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244 F. F. Ferguson, Genus *Macrostomum* O. Schmidt 1848. Part VIII.

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

By FREDERICK FERDINAND FERGUSON.

(Miller School of Biology, University of Virginia.)

(With 6 Figures.)

Eingeg. 9. September 1939.

Sexuality, egg and sperm development.

Reproduction in *Macrostomum* is entirely sexual. There is no evidence in the literature that the asexual production of zooids, as in *Microstomum*, ever occurs. Hermaphroditism is always expressed in the development of a separate and complete male and female sex apparatus.

Sexual intercourse in *Macrostomum* is accomplished by means of copulation. Animals in copula (see frontispiece) are united in such a manner that each individual suffers a half twist of the posterior body, thus keeping most of the body correctly orientated with respect to the substratum. The act of copulation involves the insertion of the penis-stilette of only one individual into the female genital atrium of the other animal. Reciprocal insemination at the same time does not occur. Copulation in *M. bulbostylum* mihi lasts for approximately two minutes. The urge to copulate is so strongly developed that very young specimens may be seen in union with mature ones. Generally, copulation takes place between animals which do not possess a trace of a developing egg. Copulation also has been found to increase when environmental conditions are ideal, while it decreases under poor conditions. Experimentally, copulation has been considerably increased by allowing large numbers of animals to remain in a strong solution of water soluble Eosin for a period of about six hours.

Since the animal is hermaphroditic, it would appear that a balance between the activities of the two systems would be productive of maximum results; yet egg-laying seems to continue at a set, uniform pace, while sperm-cell production is certainly accentuated in the summer months. Egg-laying, and to some extent sperm-cell-production, are affected by the lack of food. An immediate resumption of these functions is noticed when food again becomes plentiful.

The place at which fertilization occurs in the body is open to question. It would appear that the sperm-cell first penetrates the developing oöcyte in the common oviduct, in which spheroidal

space they may often be observed in great numbers. Moreover, since chromatic elements resembling the male nucleus have been found located near the center of the achromatized spindle, while the egg is still in the female genital atrium, it is thought that fertilization occurs here.

The study of the number and morphology of the chromosomes forms an important adjunct to the taxonomic characters expressed in *Macrostomum*. It is interesting to note that American species and varieties have a constant number ($n = 3$, $2n = 6$). The following is a complete list of the chromosome numbers in *Macrostomum* reported to date:

Chromosome number and morphology in *Macrostomum*.

Species or Variety	Number	Source	Morphology
<i>M. appendiculatum</i> (O. FABR.)	$n=3$, $2n=6$ $3 = 2$	(mihi) <i>in the 1905</i>	A large pair and two smaller pairs; all with median attachment points.
<i>M. beaufortensis</i> FER- GUSON	$n=3$, $2n=6$	(mihi)	A small pair with equal arms, a large pair with equal arms, and a large pair with unequal arms.
<i>M. bulbostylum</i> mihi	$n=3$, $2n=6$	(mihi)	A large pair, a medium sized pair and a small pair; all with median attachment constrictions.
<i>M. glochostylum</i> mihi	$n=3$, $2n=6$	(mihi)	A large slightly bent pair, a medium sized horse-shoe-shaped pair and a small V-shaped pair.
<i>M. orthostylum</i> BRAUN	$n=2$, $2n=4$ (?) $? = 2$	(BRAUN) <i>in the 1905</i>	Two short and pointed chromosomes present in mature egg.
<i>M. reynoldsi</i> mihi	$n=3$, $2n=6$	(mihi)	A large pair and two small pairs; all with median attachment constrictions.
<i>M. riedeli</i> mihi	$n=3$, $2n=6$	(mihi)	A small pair with unequal arms and two large pairs with near median spindle fiber attachment points.
<i>M. ruebushi crenato-</i> <i>stylum</i> mihi	$n=3$, $2n=6$	(mihi)	Three large pairs, three small pairs in somatic metaphase. All with median attachment constrictions.

Species or Variety	Number	Source	Morphology
<i>M. ruebushi finnlandensis</i> mihi	$n=2, 2n=4$ (?)	(LUTHER)	Two rod-shaped chromosomes are present in the maturing egg.
<i>M. ruebushi granulosum</i> mihi	$n=3, 2n=6$	(mihi)	A large, slightly bent pair, a medium sized V-shaped pair, and a small pair with spiral shape.
<i>M. ruebushi truncatum</i> mihi	$n=3, 2n=6$	(mihi)	A small rod-shaped pair, a small pair with hooked ends, a large J-shaped pair, a small horse-shoe-shaped pair, a large pair with hooked ends, and a large pair with a spiral shape (somatic metaphase plate).
<i>M. lewisi</i> mihi	$n=3, 2n=6$	(mihi)	A large V-shaped pair, a medium sized V-shaped pair, and a small pair with unequal arms.
<i>M. virginianum</i> FERGUSON	$n=3, 2n=6$	(mihi)	A pair with sub-median attachment points and two other pairs with median attachment points.

Spermatogenesis in *Macrostomum* was first studied by ZACHARIAS (1891). In this early work upon *M. viride* BENEDEN the developmental stages are outlined as spermatogonia, spermatocytes, and spermatids. Two processes are developed from an incipient spermatid, one of them becoming a "tail" thread. "Nebengeißeln" are simultaneously formed in the cell. Sometimes these lateral setae are developed before the "tail" region in the cell. The egg-shaped head becomes extended and finally, "kommt die bislang im Ruhezustande verbliebene Kernsubstanz in Bewegung, um in dem immer spindelförmiger werdenden Spermatozoonkopfe sich gleichmäßig zu vertheilen". PHILLIPS (1936) has supplemented this work with an excellent paper upon the cytology of an American form, *M. bulbostylum* mihi (*M. tuba* GRAFF of KEPNER and STIFF 1932), in which the development of the sperm-cell is stressed. Concerning this, PHILLIPS (1936, p. 324) remarks: "The chromosomes of the spermatogonia are somewhat smaller and more compact than those of either the mesenchymal cells or oögonia (Fig. 2). There is a striking similarity between the spermatogonial and meiotic chromosomes. The resting nucleus of a spermatogonium possesses a large, deeply staining nucleolus around which a clear space, or non-staining area, is observed (Fig. 3). The spermatogonia enlarge somewhat to form primary spermatocytes. At the beginning of the prophase of the first division, the six leptotene threads are distributed, apparently without any special orientation, throughout the nucleus. These threads possess small chromomeres which are spheroidal in contour (Fig. 4). No split chromomeres were observed prior to synapsis. The nucleolus

does not persist after the leptotene stage. The leptotene threads conjugate in homologous pairs to form the zygotene stage (Fig. 5). At this state no well defined matrix was observed. The three closely paired threads become slightly thicker and more compact to form the pachytene (Fig. 6). The pachytene then passes into the diplotene stage and as a result of the accumulation of extra chromatin material around the chromonemata, the separate threads are obscured (Fig. 7). The chromosomes become short and thick, and, at diakinesis, the three pairs lie scattered throughout the nucleus (Fig. 8). The synaptic pairs of chromosomes arrange themselves in a close association to form the first metaphase plate (Figs. 9 and 10). The anaphases of this first division show the dyads very plainly (Figs. 11 and 12). No metabolic nuclei are formed as a result of interkinesis; the chromosomes persist as such and pass directly to second metaphase with only a slight change in form (Fig. 13). The chromosomes of the second division are slightly smaller and more slender than those of the first division (Fig. 14). The secondary spermatocytes, which result from the first division, give rise to spermatids with granular resting nuclei (Fig. 15). When the cell-membrane and cytoplasm of the spermatid elongate to form the 'tail'-piece of the spermatozoon, the nucleus takes up a peripheral position close to the cell-membrane and near the elongated portion (Fig. 16). As the 'tail' piece becomes more elongated, the nucleus moves into it (Fig. 17). At this stage the nuclear membrane breaks down, and the chromatin material takes the form of chromonemata (Figs. 18 and 19). During the early formation and development of the chromonemata, the threads appear diffuse and irregular. The accumulation of chromatin material around the chromonemata produces distinct darkly staining threads. These form six distinct chromatin granules (Fig. 20). The granules move forward to form the head piece of the spermatozoon. Several hundred spermatozoa have been studied; each of them possesses either six, five, four, or three granules (Figs. 20, 21, 22, and 23). This variation in numbers suggests that adjacent granules have become closely associated. Further evidence for this conclusion is derived from the fact that when three granules are present, each of them is larger than a single granule of the group of six. The granules were observed when either of the fixation were used.

During their development, some of the spermatozoa become associated with accessory or nurse cells. These cells apparently play an important part in the nutrition of the spermatozoa. The connection is established after the spermatozoon has been formed and at the time the chromatin granules become differentiated (Fig. 23). The staining intensity of these nurse cells in the fixed specimens shows that the cells contain a large amount of material that may represent food. It is impossible to differentiate between the nurse cells and the spermatogonia during the early development of each group. Both may pass through mitotic stages of division, but there is no indication that the spermatogonia and nurse cells pass through their subsequent stages of development as associated units. Each shows separate and individual development. Apparently the nurse cells are modified spermatogonia which, by a physiological division of labor, contribute to the development of the sperm. A single nurse cell acts as an anchorage for from one to five spermatozoa which it may nourish, four and five being most frequently found. The heads of the spermatozoa become partly embedded in, and firmly attached to, the cytoplasm of the nurse

cell. The spermatozoa remain attached in this position until they mature; then they are released and pass from the lobules of the testes into the vasa deferentia. Unattached spermatozoa are also found in the testes. The number of nurse cells, in comparison with the number of spermatozoa, is very small; many of the spermatozoa evidently derive nourishment from the surrounding fluids.

The origin and subsequent development of the chromatin granules found in the heads of the spermatozoa is of such unusual occurrence as to warrant further investigation. A study of them throughout the complete life history of the animals would be desirable. A review of the literature shows that very little is known concerning the reproduction of '*M. bulbostylum mihi* (*M. tuba* GRAFF of KEPNER and STIFF 1932)'. In *Macrostoma tuba* GRAFF, LUTHER (1905) observed the presence of three chromatin granules in the heads

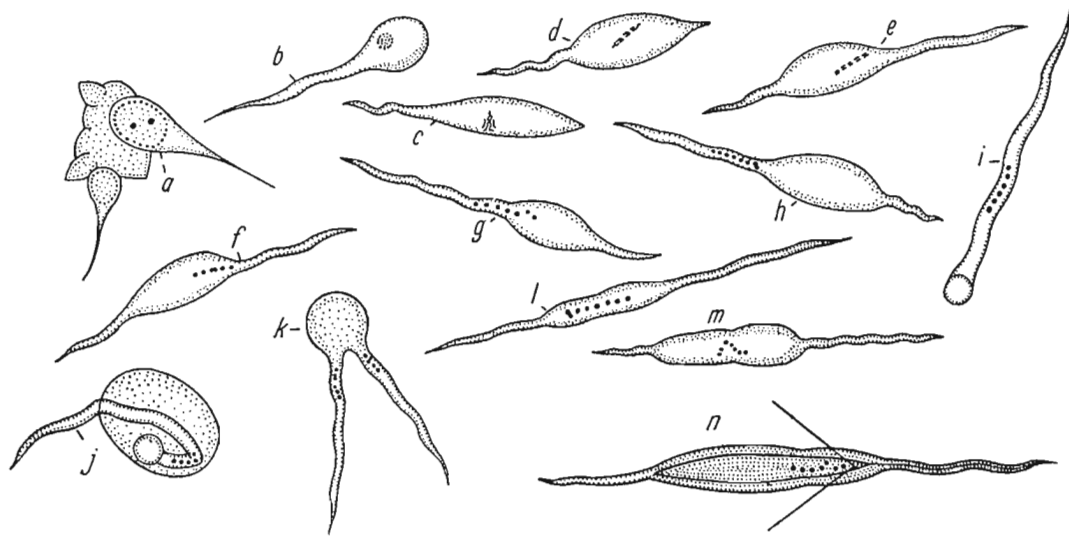


Fig. 1. *M. virginianum* Ferguson. Spermiogenesis. 900 \times .

of spermatozoa. Apparently the granules were formed from chromatin granules.

If the three chromatin granules were found to act as individual chromosomes after the egg has been penetrated by the spermatozoon, it could be assumed that the six chromatin granules represent the split or double chromosomes formed by the double chromonemata. On this assumption, the chromosomes of the spermatozoa would be double in nature.

MUSLOW (1911) described the nematode *Ancyracanthus cystidicola* as a form in which the chromosomes of the sperm remain separate and distinct. They may be readily counted even in the living spermatozoa. Since all the fixatives used produced the same results in '*M. bulbostylum mihi* (*M. tuba* GRAFF of KEPNER and STIFF 1932)', it seems hardly plausible that the chromatin granules in the fixed specimens were artifacts caused by a specific fixative. The granule-like structures are visible in the living spermatozoa, but it is impossible to trace their stages of development in the living state."

This present author has verified the observations of PHILLIPS (1936) upon the presence of chromatin granules in both living and fixed material in numerous species. Occasionally, a species is studied

in which the chromatin material is dispersed in the cytoplasm of mature sperm cells. An effort has been made to extend the commendable research of PHILLIPS (1936) in following the metamorphosis of the developing spermatid from the time in which its head is still buried in the cytoplasm of the nurse cell to the mature sperm-cell as found in the vesicula seminalis and vesicula granulorum. This study, which involves the use of living material observed in macerations, has given an interesting developmental series (Fig. 1). The following is an interpretation of this study of material taken from *M. virginianum* FERGUSON: In (a) the snow-shoe-shaped spermatids lie buried in a nurse cell associated with other very small heart-shaped ones (s'). The chromatin material of older anchored spermatids is composed of centrally located nucleoli and peripherally situated chromatic granules. The tail region now elongates (b) and the chromatin material becomes congregated near the cell-membrane. The body of the cell next assumes a spindle-shape, the chromatic content of which now appears as chromonemata (c). The disorganized shortened chromonemata become arranged as a discrete row in (d). Following this in (e), the chromonemata line up in pairs. These pairs fuse in (f), the fusion not being in accordance with any set rule. In (g) and (h) there is a tendency for the row of granules to migrate into the "tail"-region as the cytoplasmic volume of the cell becomes less. This lessening of the cellular contents would appear to be correlated in some way with the nutritional needs of a cell which is undergoing nuclear changes. The elongate cell (i) now seeks nutritional aid by again burying its spheroidal head (j) in a nurse cell. This fusion with the nurse cell (k) is quite complete. It will be noted that during the entire catabolic and anabolic stages that the chromatin granules remain in the "tail"-region. Upon severing its connection with the nurse-cell, this second phase of nutrition is terminated as the developing cell (l) next assumes a lengthened spindle-shape. In both (l) and (m) these immature spermatozoa are supplied with a row of chromatin granules located in the middle of the cell. It is thought that the sperm-cell reaches its ultimate maturity in the posterior part of the testis as it awaits passage into the vas deferens. The mature sperm-cell (n) of *M. virginianum* FERGUSON is supplied with two postero-lateral setae ("Nebelgeißeln"). These processes are developed much earlier in some species while the cell is still buried in the nurse-cell. The chromatin granules are contained within a central vesicle, from

the anterior end of which a very fine filament extends into the "feeler". It is obvious from this brief study of spermatogenesis in *Macrostomum* that there is ample opportunity for further research in this interesting subject.

The development of the egg in *Macrostomum* has been studied by LUTHER (1905), GRAFF in BRONN (1908), MEIXNER (1915), KEPNER and STIFF (1932), REISINGER (1933), and PHILLIPS (1936). Regarding egg formation KEPNER and STIFF (1932, p. 22) are quoted: "The oogonia are very small with large nuclei (*M. bulbostylum* mihi). Each nucleus contains a nucleolus, staining darkly with haematoxylin. The initial development of the oogonium takes place within the ovary. As the oogonium grows it slowly descends into the oviduct." PHILLIPS (1936, p. 328) observed that: "Oogonial divisions have been observed, but such divisions in *M. bulbostylum* mihi (*M. tuba* GRAFF of KEPNER and STIFF 1932) are rare. Very often sexually mature animals do not show a single division. The metaphase plates of these divisions show six chromosomes that are morphologically similar to the chromosomes of the spermatogonia (Fig. 24). The reduction division has not been observed in the ovaries of the specimens studied.

Sections of the egg fixed either at the time it migrates down the oviduct, or after it has reached the genital atrium, show a very large division spindle. Three chromosomes are orientated upon the equatorial plate of this spindle (Fig. 25). It was suggested by BARRETT (1930) that in *Macrostomum appendiculatum* O. FABR. this division represents the first cleavage of a parthenogenetically developing egg. But, the structure of the chromosomes and the fact that no reduction divisions were observed in the ovaries indicate that the division is a maturation metaphase. The apparent non-occurrence of haploid individuals also suggests that parthenogenesis does not occur, but it is possible that diploidy is established by a division of the chromosomes without a subsequent cell division."

Before the oogonium descends the oviduct it takes on shell droplets and yolk granules. LUTHER (1905, p. 44) first commented upon the nutrition of oogonia: "Ich muß daher die starke Größenzunahme der Eier am Anfang des Oviducts durch Wachstum mittelst Aufnahme von Nahrung aus den umgebenden Körpersäften und durch Imbibition mit Wasser erklären." Regarding the origin of the shell droplets and yolk granules KEPNER and STIFF (1932, p. 227) comment: "MEIXNER (1923) describes the yolk and shell formation and states that the pale yellow shell droplets are formed in rich masses by the young, indifferent germ cells, and that these masses are discharged between the oogonia and are to be found in the ovary and in the oviduct, where they are picked up by the pseudopodial processes of the egg. He concludes that, in *Macrostomum* the production of the shell-substance and at least a part of the yolk-material is carried on by the indifferent germ-cells. These cells function for life as shell or yolk cells, but they keep their ability undamaged to develop into egg cells when necessary.

If this method of shell production holds good in *Macrostomum tuba* (*M. bulbostylum* mihi), it is certainly not sufficient for the great amount of shell-material needed for the developing eggs. We have seen but a few free shell droplets in the ovaries and none in the oviducts. It is our opinion that

each oögonium elaborates its own shell and yolk material and that there are no indifferent germ cells that perform this function for the benefit of the oögonia. Germ cells disintegrate at times, as do body-cells, and thereby incidentally expel shell material. This would explain the presence of the very few shell droplets seen in the ovaries.

As the oögonium starts its development, shell droplets are elaborated, and by the time the enlarged oögonium reaches the oviduct, the cytoplasmic body is profusely sprinkled with shell-droplets. But at this period, they move to the periphery of the egg, thus forming its shell.

The shell-covered oöcyte drops into the common oviduct over the female genital atrium, whence it descends into the atrium." MEIXNER (1915, p. 473) states that occasionally abortive eggs lacking both yolk and shell material may appear in the female genital atrium of *M. orthostylum* BRAUN. KEPNER and STIFF (1932, p. 228) further comment: "We could not determine what took place at the time of the slipping of the egg into the genital atrium in the living animal. But, in our slides, the columnar epithelial cells seemed to have disappeared in all regions except that near the oviduct opening. Even here the cells seemed distorted. At first it was thought that the epithelial cells had disintegrated, but upon closer examination we found a very small ring of granular material around the inner edge of the atrium, and in this ring there were scattered, at fairly regular intervals, nuclei. This evidence forced us to conclude that the epithelial cells were still present, but greatly contracted along their axis, so as to be almost flat. Comparative measurements of the preatrial oöcyte and the atrium showed conclusively that the atrium must distend to receive the oöcyte. This distension, then, of the muscular female genital atrium is accompanied by a great flattening of the epithelial cells, thus providing a lumen capable of accommodating the egg."

Embryology.

The information upon the embryology of *Macrostomum* is sparse. Our knowledge at present is limited to these facts: The two cell stage consists of a large and a small blastomere, each of which is bisected. The ectoderm is developed from the large cell while the endoderm arises from the small cell. The embryo arrives at gastrulation by means of epibole, the blastopore being located at the posterior (?). Two lateral invaginations produce the nervous system. This short and incomplete description of the embryology of *M. hystrix* OERSTED (*M. appendiculatum* O. FABR.) (PEREYASLAWZEWA, 1892, p. 178—187) has received earlier criticism in the literature. REISINGER (1923, p. 51) gives a short note upon the development of *M. viride* BENEDEN in which it is stated that the total, unequal cleavage follows the spiral type. Four primary blastomeres develop from the blastomeres of the first cleavage, in a laetotropic division. The subsequently appearing non-synchronous first ectomeric quartet (1a and 1d) displays

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a dextrotropic development. Further stages in this form were not studied, however it is known that *Macrostomum* undergoes no metamorphosis during development but emerges from the egg resembling the parent except for the lack of sex organs.

An embryo of *M. bulbostylum* mihi (Fig. 2) shows that the animal is fairly well developed before leaving the case. The embryo is always folded upon itself so that the ventral side is divided into two divisions which touch. The animal constantly rotates within its membrane at this stage of development. In this form the distal part of the penis-stilette develops first (Fig. 3). At this point the



Fig. 2. *M. bulbostylum* mihi. Embryo within membrane. 210 \times .
Fig. 3. *M. bulbostylum* mihi. Early stage in development of penis-stilette. 1200 \times .

bulbous penis termination is situated in a hyaline spheroidal vesicle. The testes at this stage are hardly discernable, while the male gonopore has not yet appeared.

Physiology.

As a general statement, *Macrostomum* may be said to be omnivorous. My observations, however, lead me to believe that although a large amount of plant material may be taken into the enteron, that very little of it is actually digested, the animal preferring to retain and digest animal tissues and to eject most plant material. It is possible that any plant material observed in the enteron may have been taken in adventitiously.

The ingestion of food is accomplished through the animal's ability to greatly distend the pharynx simplex, completely surround the mass of food, and cause it to move posteriorly into the lumen of the enteron by the peristaltic action of the muscular fibers. Thus, there is possible a degree of sucking action which allows the animal to maintain its hold upon smaller invertebrates which are making an effort to escape. Apparently the ciliary action has no effect upon driving food into the pharyngeal cavity as WESTBLAD suggests.

WESTBLAD (1923) has furnished an excellent study of the physiology of the Turbellaria in general which gives numerous suggestions as to the physiology involving this genus. In this paper,

the gland-cells in the pharynx, which appear as radiating streamers from the mouth into the parenchyma, are functionally divided into cyanophilic mucous glands and erythrophilic salivary glands. As food passes through the mouth and pharyngeal cavity it is infiltrated with digestive ferments, thus here, as with higher forms, digestion may be said to start in the pharyngeal cavity. The mucus, with which the food is covered as it passes through the pharynx, remains intact as a coating long after the bolus of food has been carried about in the enteron. This has been ascertained by intravital staining with muci-carmin in *M. bulbostylum* mihi. This mucus-covering serves to protect the enteric walls from the sharp processes of the animals eaten.

The epithelium of the enteron consists principally of assimilatory cells and gland-cells. The "Körnerkolben" which serve as secretory cells generally do not possess flagella. The presence of "braune Drüsen" is questioned in *Macrostomum*. The assimilatory cells are divided into ameboid and flagellated cells (Fig. 5). In *M. tuba* GRAFF the flagellated assimilatory cells (Fig. 4) are about 22μ in diameter, with flagella one and a-half times as long as the diameter of the isolated cell. The cell plasma is finely granular, containing many centrally located angular granules, and droplets with the same optical refraction as the plasma. The droplets respond to both Sudan III and neutral red. Many small vacuoles are present. WESTBLAD (1923) found that there were, generally speaking, three types of flagellated assimilatory cells: (a) cells with large or small fat droplets, small vacuoles, and a few refractive granules, (b) cells with large vacuoles, without fat drops, few granules and with a thin flagellated border, (c) cells with a mass of refractive granules, small vacuoles, and no fat droplets (Fig. 4).

The ameboid cells (Fig. 4) move with quick pulsative actions. Inclusions in these cells are rare, however there is present a small amount of digested material. Fat droplets are rare. Since these cells have a primitive appearance with their small size, hyaline plasma and their high activity, it is inferred that they are transformed into flagellated cells. BÖHMIG (1890) earlier expressed this idea.

Extra cellular digestion is carried on by extracellular digestive ferments in which a lipolytic and possibly a proteolytic enzyme are involved. There is, however, no amylolytic enzyme, since ingested starch granules do not undergo the slightest digestion in the enteron. Remarking upon digestion in *Macrostomum*, HYMAN

(1936, p. 17) notes: "Although it is stated that digestion is extra-cellular in these rhabdocoels, the intestinal epithelium certainly resembles that of planarians during digestion and strongly suggests intracellular digestion in progress." WESTBLAD (1923, p. 91) infers the possibility of the digestion in *Macrostomum* being a process in

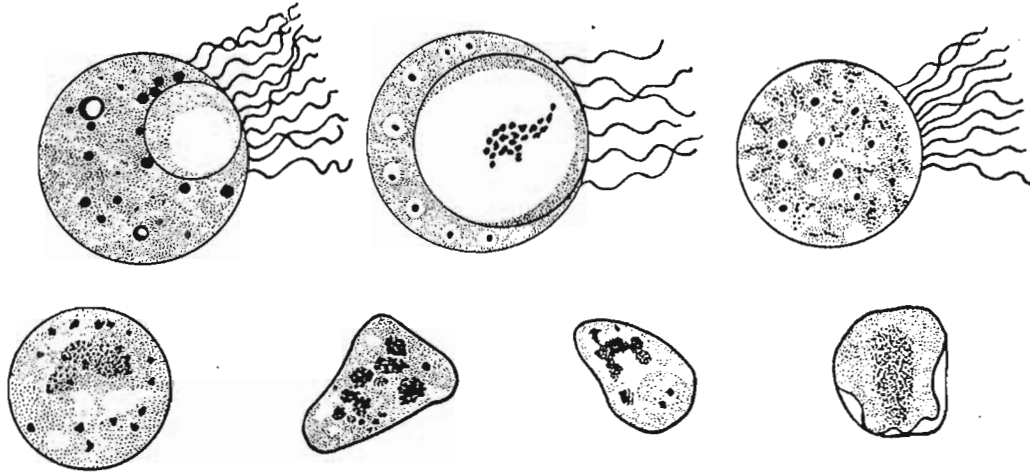


Fig. 4. *Macrostomum* sp. Cells in maceration. Upper row; atriocytes in Methyl blue. ? \times . Lower row; enteric cells. ? \times . (After Westblad, 1923.)

which intracellular and extracellular digestion plays distinct and separate roles. However, the enteron cells do not appear to possess the ability to engulf food masses.

Circulation of the various body fluids in *Macrostomum* is confined principally to the semi-liquid plasma of the parenchyma. In

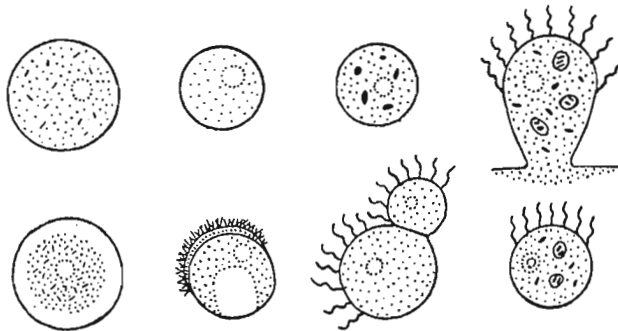


Fig. 5. *M. appendiculatum* O. Fabr. Cells in maceration. 330 \times .

the anterior body numerous granules and droplets of many colors and sizes appear in the parenchyma. These parenchymal inclusions respond positively to neutral red and methylene blue. The blind enteric sack acts in part as a circulatory element, since it is in contact with the fluid filled space, the parenchyma, which is composed of a loose jelly-like syncytium of cells. This space receives the products of digestion, as well as oxygen absorbed through the epidermis. Thus, the materials necessary for assimilation and dissimulation reach the protoplasm of the body in *Macrostomum*.

Excretion is thought to be principally handled by the conspicuous protonephridial system with its complement of flame cells, secondarily branches and primary lateral stems. The excretory function seems to be limited to only a restricted glandular region. There are relatively numerous atrocytic gland-cells (Fig. 4) connected to be excretory system, which facilitate the absorption and the further delivery to this system of the dissolved waste products. In consideration of the secondary organs of excretion it must be stated that the enteron serves as an important organ of elimination in that waste products may be delivered to and made innocuous in the enteric secretions. The body-epithelium may play an unusual role, since the amebocytes may carry excretory products to the surface where they are discharged. Pigment cells may also serve in excretion as store-houses for waste products.

WESTBLAD (1923, p. 89) presents an interesting discussion of the action of the "Stäbchendrösen". Here, it is pointed out, the "Stäbchen" penetrate the weaker parts of other animals which become stupified or die. There is a question as to whether or not digestive secretions are not simultaneously squirted into the victim through the agency of these anterior glands. Thus the "Stäbchen" may therefore be a precursor for the digestive enzymes. Remarkable enough, the "Stäbchen" apparently imbibe water inside the victim and upon swelling loosen up the tissues in acceleration of the subsequent digestive processes! The "Rhabditendrösen" of the fore body may also secrete a narcotic or poison upon the victim.

The above discussion of physiology has been taken primarily from the excellent paper of WESTBLAD (1923).

Experimentation.

Regeneration of parts is evidence of the ability to respond to various injuries. Such faculty is fairly well developed in *Macrostomum*. Four separate sections were made upon specimens of *M. bulbostylum* mihi: (a) a cut was made across the body at the posterior one-quarter mark. The posterior portion failed to regenerate, while the anterior three-fourths resumed normal activity; (b) a cross-section of the mid-body was made in which the posterior half failed to survive; (c) a cross-section was made at the anterior one-quarter mark in which the portion containing only the brain, eyes and part of the mouth succumbed the second day and the posterior three-fourths gradually developed a mouth and seems on

the road to recovery; (d) a longitudinal cut was made up the body from the posterior tip to the level of the mouth. The animal soon joined these sagittal halves and recovered rapidly. A sort of gelatinous covering seems to be deposited over such wounds.

A normal culture of *M. bulbostylum* mihi was subjected to the light of a 100 watt lamp. One-half of the culture dish was light-proofed by wrapping in heavy black cloth. In one hour's time all of the worms had moved out of the path of light into the darkened area. While this example is in the extreme, light does seem to play a part in their choosing the deeper, unlighted levels of the body of water in which they live. In the low land areas, these animals are more generally found in water through which light does not easily penetrate. The Gymnasium reflection pool of the University of Virginia, with its turbid water, is an excellent example of this factor. In the alpine habitats, since the streams are generally clear, they are found at the very bottom of the creeks, living in the protection of the aquatic vegetation. In the laboratory I find that they do best in cultures containing a shelter of some sort of water plant.

In order to test their responsive ability to radical changes in their environment, mature specimens of *M. bulbostylum* mihi were subjected to various solutions and conditions.

Specimen (1).

This animal survived for four hours in a normal saline solution, first reacting by twitchings of the body, after which an effort was made to keep constantly at the surface. The animal finally settled down to complete circles by holding the body in a rigid curve. Recovery in fresh water was rapid.

Specimen (2).

This animal was subjected to a weak Methyl Blue solution. In three hours an apparent adjustment had been made to this treatment. Methyl Blue ordinarily has a high lethal rate for Protozoa in such concentrations.

Specimen (3).

This animal was placed in a weak Light Green solution. In two hours it had reached adjustment. Recovery was rapid in fresh water.

Specimen (4).

This low-land specimen was subjected to a very weak Eosin solution. Death ensued in five minutes. Alpine forms may live for hours in a fairly strong Eosin solution.

Specimen (5).

This animal was placed in freshly distilled water. An unexpected reaction produced death and total cellular disintegration in five minutes. This experi-

ment was repeated with the same results. *Stenostomum* are known to live for several hours under such conditions.

Specimen (6).

India Ink of quite strong solution was used in this case. Concentrated black patches, which changed to brown, were produced in the epidermis as the animal came to complete adjustment. These brown patches disappeared during recovery.

Specimen (7).

This animal, when placed in a weak Neutral Red solution, succumbed in about fifteen minutes.

Specimen (8).

Bismarck Brown, in a weak solution, gave a slow, but definitely lethal reaction. Animals rescued from this solution slowly lost their intense color and returned to normalcy.

Specimen (9).

This animal was placed in an apparatus especially designed to test the effect of a six-volt alternating current upon ameba. When the current was applied, the animal responded in exactly the same manner as the ameba, travelling away from the electrodes in a right angle to the path of the current. After the deposition of a mucous-layer, there was a distinct cellular disintegration of the general epidermis. The animal recovered rapidly from the shock.

Specimen (10).

This subject was given a gradually increased dose of 15% alcohol. The animal soon lost all sense of balance and coördination, and began to describe curious circles with the body tightly rolled in a ball. Recovery was slow.

Specimen (11).

At it was desirous to know something of the pH range of the animal, it was subjected to McILVAINE's Buffer of a pH of 2.2. The animal instantly ceased all activity. In a few seconds there was a noticeable disintegration of the epithelial lining of the pharyngeal cavity and also of the flattened extensions of the body proper. Upon being rescued, the body assumed a roughly spherical shape with an unusually large mouth due to injury. The animal recovered.

Specimen (12).

This animal was placed in McILVAINE's Buffer of pH of 8.0. The effect here is to produce a loss of the proper geotropic orientation since the animal is caused to move slowly upon its back. Regurgitation of the enteric contents and the production of a thick layer of mucus also resulted. The specimen recovered rapidly. McILVAINE's Buffer is known to have a low toxicity. The formula and concentration:

- | | |
|------------------------------------|----------------------|
| (1) .2 M Na_2HPO_4 | } in a .1% solution. |
| (2) .1 M Citric acid | |

pH = 2.2 = .4 c. c. of (1) — 19.6 c. c. of (2).

pH = 8.0 = 19.45 c. c. of (1) — .55 c. c. of (2).

Specimens (12), (13), and (14).

The last of the experimental efforts to show the animal's ability to withstand radical changes in its environment concerns the raising and lowering of the temperature of the culture. Number 12 was placed in the apparatus designed for the purpose and the temperature was very slowly raised. There was no visible reaction before 40° C. was reached. Then the animal exhibited avoidance reactions in all directions. Finally, at 44° C., all movement ceased. The animal was quickly placed in a normal bath in which it recovered shortly. Number 13 and Number 14 were placed in separate containers and the temperature was lowered to 4° C. and kept there for 15 minutes. Number 13 was quickly placed in ordinary culture water of room temperature. Number 14 was allowed to recover slowly as the water gradually returned to room temperature. Apparently there was no difference in the recovery ability of the two. Number 14 was then subjected to a temperature between 4° C. and 6° C. for thirty minutes, during which time even ciliary motion ceased and the protoplasm assumed a glazed appearance. Recovery was very slow. Number 13 was next frozen solidly for 5 minutes. The animal failed to recover upon a slow restoration to room temperature. This leaves the perplexing question as to how species over-winter in such low temperature areas as Skyline Drive, Greene County, Virginia.

These temperature experiments indicate an unusual ability in the genus which allows its species to withstand such different environments as the cold waters of the Cascades, Giles County, Virginia, in comparison to the tepid content of the Gymnasium reflection pool, University of Virginia.

An effort was made to ascertain the mucus-content of the tissues of *Macrostomum* by placing several specimens of *M. bulbo-stylum* mihi in a weak solution of Mucicarmine. The results obtained were uniform for all of this group of animals and for other groups tested at a later date. In from three to ten minutes there appeared in the epidermis two laterally situated rows of colored patches which extended the length of the body. The center of these small, roughly spheroidal patches was lightly stained in comparison to the heavily stained periphery. In the same period a posterior region at the very tip of the body and the glandular rim of the mouth region respond to the staining. After twenty minutes had passed the mucous coating of various food masses in the enteron gave a positive reaction. While it is logical to assume that food masses and the stomatal rim would respond to Mucicarmine, the reaction of the dorsal epidermal patches is most perplexing, since mucous glands are numerous and uniformly dispersed over the entire body surface in *Macrostomum*.

It was thought desirable to study the penis-stilette's size-variation in a species in which there is a slight difference in size

of stilettes of mature animals. With this in mind, a pedigreed culture of *M. bulbostylum mihi* was established from the union of two average sized mature animals. As the first filial generation appeared its members were separated from the parents and carefully raised to maturity. Following this, a second filial generation was raised. Next, the progeny of these animals, the third filial generation, were brought to maturity and ten of these animals were selected at random and their stilette measurements recorded in the following table according to the scheme of Fig. 6:

	(1)	(2)	(3)	(4)	(5)
(a)	19.2 μ	6.4 μ	4.8 μ	11.2 μ	394.2 μ
(b)	16.6 μ	6.4 μ	4.8 μ	12.8 μ	379.6 μ
(c)	17.6 μ	4.8 μ	3.2 μ	11.2 μ	394.2 μ
(d)	16.0 μ	4.8 μ	3.2 μ	11.2 μ	408.8 μ
(e)	17.6 μ	4.8 μ	3.2 μ	11.2 μ	394.2 μ
(f)	20.8 μ	4.8 μ	4.8 μ	12.8 μ	467.2 μ
(g)	19.2 μ	4.8 μ	4.8 μ	11.2 μ	292.0 μ
(h)	11.2 μ	6.4 μ	4.8 μ	12.8 μ	248.2 μ
(i)	17.6 μ	6.4 μ	4.8 μ	12.8 μ	467.2 μ
(j)	16.0 μ	6.4 μ	4.8 μ	12.8 μ	292.0 μ
Av.	17.28 μ	5.60 μ	4.32 μ	12.0 μ	373.76 μ

Since the stilettes of the parents averaged 312 μ in length it is seen that the length of the measured stilettes vary both above and below this figure. While there is some discrepancy in size relations in the various regions of a single stilette, most of them remain fairly constant, the greatest difference lying in the length of the tube. Thus the mature animals of an average size in a clone may be expected to display variations in the length of their stilettes. Also it must be observed that a difference in size in stilettes is not a valid basis for new species or varieties.

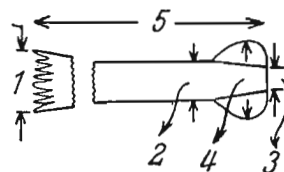


Fig. 6. *M. bulbostylum mihi*. Diagram showing method of measuring penis-stilette.

Discussion.

This work has been accomplished with two objects in mind; firstly to bring before others an up-to-date account of the knowledge pertaining to the genus *Macrostomum*, and secondly, to indicate some of the problems which as yet remain unsolved. These problems are to be found chiefly in the fields of ecology, spermatogenesis, oögenesis, embryology and physiology. The preliminary experiments of this author shows *Macrostomum* to be an excellent subject for physiological experimentation.

An effort has been made in this monograph to place the genus *Macrostomum* upon a firmer taxonomic basis. With this in view, the author has essayed to incorporate within the text those principles which have distin-

guished the better papers written upon Turbellaria. Pertaining to the descriptions of the valid species and varieties, these standard questions must be answered in simple, easily translatable language:

1. Does the specimen have the generic characters?
2. Would a future worker be able to distinguish this animal from all others by the use of the written and graphic description given?
3. Is the animal a valid sub-species or variety?
4. What are the diagnostic features of value in this animal?

It is of the utmost importance that the shape of the animal be recorded while it is moving slowly. The color is best studied when the enteron is nearly empty. Above all, the size should be obtained from an average taken in the study of many sexually mature animals. Descriptions taken from one or two specimens are obviously grossly insufficient.

The species dubiae in the genus have been discussed at length and drawings have been given in the event that they may aid in the future accurate depiction of the animal in question.

The valid species and varieties in this genus are 43 in number according to the present writing. Of this number 23 are from the eastern United States. This paper contains 27 new *Macrostomum* through this author's efforts.

While the key method of study has been indicated in this work, its value is questionable; only an authority may properly employ one and they finally have no real use for it. It is held by this author that accurate drawings are of greater diagnostic value than a key may be.

The description of the chromosome morphology is presented as a diagnostic feature of value in this genus. In this connection, the morphology of the mature sperm-cell has a role of increasing importance in the taxonomy of *Macrostomum*.

I am prone to believe that the best descriptions in the literature are those which have resulted from the study of live material. While sectioned material is of great value in checking results, the tissues in these animals are such that the fixation image is often misleading. Inaccuracies in the reconstructed drawings follow as a natural result of such work.

The bibliography has purposefully been made extensive in order to concentrate all of the literature up to date in one place. It is felt that research upon the genus may be stimulated by making the references more available.

In conclusion I gratefully salute the patience and intelligent cooperation of Dr. BERTHOLD KLATT and his co-workers who have made the publication of this work possible. The author invites criticism of the monograph through his permanent address.

List of abbreviations.

ad, antero-dorsal nerve; *av*, antero-ventral nerve; *b*, body of sperm-cell; *br*, "brain"; *c*, cilia; *cc*, ciliated chambers; *ce*, ciliated entrance to vesicula seminalis; *cod*, common oviduct; *cp*, ciliated pit; *e*, eye; *eg*, egg; *el*, ellipsoid; *en*, enteron; *ep*, epidermis; *de*, ductus ejaculatorius; *f*, feeler of sperm cell; *fg* and *fgp*, female gonopore; *fl*, flagellum; *fvs*, false vesicula seminalis; *g*, ganglion; ♀ *ga*, female genital atrium; *gc*, ganglion cells; *gl*, glands cells; *gm*, granular material; ♀ *gp*, female gonopore; ♂ *gp*, male gonopore; *hp*, "Haftpapillen"; *i*, inclusion; *le*, lumen of enteron; *ln*, lateral nerve; *m*, mouth;

mc, muscle cells; *mg*, male gonopore; *mjp*, male gonopore; *mr*, "Mittelrippe"; *ms*, muscle sheath; *my*, myoid; *nc*, nurse cell; *od*, oviduct; *oo*, oöcyte; *op*, opening; *ov*, ovary; *p*, penis-stilette; *phc*, pharyngeal cavity; *pm*, protractor muscles; *pn*, protonephridium; *ps*, pseudocoele; *rc*, rhabdite cell; *rd*, rhabdoid; *rh*, rhabdite; *rm*, rhamiten; *rs*, "Rhabditenstrassen"; *s*, sperm cell; *sh*, sensory hairs; *sp*, spines; *sph*, sphincter; "*t*", "tail" of sperm cell; *t*, testes; *vd*, vas deferens; *vg*, vesicula granulorum; *vs*, vesicula seminalis.

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Über ein neues Organ an der Basis des Abdomens von Acidalia.

VON TONI PODESTÀ.

(Aus dem Zoologischen Institut der Universität Kiel.)

(Mit 2 Abbildungen.)

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Im Laufe von Untersuchungen über das Vorhandensein von Duftschuppen an Schmetterlingsbeinen — die auf Anregung meines verehrten Lehrers, Herrn Prof. Dr. EGGERS, erfolgt waren — fand ich bei Spannern ein interessantes abdominales Organ. In der Gattung Acidalia zeigte sich bei männlichen Tieren einiger Arten an der Abdomenbasis, gleichsam dem ersten + zweiten Sternum aufgelagert, ein chitiniges, häutiges Gebilde, das in seiner Form einer runden Tasche ähnelt (Abb. 1). Meine bisherigen histo-

