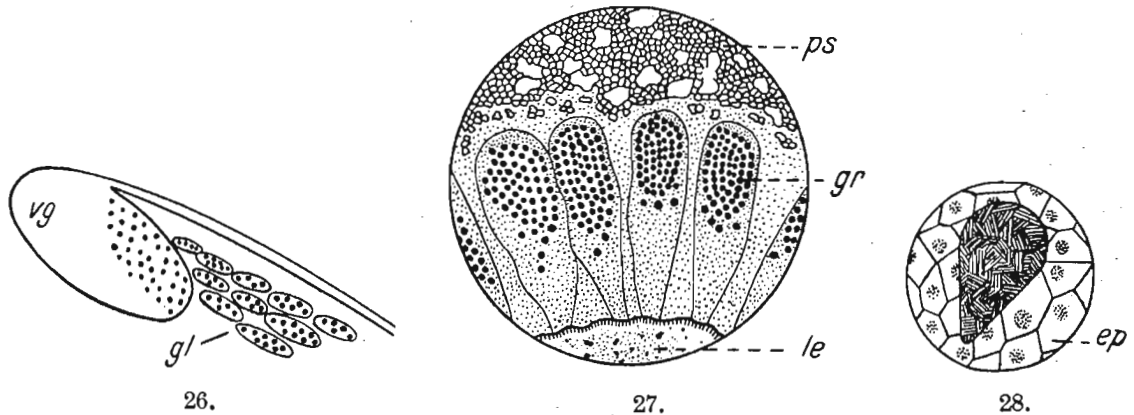


Fig. 26. *M. bulbostylum* mihi. Azure-eosin preparation of accessory gland cells to vesicula granulorum. 35 ×.

Fig. 27. *M. bulbostylum* mihi. Detail of enteric gland cells. 225 ×.

Fig. 28. *M. bulbostylum* mihi. Detail of epidermal inclusion. 85 ×.

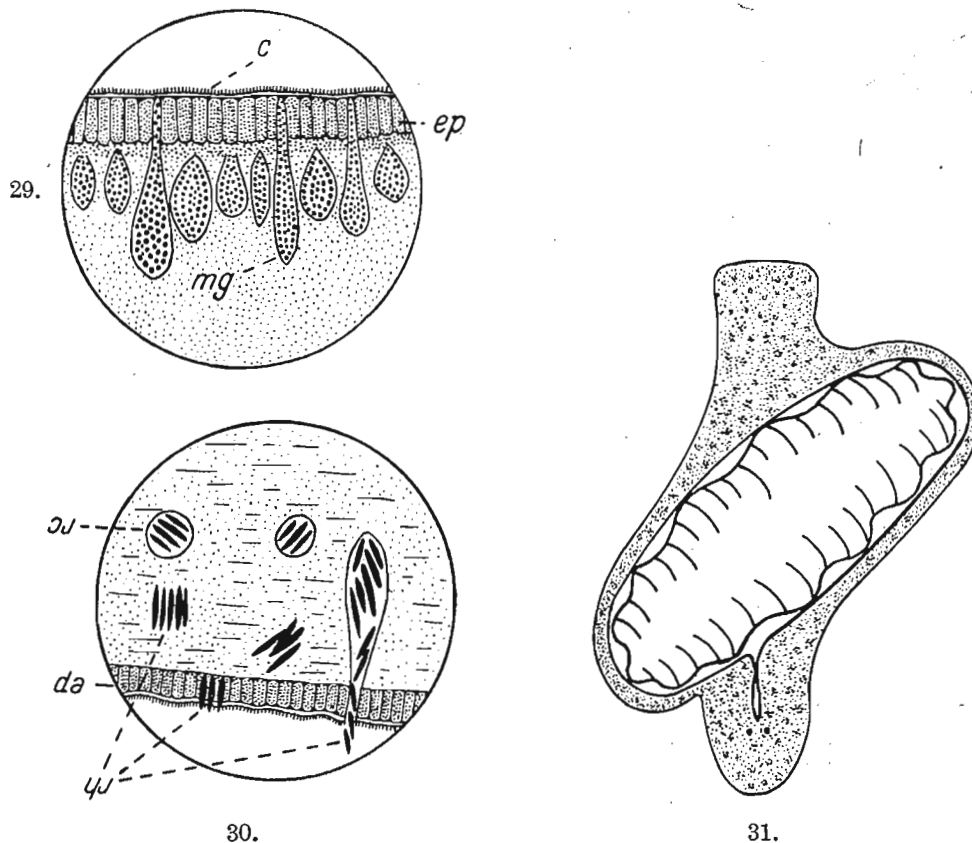


Fig. 29. *M. bulbostylum* mihi. Detail of mucous glands, 66 ×.

Fig. 30. *M. bulbostylum* mihi. Detail showing elaboration of rhabdites. 460 ×.

Fig. 31. *M. bulbostylum* mihi. Diagram showing enteron distended with food. 18 ×.

are oval in transverse section (Fig. 32). Both mesial and lateral walls are highly irregular in contour. A central collecting space sends off many branches into the testes. These alley-ways are filled with sperm cells in various stages of development (Fig. 33).

The vasa deferentia parallel the contour of the enteron to its posterior tip where they unite to empty into the vesicula seminalis. Occasionally the enteron may overlap the vasa deferentia as shown in (Fig. 22). The vesicula seminalis is a lengthened thick walled sack whose cilia keep the sperm-cells in motion. The normal shape of the vesicula granulorum is oval. Ciliated chambers are present at the entrance to the vesicula granulorum.

The penis-stilette (Fig. 21), whose proximal portion is buried in the tissues of the vesicula granulorum, is a very long funnel which is gradually reduced from its crenate basal part to its bulbous termination. The cuticular tube is straight for its entire length. The bulbous end (Fig. 34) of the stilette has two latero-terminal thickened walls. There is a definite enlargement of the lumen of the genital canal just distal to the beginning of the thickened walls. The

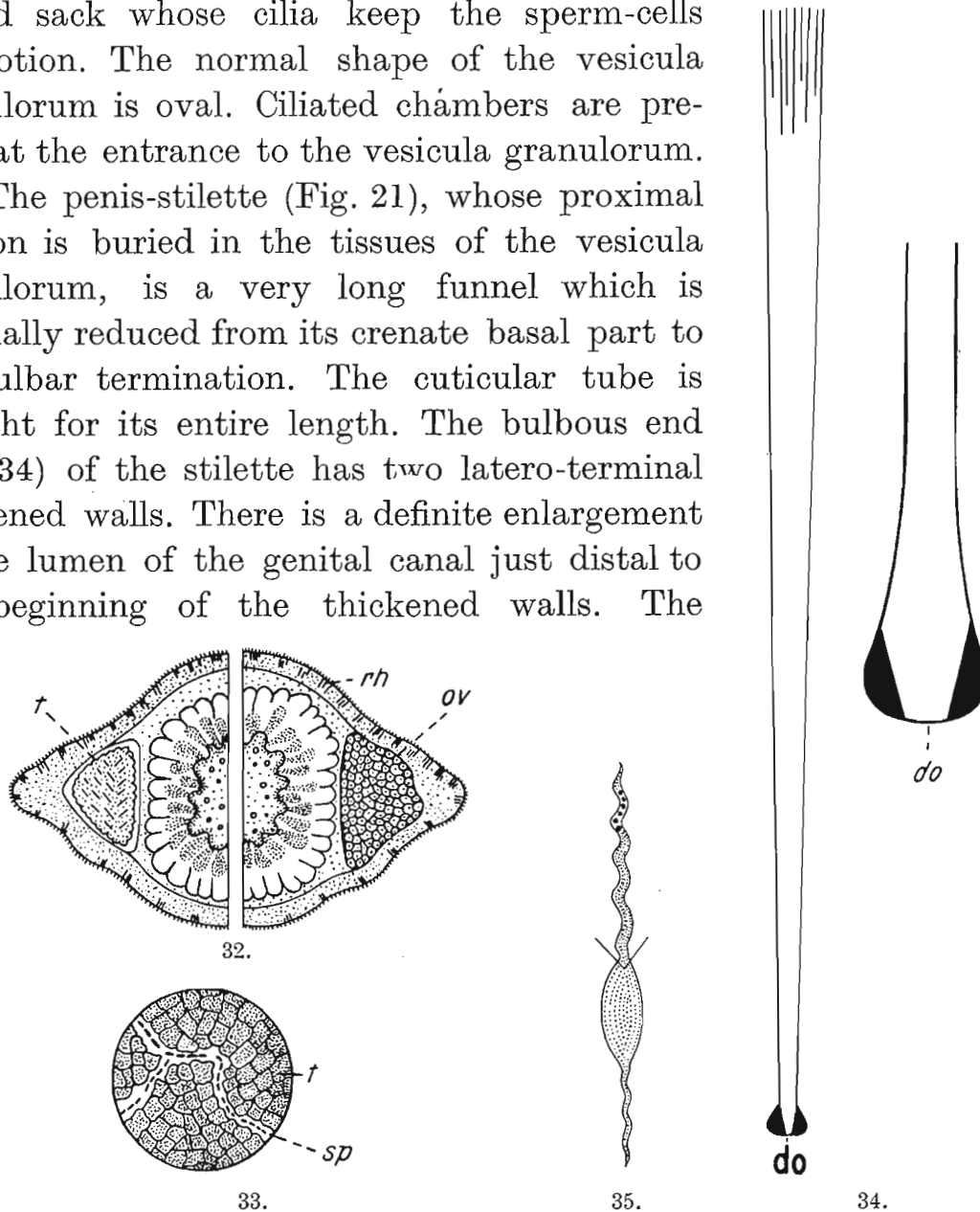


Fig. 32. *M. bulbostylum* mihi. Detail showing position of gonads in transverse section. 66 ×.
 Fig. 33. *M. bulbostylum* mihi. Detail of sectioned testis. 40 ×.
 Fig. 34. *M. bulbostylum* mihi. Gross anatomy of penis-stilette (350 ×) plus detail of stilette terminus (1330 ×).
 Fig. 35. *M. bulbostylum* mihi. Mature sperm-cell. 1000 ×.

external opening is circular and is smaller in diameter than the genital canal. The basal crenations are twice as deep as the diameter of the genital canal in that part. The walls of the long tube have a uniform thickness up to the bulbar termination. The longest penis-stilette that the author has studied measured 312.8 μ in length and 11 μ in diameter at its proximal end.

A muscular tunic clothes the stilette. The bulbar end of this structure remains directed toward the ventral ciliated male gonopore which is approximately twice as far from the posterior end as it is from the female gonopore.

Mature sperm cells, as studied in living material from the vesicula seminalis, measure 40μ in length. The cell is divided (Fig. 35) into anterior feeler (*f*), body (*b*), and posterior tail regions (*t*). The feeler is very thin and vibratile. The body of the cell is constituted of homogeneous cytoplasm and is provided with a pair of latero-posterior setae which originate at the connection of the tail to this region. The tail is as long as the combined feeler and body regions. In its terminal portion there is located a moniliform series of chromatic granules. Setae are to be found in sperm cells whose anterior ends are yet buried in nurse cells.

The female reproductive system has no particularly distinguishing characters except that the oviducts occupy about two-thirds of the distance from the genital atrium to the anterior origin of the ovaries. The ovaries (Fig. 22) are compact, indented and translucent structures. The oviducts which extend posteriorly from the mesial border of each ovary join in the posterior mid-ventral line to produce a slight enlargement, the common oviduct, as shown by KEPNER and STIFF (1932, Fig. 5, *cod*). The egg remains in this spheroidal receptacle before reaching its final position in the genital atrium. The structure of the female genital atrium is such that it never collapses without eggs as in most *Macrostomum*, but maintains itself as a discrete structure throughout. It is lined by large columnar cells. The lumen generally contains sperm cells which adhere to the anterior wall. The female gonopore lies ventral to the genital atrium. The eggs are dark gray in immaturity and red brown in maturity.

PHILLIPS (1936, p. 322) reports and recognized the spermatogonial chromosome number to be $n = 3$, $2n = 6$. The chromosome complement consists of one large pair, one medium sized pair and one small pair of chromosomes, all of which have median attachment constrictions. The oögonial divisions show six chromosomes. In the developing egg a large spindle is present which bears three chromosomes and is ostensibly a maturation division.

Taxonomically, *M. bulbostylum* mihi must be compared with *M. reynoldsi* mihi, *M. lewisi* mihi, *M. tuba* VON GRAFF, and *M. tuba gigas* OKUGAWA. These species, whose tube-like stilettes have thickened terminations, are the only ones which the literature presents that resemble *M. bulbostylum* mihi.

The stilette of *M. reynoldsi*, as shown in (Fig. in part V) is a slender curved tube containing two right angle bends and extending from a broadened base to a slightly knobbed end. The opening is subterminal. *M. reynoldsi* mihi measures up to .9 mm. in length. Obviously *M. reynoldsi* mihi and *M. bulbostylum* mihi may not be confused.

The stilette of *M. lewisi* mihi (Fig. in part V) measures about 104 μ in length and is a greatly bent tube containing two right angle bends. The tube extends from a dentate base to a reduced knobbed termination. The bulbar region is asymmetrical in that one side wall is always much thicker than the other one. It appears that this bulbar condition is an outgrowth of a cuticular ring around the end of the tube of the genital canal. A dentated ring encircles the proximal portion of the terminal bulb. The entirely straight tube of the stilette of *M. bulbostylum* mihi, with its symmetrical bulbous end, has nothing in common with the morphology of the stilette of *M. lewisi* mihi.

The comparison of *M. bulbostylum* mihi with *M. tuba* VON GRAFF is of especial interest:

(1) *M. bulbostylum* mihi is elongated and greatly flattened dorsoventrally. It measures about 3 mm. in length in the mature, distended condition. The anterior end is rounded while the posterior end is thin and spatulate dorso-ventrally. *M. tuba* VON GRAFF has a length of about 2.5 mm., has a weakly arched dorsal crest and is much more plump than *M. appendiculatum* (O. FABR.) The anterior end is broadly rounded, the posterior is reduced and the body has its widest part just behind the pharynx.

(2) The rhabdites of *M. bulbostylum* mihi have a singular structure (Fig. 23), measure about 17 μ in length and are one-fourth as numerous ventrally as dorsally. They are particularly numerous on the lateral extensions of the body. The rhabdites of *M. tuba* VON GRAFF are thicker on one end than the other and measure about 15 μ in length. They are dispersed in groups of from two to seven over the body surface.

(3) *M. bulbostylum* mihi does not possess "Haftpapillen" (Fig. 12). The peripheral rim of the spatulate tail in *M. tuba* VON GRAFF is thickly supplied with "Haftpapillen" (Fig. in part VII).

(4) The nervous system of *M. tuba* VON GRAFF is stated by GRAFF (1882) to be similar to the drawing given for *M. appendiculatum* (O. FABR.) (*M. hystrix* OERSTED in Taf. IV, Fig. 2, of that publication). *M. bulbostylum* mihi has a nervous system which does not agree to that shown in the drawing mentioned above. The commissure of the "brain" in *M. bulbostylum* mihi is so very narrow that the ganglionic halves of the so-called "brain" are in contact. In (Fig. in part VII) the ganglion cells of *M. tuba* VON GRAFF which are absent in *M. bulbostylum* mihi are demonstrated as discrete features. The lens in the eye of *M. bulbostylum* mihi is larger than that in *M. tuba* VON GRAFF.

(5) The sperm cell of *M. bulbostylum* mihi is an elongate spindle with homogeneous cytoplasm and is possessed of two latero-posterior setae. The cell measures 40 μ in length. Chromatic granules are present in the tail region. The sperm cell of *M. tuba* VON GRAFF is an elongate filament with a very delicate anterior feeler. The body region in the cell is provided with three strongly developed sharpened setae. There are no chromatic granules in the cell (Fig. in part VII).

(6) The penis-stilette of *M. bulbostylum* mihi is a straight elongated tube which extends from its highly crenate base to its bulbar termination. At the end of the stilette there is an enlargement in the genital canal, the walls are thickened and the opening to the exterior is smaller than the diameter of the genital canal. The penis-stilette of *M. tuba* VON GRAFF is a gradually reduced funnel which extends from a non-crenated base to its terminally bent bulbar end. The walls of the bulbar end are not thickened. If the drawings of GRAFF (1882, Taf. IV, Fig. 14, 15, 16) from which the above comparison has been made are correct, then the stilette of *M. bulbostylum* mihi is approximately twice as long as that of *M. tuba* VON GRAFF.

A variety of *M. tuba* VON GRAFF has recently been described in Japan by OKUGAWA (1930). This variety, *M. tuba gigas* OKUGAWA, is a very large animal (3.5 mm. \times .8 mm.) with an acuminate pointed head and eyes whose pigment cups are composed of an irregular massing of granules. The penis-stilette measures 200 μ in length and is an elongated slightly curved tube which does not appear to be funnel-shaped in the figures of OKUGAWA (1930, Pl. III, Fig. 3 and 4). The bulbous end of the stilette (Pl. III, Fig. 4) has a circular opening whose diameter is the same as that of the genital canal and which has a pair of asymmetrical thickenings in the walls. The stilette (Fig. in part VII) appears to be two and a half times as long as the vesicula granulorum. The excretory system has a posterior commissure in the tail region which is supplied with "Haftpapillen". The above description of the anatomy of *M. tuba gigas* OKUGAWA only includes those features which mark it as separate and distinct from *M. bulbostylum* mihi.

Species Diagnosis.

Macrostomum bulbostylum new species: Body elongate, flattened dorso-ventrally, anterior end rounded while posterior end is spatulate and thin, rhabdites more numerous at extremities, rhammiten present near mouth, postero-lateral nerve fibers enlarged, retinula of eye composed of rhabdome, ellipsoid, and myoid, penis-stilette is an elongated straight tube with a bulbar end whose walls are symmetrically thickened (length 312 μ), mature sperm cell measures 40 μ and has two postero-lateral setae plus chromatic granules, chromosome number is $n = 3$, $2n = 6$ including a large pair, a medium sized pair and a small pair all with median attachment constrictions.

Paratype: U. S. N. M. No's. 20431, 20432, 20433, 20434, 20435, 20452, 20453, 20454, 20455, 20456, 20457, 20458, 20459, 20460, 20461, 20481, 20482, and 20483.