

**Studies on the Morphology and Histology
of
Burnupia mooiensis (Walker)
(Mollusca, Basommatophora, Ancyliidae)**

by

G. OBERHOLZER

INSTITUTE FOR ZOOLOGICAL RESEARCH,
DEPARTMENT OF ZOOLOGY,
POTCHEFSTROOM UNIVERSITY FOR C.H.E.,
POTCHEFSTROOM

THESIS

PRESENTED FOR THE DEGREE OF MAGISTER SCIENTIAE
IN THE POTCHEFSTROOM UNIVERSITY FOR C.H.E.

**SUPERVISOR
PROFESSOR J. A. VAN EEDEN**

DECEMBER, 1963

STUDIES ON THE MORPHOLOGY AND HISTOLOGY
OF BURMUPIA MOOIENSIS (WALKER)
(MOLLUSCA, BASOMMATOPHORA, ANCYLIDAE)

by

G. OBERHOLZER.

(Institute for Zoological Research, Department
of Zoology, Potchefstroom University for C.H.E.)

<u>CONTENTS</u>	<u>PAGE</u>
1.0 Introduction	1.
2.0 Materials and methods	1.
2.1 Field methods	1.
2.2 Maintenance in laboratory	3.
2.3 Narcotization, dissection and microtomy	4.
3.0 Morphology and anatomy	5.
3.1 Shell	5.
3.2 External morphology	6.
3.3 Pseudobranch and mantle cavity	9.
3.4 General topography of the internal organs	11.
3.5 Alimentary canal and digestive gland	11.
3.6 Radula	19.
3.7 Excretory system	22.
3.8 Sense organs	24.
3.9 Circulatory system	26.
3.10 Morphology and histology of the reproductive system.	30.
3.11 Summary	53.
3.12 Literature cited	55.
3.13 Acknowledgements	58.

1.0 INTRODUCTION

The taxonomy of the Ancyliidae of South Africa is in a very unsatisfactory condition owing to the fact that, excluding a few radulae, nothing is known of their soft anatomy. The simple form of the shell of the genus Burnupia Walker, 1912 renders determination of the different species exceedingly difficult and sometimes impossible.

At present the South African species have to be identified exclusively by reference to descriptions and drawings of the shell and radula where such are available, and by taking into consideration the locality where the specimens were collected. The degree of variation exhibited by these structures, however, greatly limits their value in species discrimination. The only publications which contain all this information are those of Walker (1923) and Connolly (1939).

The purpose of the present investigation was to establish the anatomical details of a single South African species which could serve as a basis for future research work on the South African representatives of this family.

2.0 MATERIALS AND METHODS

2.1 FIELD METHODS

Walker (1923) records the type locality for Burnupia mooiensis (Walker) as Mooi River, Potchefstroom, Transvaal. It was however, impossible to trace the exact locality.

The material for this study was taken from the Mooi River at the Boskop Dam effluence, district Potchefstroom. All collections were made at the same spot,

more or less 450 yards from the concrete effluence. The collecting area covered a stretch of 15 yards. Monthly collections were made from March to July 1962.

The river is small (South African standards) fairly fast flowing and the water is clear. The bottom is muddy, sandy, and rich in decomposing organic matter such as willow leaves, sticks and logs.

The snails were secured by examining the submerged debris and stones about one to one and a half feet beneath the water surface and removing them gently with the finger tips, without damaging the shells. The use of a sharp object such as a scalpel was found unnecessary.

The animals showed a marked preference for the smooth hard surfaces of stones and were found in fairly large numbers on such objects as pieces of porcelain, bottles and tins. On all these objects they were found on the bottom surfaces and the impression was gained that they preferred the wake side to the front side.

The snails were identified as B.mooiensis by Prof. J.A. van Eeden of this Institute. A number of shells were compared with two paratype specimens from the Natal Museum, Pietermaritzburg. No soft material of the paratype was available for comparison.

Two shells were selected, one of which is figured in figs. 1 and 2. These differ only slightly from the paratype shells. The radulae of these two animals were prepared as permanent mounts (figs. 31 & 5, appendix). Unfortunately, however, these radulae cannot be considered as "mode radulae" for the species.

The radulae were removed by placing the buccal masses of specimens in a 5% caustic soda solution and

boiling them for a while in a water bath until separated from the surrounding tissues. The radulae were mounted and stained according to the method of Van Eeden et al. (1962). These mounts were examined with the normal research microscope at magnifications of up to 1000 times.

The jaws were dissected out together with a small portion of the surrounding tissues and examined as glycerin mounts. Staining of the jaws for examination purposes was found unnecessary.

2.2 MAINTAINANCE IN THE LABORATORY

A number of live ancyliids were kept in the laboratory in order to have fresh material at hand during the course of the study. The shallow aquarium measured 10" X 10" X 4". The bottom was filled with sand from the locality in which the snails were collected, together with a few sticks, rocks and pieces of porcelain. To simulate the natural stream, fresh water, directly from the tap, was led into the aquarium after passing through a glass tube coiled around an electric bulb suspended about four inches above the water surface. The latter served the dual purpose of raising the temperature of the water by more or less 1°C (this was necessary as the winter was fast approaching) and also producing enough light for the algae to grow indoors where sunlight did not reach the aquarium at all. A chip in the top edge of one of the walls of the aquarium acted as an overflow. This chip was covered with a piece of plastic gauze.

The snails probably found enough nourishment in the thin layer of algae on the sides of the aquarium, where they could be seen browsing, especially during the first four

or five days after being placed into the aquarium. Afterwards they settled down underneath the rocks and pieces of porcelain, where the majority died three or four weeks later. In my opinion this could be ascribed to the chemical properties of the municipal water. Borehole water which, unfortunately was not available, might have given better results.

2. 3 NARCOTIZATION, DISSECTION AND MICROTOMY

Three narcotization methods were tried out.

The method described by Van Eeden (1958), although excellent for narcotizing larger freshwater mollusc species, proved to be too slow and consequently to be associated with macerative changes which ruin the material for biological studies.

The method of Joosse and Lever (1959) proved successful except that the animal could not be removed from its shell without breaking it or damaging the mantle and other organs.

By using a 1% nembutal solution with a relaxing period of approximately 25 minutes at a temperature of 22 °C the snails drooped out of their shells and showed no reaction to mechanical stimuli. The snails were then instantly killed by dipping them into boiling water for about three seconds. This method of killing, which was successfully used by Schutte and Van Eeden (1959b) in their studies on Biomphalaria pfeifferi (Krauss), greatly facilitates the removal of the animal from its shell without damaging either the latter or the soft parts.

Specimens to be sectioned were relaxed as described in the third method above and then killed instantly by dropping them into a 4% formalin solution that had pre-

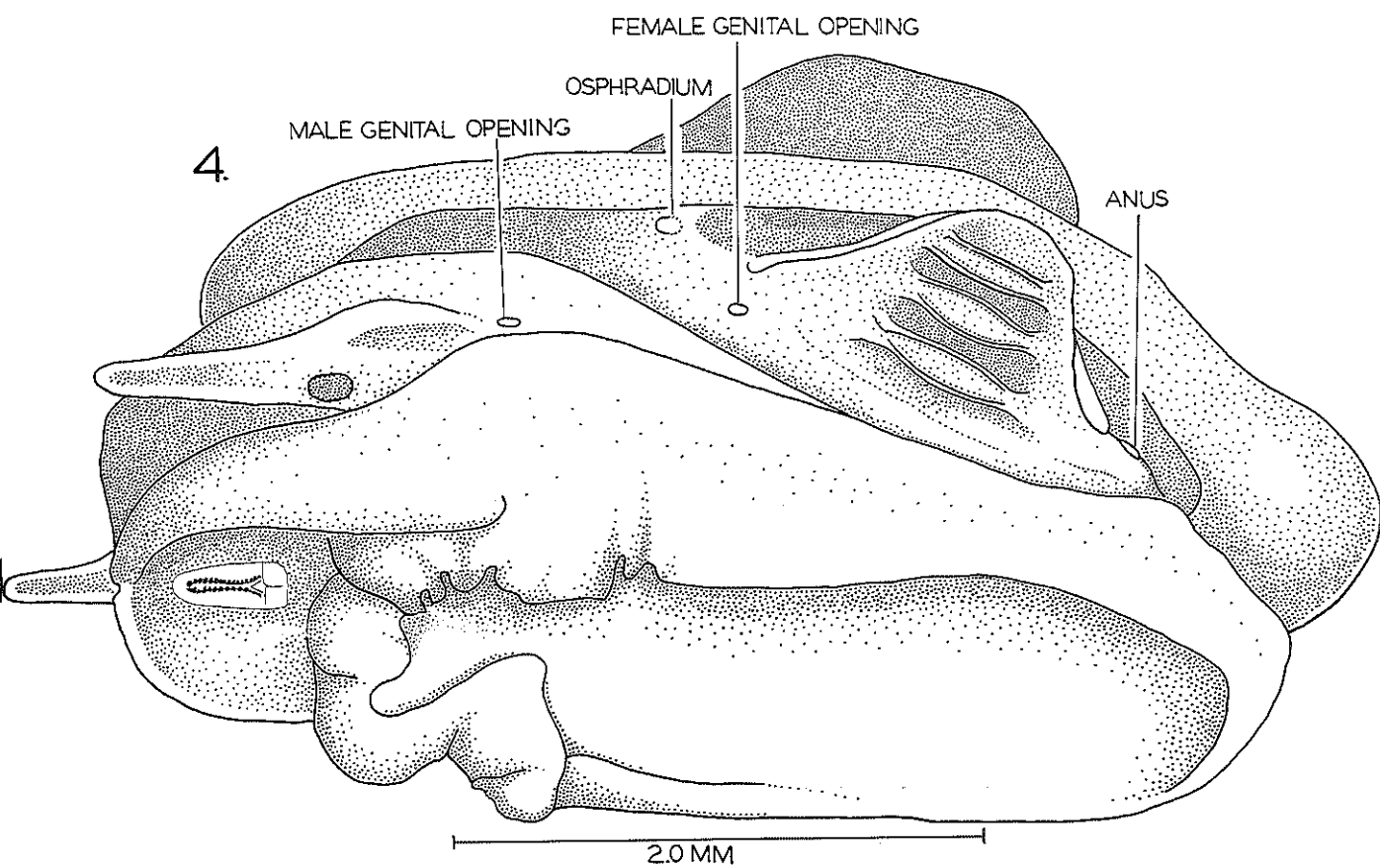
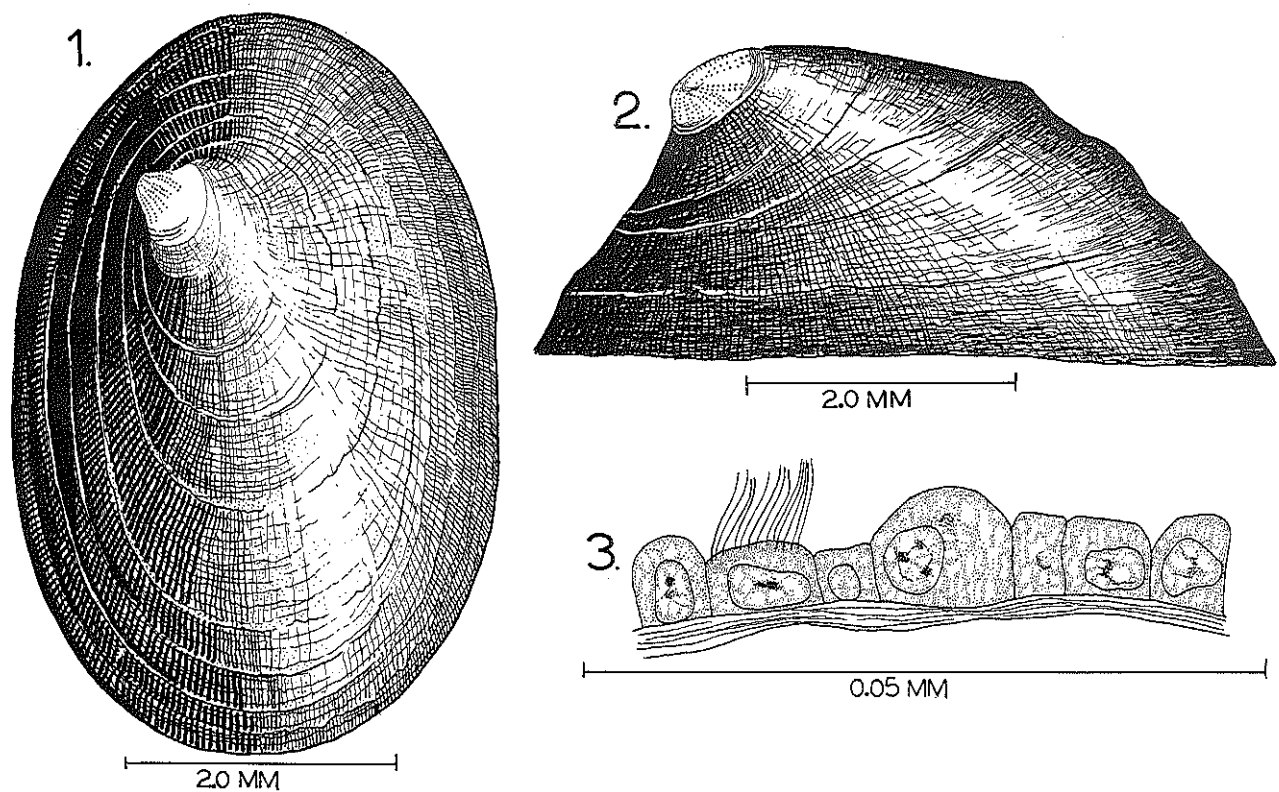
viously been heated up to 60^o C. For fixation the animals were left in the same fluid for 12 to 24 hours. The snails were embedded in paraffin by the alcohol xylol method and sectioned transversely, frontally and sagittally at 2 to 5 . Staining with Mallory's triple stain was found satisfactory.

3. 0 MORPHOLOGY AND ANATOMY

3. 1 SHELL

Walker (1923, p. 47) described B. mooiensis under the name Ancylus (Burnupia) mooiensis as follows: "Shell slightly obovate, the greatest width being in front of the centre; thin, translucent light horn colour; surface with regular, but very fine, growth-lines, and exceedingly delicate, wavy radial striae; apex about half-way between the centre and posterior margin, subacute, not prominent, but slightly turned to the right and very little deflected; anterior slope convex, but flattened above and nearly straight as it approaches the anterior margin; posterior slope long and regularly, but not deeply concave; left slope slightly convex; right nearly straight, slightly concave about half-way down."

Connolly (1939, p. 523) described the shell as follows: "Shell large, elevated, slightly obovate, ends nearly equally rounded, left margin a little more so than right, front and left slopes more or less convex, rear long, regularly but not deeply concave, right slightly so half-way down, apex about one-third length from rear and half-way between median line and margin, subacute, not strongly beaked, more or less turned to right but seldom extending near margin, punctate area large, first 4 or 5 dots



FIGS.1-2. SHELL.

FIG. 3. EPITHELIAL LINING OF MANTLE CAVITY.

FIG.4. EXTERNAL MORPHOLOGY, LATERO-VENTRAL ASPECT.

in each row single, next 5 double, growth lines strong, crossed by equally strong wavy radials. The type is 6.25 x 4 x 2.5 mm. and my largest topotype 7 x 5.2 x 3.0 mm."

The shells of B. mooiensis in my possession are rather variable and seem to be quite susceptible to ecological variation. For instance, the shells of some animals that have been living attached to reeds since hatching from the egg fit perfectly on the contours of the reed, therefore diverging completely from the normal shape of the shell of an animal that has been living on the surface of a smooth rock. The height and relative convexity of the left and right margins of the shell could therefore be very misleading, and should be applied with caution in species discrimination.

The shell alone could be a study in itself. However, the cited descriptions of the shell of B. mooiensis are fairly complete and it is not necessary to add to or repeat a similar description here. The cited statement of Connolly (1939) "next 5 double", referring here of course to the punctate area, was found to be incorrect. In some well preserved specimens in my own collection counts up to six and twelve double dots per line were made.

3.2 EXTERNAL MORPHOLOGY

The body of B. mooiensis resembles other ancyliid genera in being superficially bilaterally symmetrical. It may be divided into three regions viz. the head, the foot and the visceral mass.

The head and the foot are of a light grey colour while the translucency of the integument permits the colour

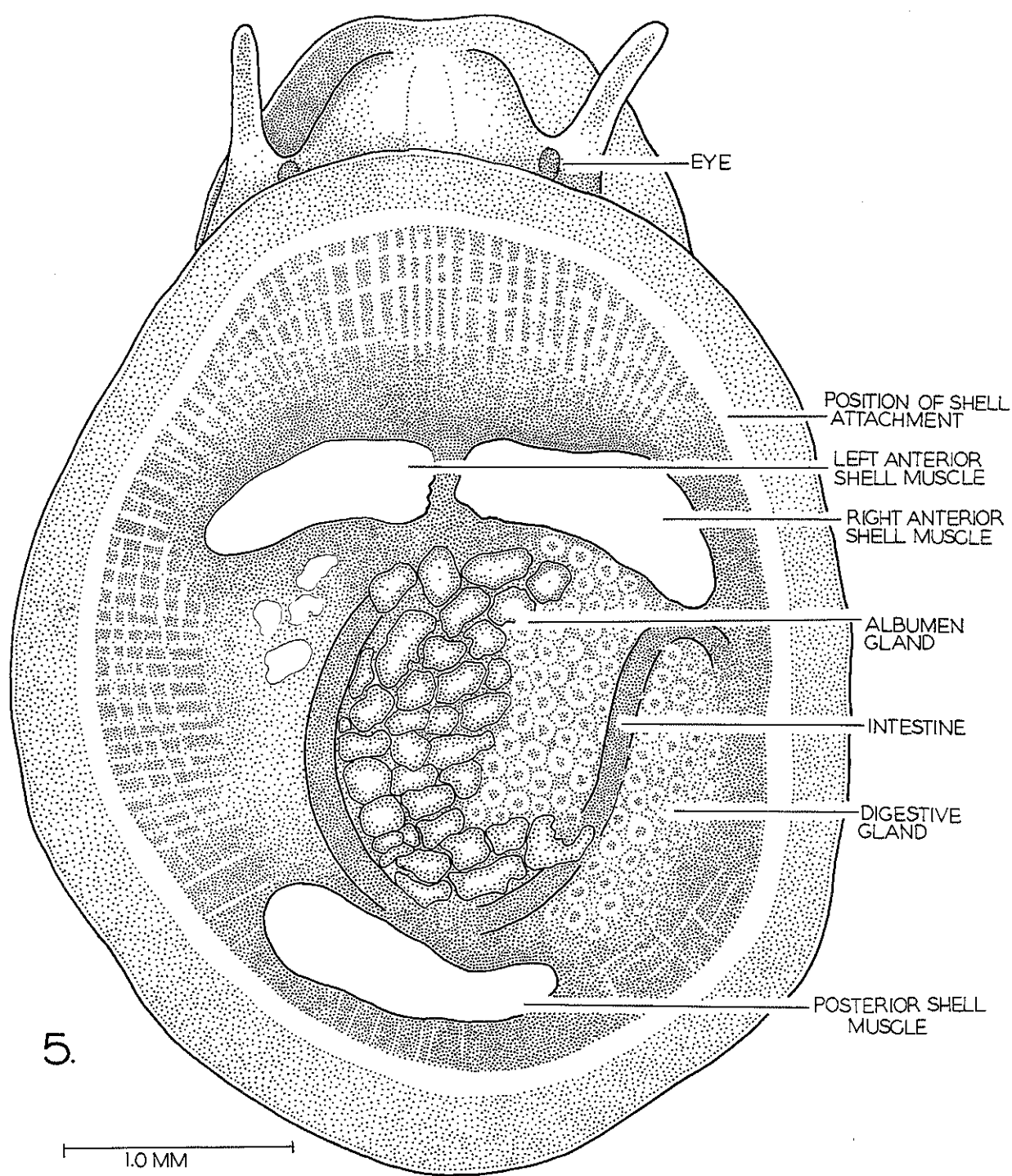


FIG. 5. EXTERNAL MORPHOLOGY, DORSAL VIEW WITH SHELL REMOVED.

and shape of the internal organs, especially the pinkish blood sinus of the buccal mass, to be discernable externally. The tentacles are subcylindrical, becoming roughly triangular at the base, thus giving the impression of a poorly defined ventrally directed flap. The conspicuous hollow core of black pigment described for Laevapex fuscus Adams by Basch (1959) is absent in B. mooiensis, and, although pigment is present in a limited quantity, it is mainly concentrated in the distal half of the tentacle. The eyes are situated in the usual basommatophoran position.

The muscular foot is suboval and broadest at its anterior end. The three shell muscles are intimately connected with the tissues of the foot and forms the basket work in which the viscera lies. Of the three shell muscles the right anterior one seems to be the largest while the posterior and the left anterior shell muscles are more or less of equal size and slightly smaller than the former. The posterior shell muscle is situated slightly to the left of the median sagittal plane of the body.

The mantle is translucent in certain areas, allowing such structures as the digestive gland and parts of the intestine and albumen gland to be distinguished externally (fig. 5). Black pigment granules, distributed over the dorsal surface of the mantle, are more densely concentrated around the periphery of the shell muscles. Unlike L. fuscus, the location of the kidney is not frequently outlined by black pigment. The kidney, however, is opaque and could sometimes be seen vividly through the mantle in freshly killed specimens.

The margin or swollen edge of the mantle is not free of pigment as in L. fuscus. In some specimens the pigment is concentrated over the whole of the mantle surface leaving only the dorsal surfaces of the shell muscles and a slightly larger portion of the dome fitting into the apex of the shell, free of pigment. As in the case of L. fuscus the rest of the animal is flecked with scattered, small, concentrated black pigment spots. A variable pattern is sometimes seen running backwards from the left anterior shell muscle and also running forwards from, and between the anterior shell muscles.

The sinistrally placed pseudobranch is a roughly rounded triangular extension of the body wall and protrudes ventrally from underneath the mantle border (figs. 4 & 6). In B. mooiensis this structure consists of two lobes. A larger ventral lobe lies underneath a smaller dorsal lobe. The anus is situated at the posterior junction of these two lobes. By lifting the overhanging mantle, the pneumostome can be seen directly above the junction of the anterior margin of the pseudobranch with the body. Vertically below this point, the female genital opening, which is sometimes difficult to locate externally, can be seen. By lifting the mantle still further, the osphradium can be seen as a minute white speck, situated on the ventral mantle surface almost in line with the pneumostome. The tiny urinary orifice, which could be seen in some specimens of L. fuscus (Basch, 1959), could not be seen in B. mooiensis in gross dissection. The male genital opening is situated at the base of and slightly

behind the left tentacle.

3.3 PSEUDOBANCH AND MANTLE CAVITY

Two lobes are differentiated viz, an upper lobe and a slightly larger subtending ventral lobe. Each of these lobes (figs. 4, 6 & 8) is thrown into three transverse folds, alternately projecting on the dorsal and ventral surfaces, and corresponding to the primary folds described for Bulinus tropicus (Stiglingh et al, 1962). Similar folds seem to be indicated in L. fuscus (Basch, 1959, fig. 3A). In respect of its pseudobranch B. mooiensis seems to be intermediate between L. fuscus (Basch, 1959) and Ancylus fluviatilis (Sharp, 1883), a condition which may be correlated with the fact that, whereas L. fuscus normally lives in practically stagnant water, both B. mooiensis and A. fluviatilis seem to be adapted to well aerated running water. If this conclusion be correct, then it seems obvious that the pseudobranch of B. mooiensis is less important as a respiratory organ than it is in L. fuscus and is, consequently, less well developed.

Basch (1959) considers the dorsal lobe of L. fuscus to be homologous with the auriform lobe of authors which, in turn, might be homologous with the lower mantle lobe (Hubendick, 1947, quoted from Basch, 1959) of the Planorbidae. The condition obtaining in B. mooiensis apparently lends stronger support to this view than does that in L. fuscus. In the former species, the anus is not situated on the anterior part of the anal lobe, as is figured for L. fuscus, but rather behind it

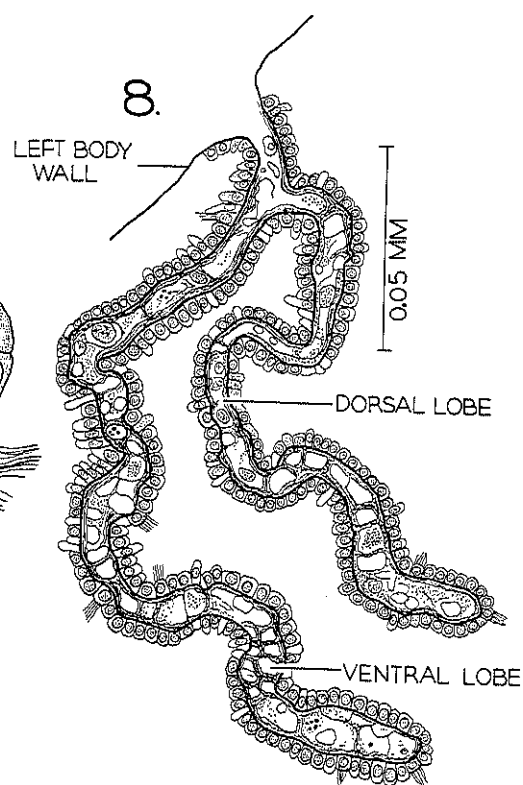
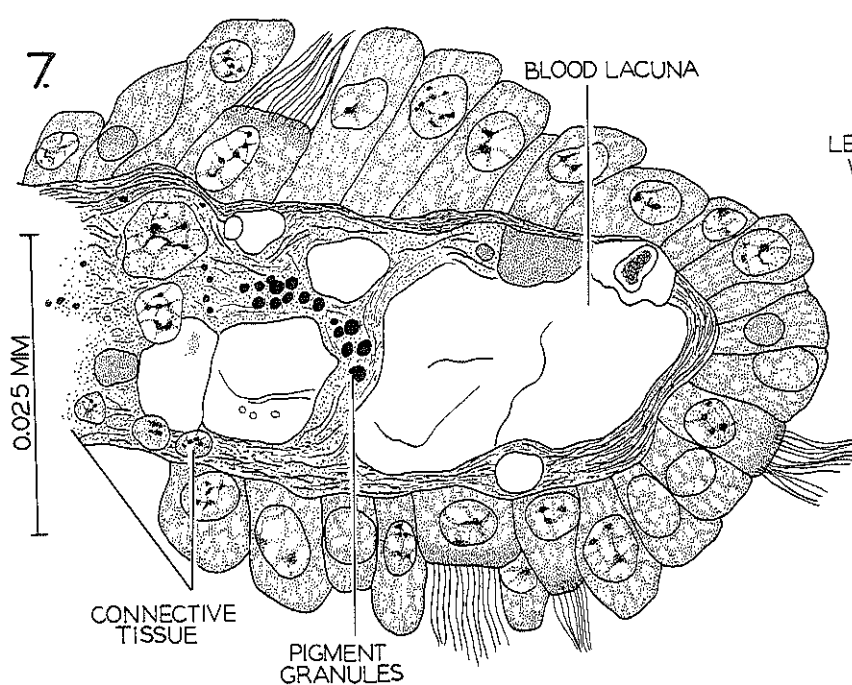
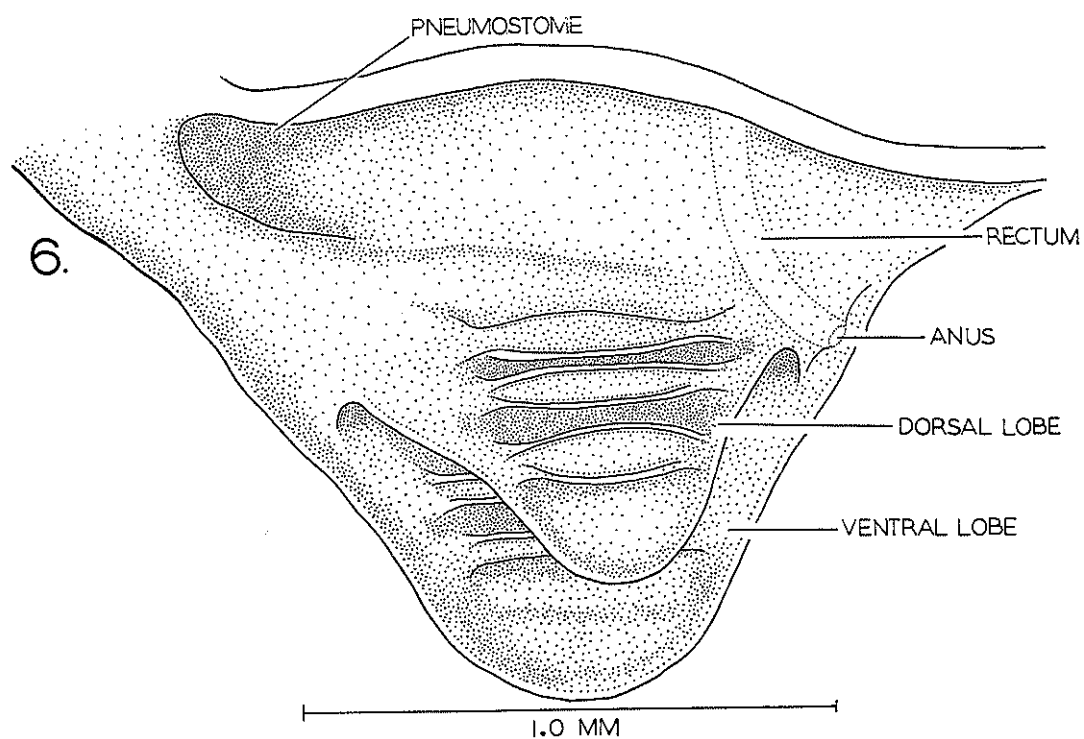


FIG. 6. PSEUDOBANCH, DORSAL VIEW.

FIG. 7. SECTION THROUGH TIP OF VENTRAL LOBE OF PSEUDOBANCH.

FIG. 8. SECTION THROUGH PSEUDOBANCH.

at the level of the junction of this lobe to the lower respiratory lobe (figs. 4 & 6), thus bearing relations to the anal lobe approaching those between the anus and lower mantle lobe in the Planorbidae. The anal lobe of B. mooiensis is obviously better developed than that of L. fuscus and the former species is the only ancyliid thusfar known to bear a respiratory lobe similar to that of the latter.

Histologically the pseudobranch consists of loose connective tissue fibres with lacunae, bounded on either side by a single layer of cuboidal and club-shaped cells (fig. 7). Only some of the cuboidal cells possess dense tufts of cila nearly as long as the cells are high. Interspersed between the connective tissue fibres, pigment granules are found.

A continuous canal, similar to that found in L. fuscus (Basch, 1959) and A. fluviatilis (Sharp, 1883), runs along the borders of both lobes. It is, however, less well developed than in either of these species, and seems to support the conclusion reached earlier on, that the pseudobranch of B. mooiensis is of less importance as a respiratory organ than that of L. fuscus.

The pneumostome is placed directly above the anterior margin of the pseudobranch and is a narrow horizontal slit, lying roughly between the left anterior and posterior shell muscles (fig. 9). The mantle cavity extends dorsally into the body at an angle of more or less 45° . It extends anteriorly beyond the point of junction of the atrium with the ventricle

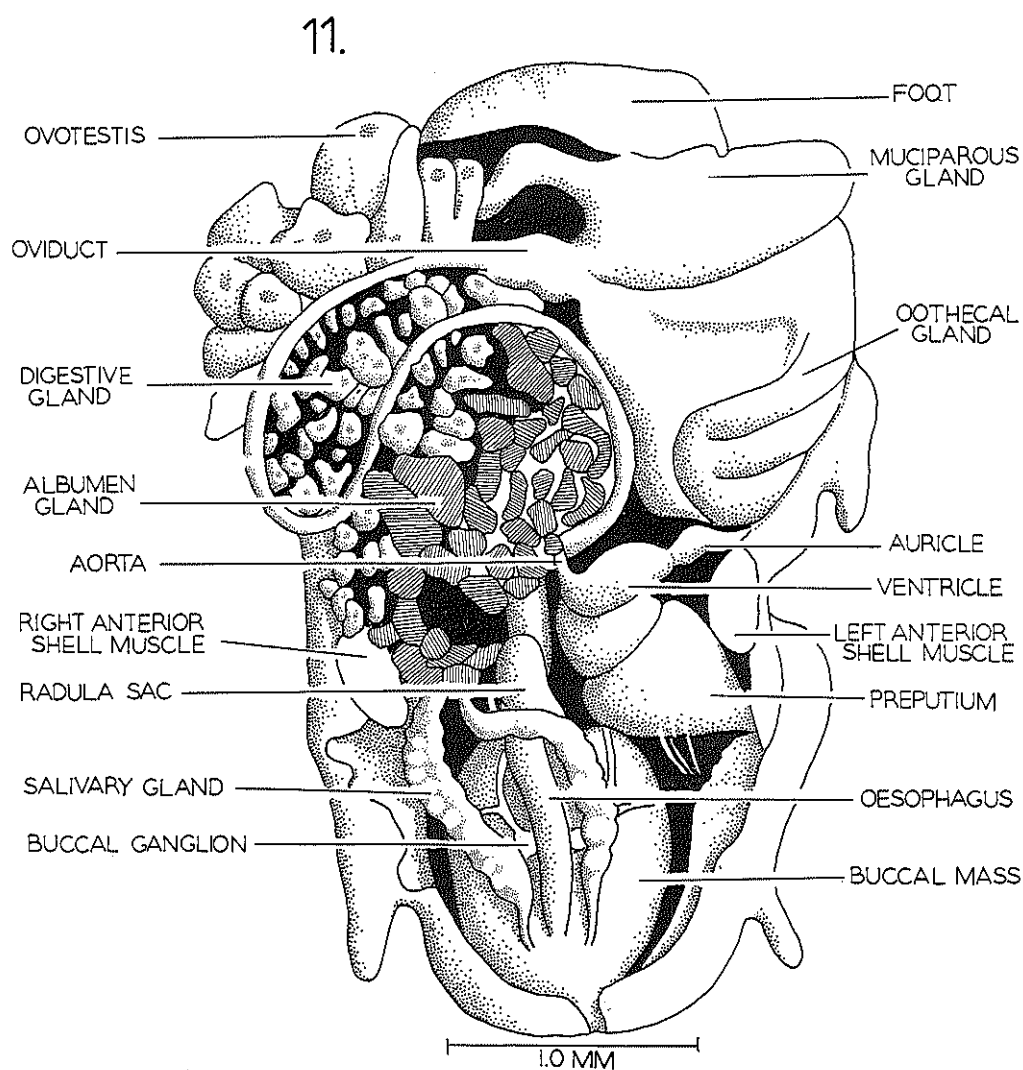
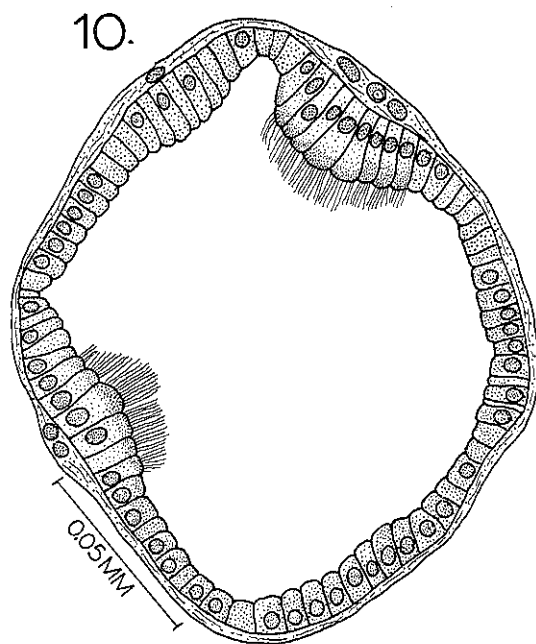
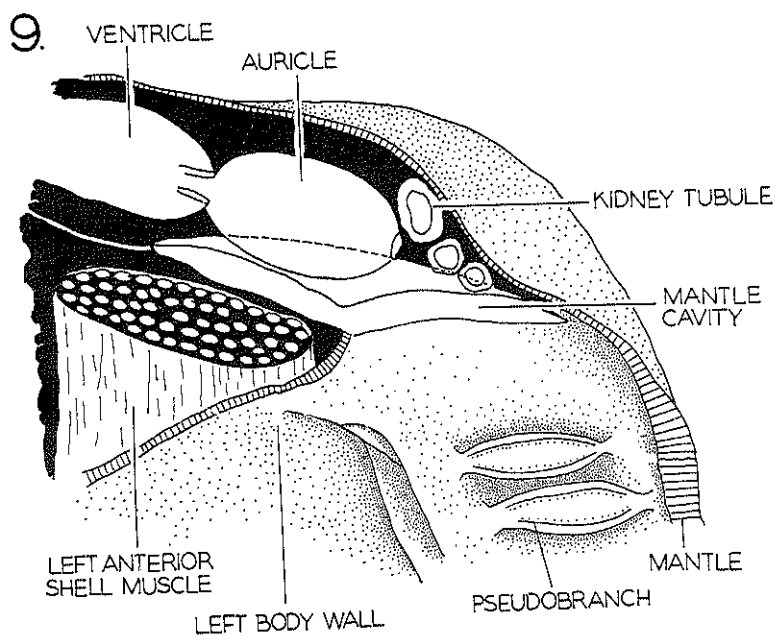


FIG.9. DIAGRAMMATIC SKETCH SHOWING TOPOGRAPHICAL RELATIONS OF MANTLE CAVITY.

FIG.10. CROSS SECTION THROUGH OESOPHAGUS WHERE IT PASSES THROUGH THE CIRCUMOESOPHAGEAL CONNECTIVE.

FIG.11. GENERAL TOPOGRAPHY OF INTERNAL ORGANS IN A FRESHLY DISSECTED SPECIMEN.

which lies directly above in the pericardium. From this point backwards the right wall of the cavity proceeds obliquely towards the left body wall which joins it above the pseudobranch. Its shape therefore roughly conforms to the description given for L. fuscus (Basch, 1959), with the ceiling consisting of the ventral surface of the pericardial membrane and a portion of the mantle. The epithelium of the floor of the mantle cavity is continuous with that of the dorsal surface of the pseudobranch. It is lined with low columnar epithelium with scattered ciliated cells (fig. 3) and the epithelium of its floor gradually merges into the epithelium on the dorsal surface of the pseudobranch. Unidentified flatworms were frequently found in this cavity.

3.4 GENERAL TOPOGRAPHY OF THE INTERNAL ORGANS

The mutual relations of the internal organs, as exposed by removal of the mantle, are depicted in fig. 11 and need not be supplemented by verbal description.

3.5 ALIMENTARY CANAL AND DIGESTIVE GLAND

The digestive system is discussed in the following order: Mouth and jaw, buccal mass, salivary glands, oesophagus, crop, gizzard, caecum and pylorus, intestine, rectum and anus, digestive gland and radula.

The jaw consists of approximately 30 chitinous plates arranged as shown in fig. 12. Each of these plates has a coarse, longitudinal striation, giving the impression of bars lying very close together and thus providing the cutting edges. Each of these bars

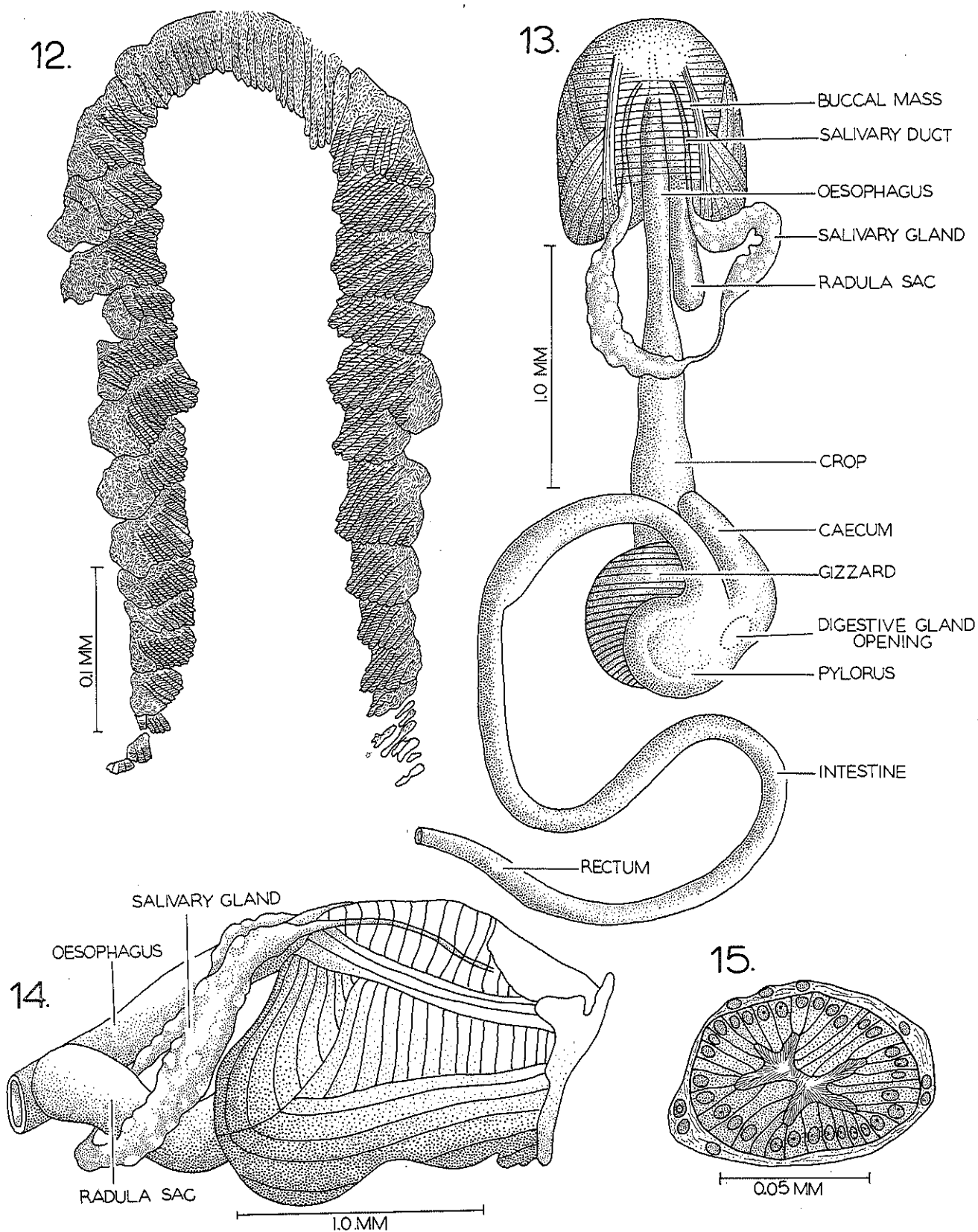


FIG.12. JAW, VIEWED FROM VENTRAL ASPECT OF ANIMAL.

FIG.13. ALIMENTARY TRACT, DORSAL VIEW.

FIG.14. BUCCAL MASS, RIGHT LATERAL ASPECT.

FIG.15. CROSS SECTION THROUGH OESOPHAGUS DIRECTLY ABOVE THE BUCCAL MASS.

in turn is finely striated transversely. This more or less agrees with the condition obtaining in Ferrissia junodi Conn. (Connolly, 1925).

The general shape of the buccal mass is essentially the same as that described for other ancyliids (figs. 14 & 16). The mouth and buccal cavity are covered with a layer of columnar epithelium. An unusual feature of the pharynx of B. mooiensis is the presence of a blind evagination which extends backwards into the buccal mass for a short distance (fig. 16). The lumen of this evagination is also lined by a single layer of columnar epithelium. I have not come across any reference to a similar structure in any mollusc species thusfar examined. Although Mortons (1958) figure 10 C on page 87 may possibly be interpreted as representing a structure of this nature, he, unfortunately, neither labels it nor does he refer to it in the text. In the present state of our knowledge it seems inadvisable to venture any suggestion as to its possible function.

In general appearance the two salivary glands resemble those of the Planorbidae. The glands are composed of rather large irregularly shaped secretory cells which surround a poorly defined lumen (fig. 18). The cell walls are not well defined. Only a basement membrane with scattered pigment granules underlie the epithelium. Anteriorly each gland narrows down to a fine salivary duct which debouches into the pharynx in the antero-dorsal region of the buccal cavity (figs. 16 & 19). Each of these ducts is lined by low columnar epithelium and, in cross section, the

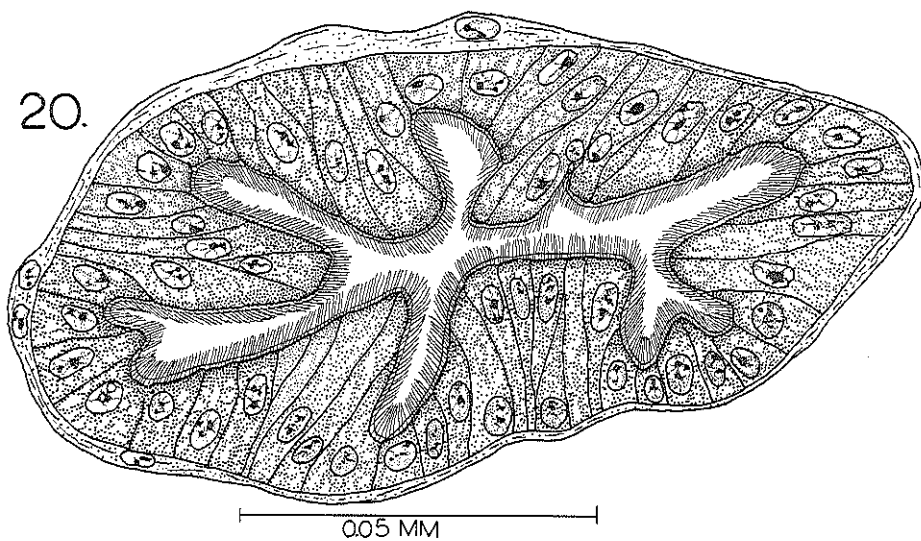
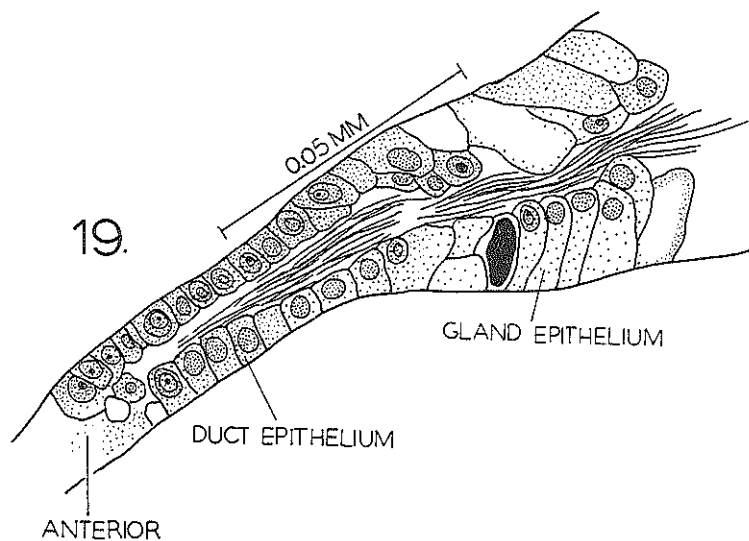
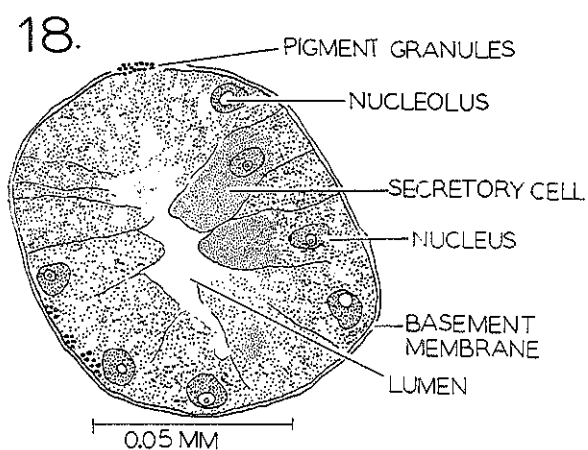
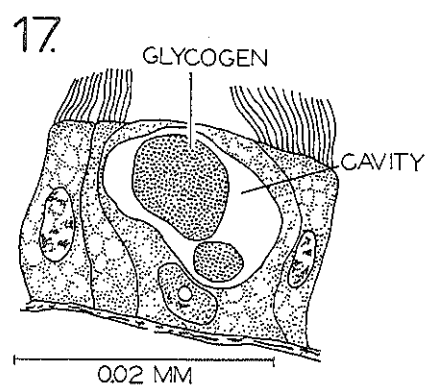
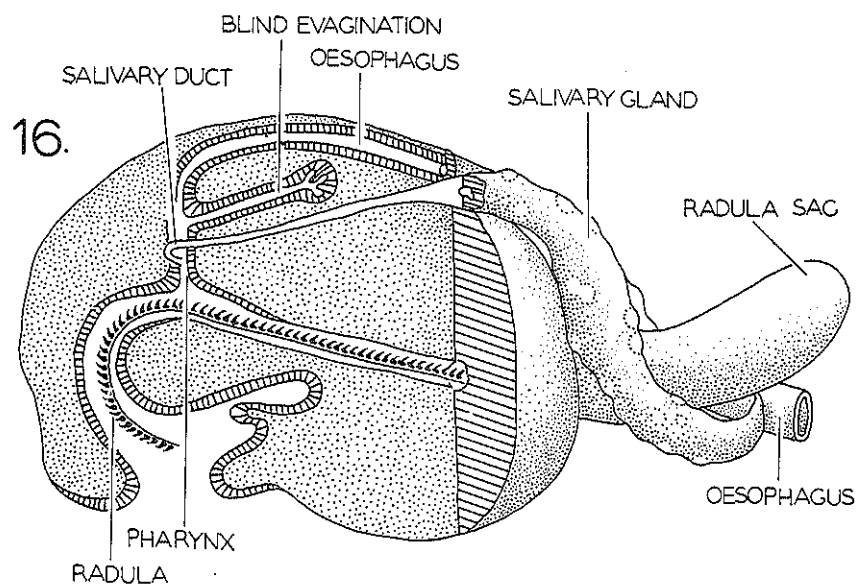


FIG.16. DIAGRAMMATIC LONGITUDINAL SECTION THROUGH BUCCAL MASS.
FIG.17. RESORPTION CELL FROM INTESTINAL LINING.
FIG.18. CROSS SECTION THROUGH SALIVARY GLAND.
FIG.19. LONGITUDINAL SECTION THROUGH DUCT OF SALIVARY GLAND.
FIG.20. CROSS SECTION THROUGH TERMINAL PORTION OF RECTUM.

lumen of this duct appears to be filled with structures resembling unusually long cilia whose origin, unfortunately could not be traced down to the epithelium. To my knowledge this feature has not yet been described for any ancyliid.

The radula sac is situated between the buccal or radula cartilages and extends postero-dorsad from beneath the buccal mass as indicated in figs. 13, 14 & 16 passing through the loop formed by the junction of the distal ends of the salivary glands.

After leaving the buccal mass, the oesophagus dips ventrally and, in the majority of cases, bends to the right in order to pass round the posterior extension of the radula sac. In some specimens this relation to the radula sac is reversed. Immediately after this it passes through the nerve ring.

The short oesophagus is lined by a single layer of ciliated columnar epithelium underlain by a narrow layer of muscle fibres and connective tissue (fig. 15). Where it merges into the crop, the ciliated cells become reduced to two narrow tracts on the left latero-dorsal and right latero-ventral sides respectively (fig. 10). For the rest the crop is lined by lower, unciliated columnar epithelium.

The description for the gizzard, as given by Basch (1959) for L. fuscus, can well be applied to that of B. mooiensis. The gizzard is tilted forwards and consists of columnar epithelium thrown into folds or costae, like brain coral, and covered internally by a rather thick cuticle seam consisting of rodlike

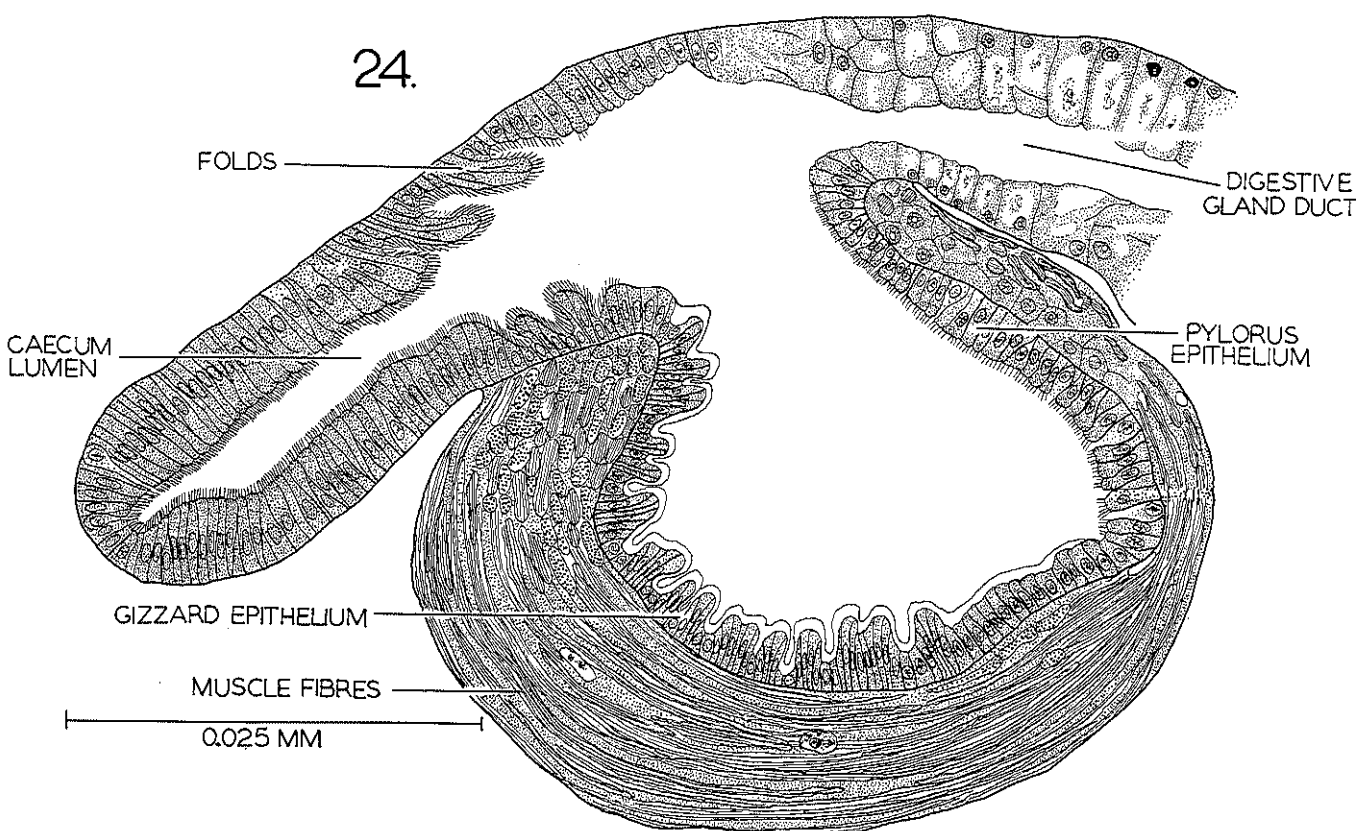
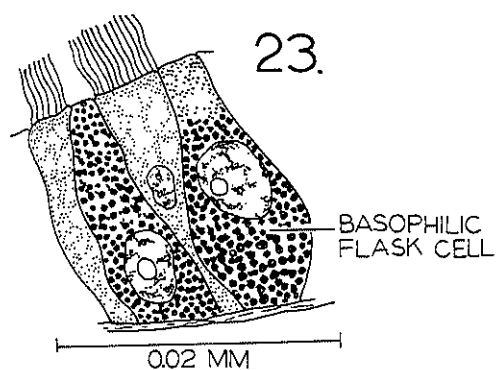
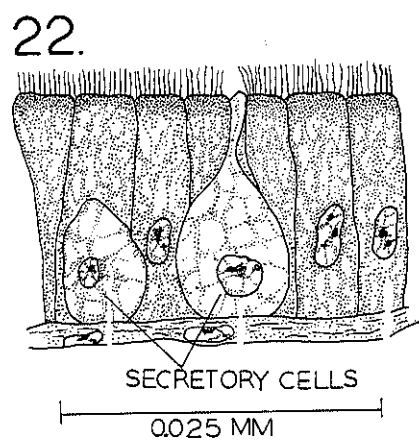
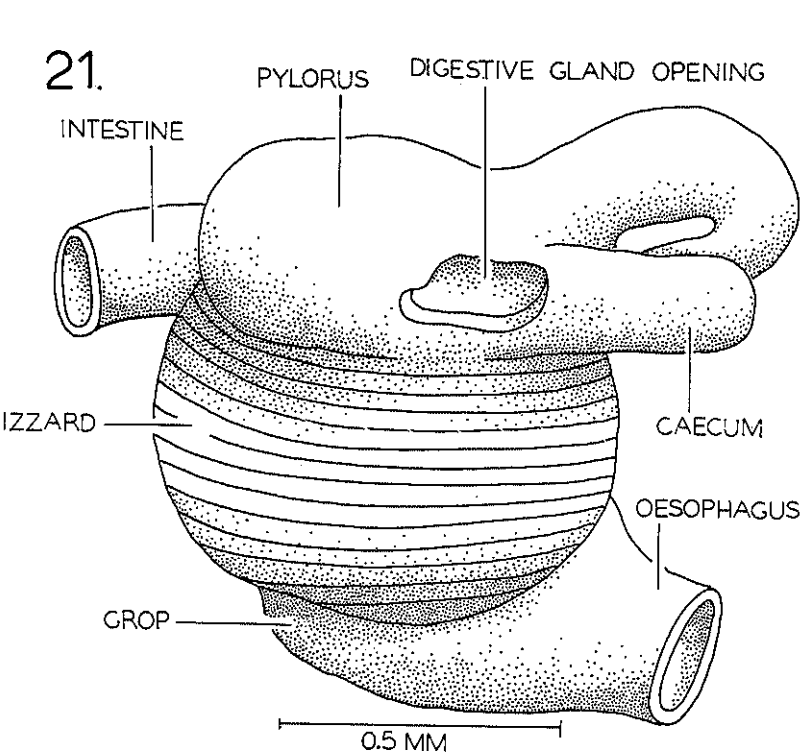


FIG. 21. STOMACH, RIGHT LATERAL ASPECT.

FIG. 22. INTESTINE EPITHELIUM, IMMEDIATELY BEYOND PYLORUS-INTESTINE JUNCTION.

FIG. 23. BASOPHILIC FLASK CELL FROM INTESTINAL LINING.

FIG. 24. OBLIQUE HORIZONTAL SECTION SHOWING OPENINGS OF CAECUM AND DIGESTIVE GLAND DUCT INTO PYLORUS AND GIZZARD OF STOMACH.

particles (figs. 24 & 25). Externally the epithelial lining is bounded by a thick sheath of alternating longitudinal and circular muscles (fig. 24).

The pylorus is a flattened sac-like structure lying on the right dorsal side of the gizzard (figs. 13 & 21). It has no muscular wall. This agrees with the condition described for Ferrissia tarda Say (Hoff, 1940) where, however, the pylorus is separated from the gizzard by a constriction. The lining of the pylorus consists of tall ciliated columnar cells interspersed with flask-shaped cells (fig. 26). Carriker and Bilstad (1946) are of the opinion that the latter cells secrete a transparent mucoid material which envelopes the faecal residues and certain other portions of the faecal pellets passing from the caecum.

On its right ventral aspect the pylorus receives the opening of a cylindrical, slightly tapering blind tube, the caecum (figs. 13, 21 & 24) which is directed forwards and obliquely to the left and which is lined by ciliated columnar epithelium. In its distal right lateral aspect this lining is thrown into longitudinal folds or costae (figs. 24 & 42) which increases in extent towards the opening of the caecum into the pylorus, so that at the point where it debouches into the pylorus the entire internal surface of the caecum is thrown into these folds. Hoff (1940) maintains that in F. tarda it is the bile duct which exhibit these plaits or costae. However his fig. 6 on page 229 shows the ventral aspect of the caecum to be folded in this manner. In the other ancyliids thusfar described no mention is made of the

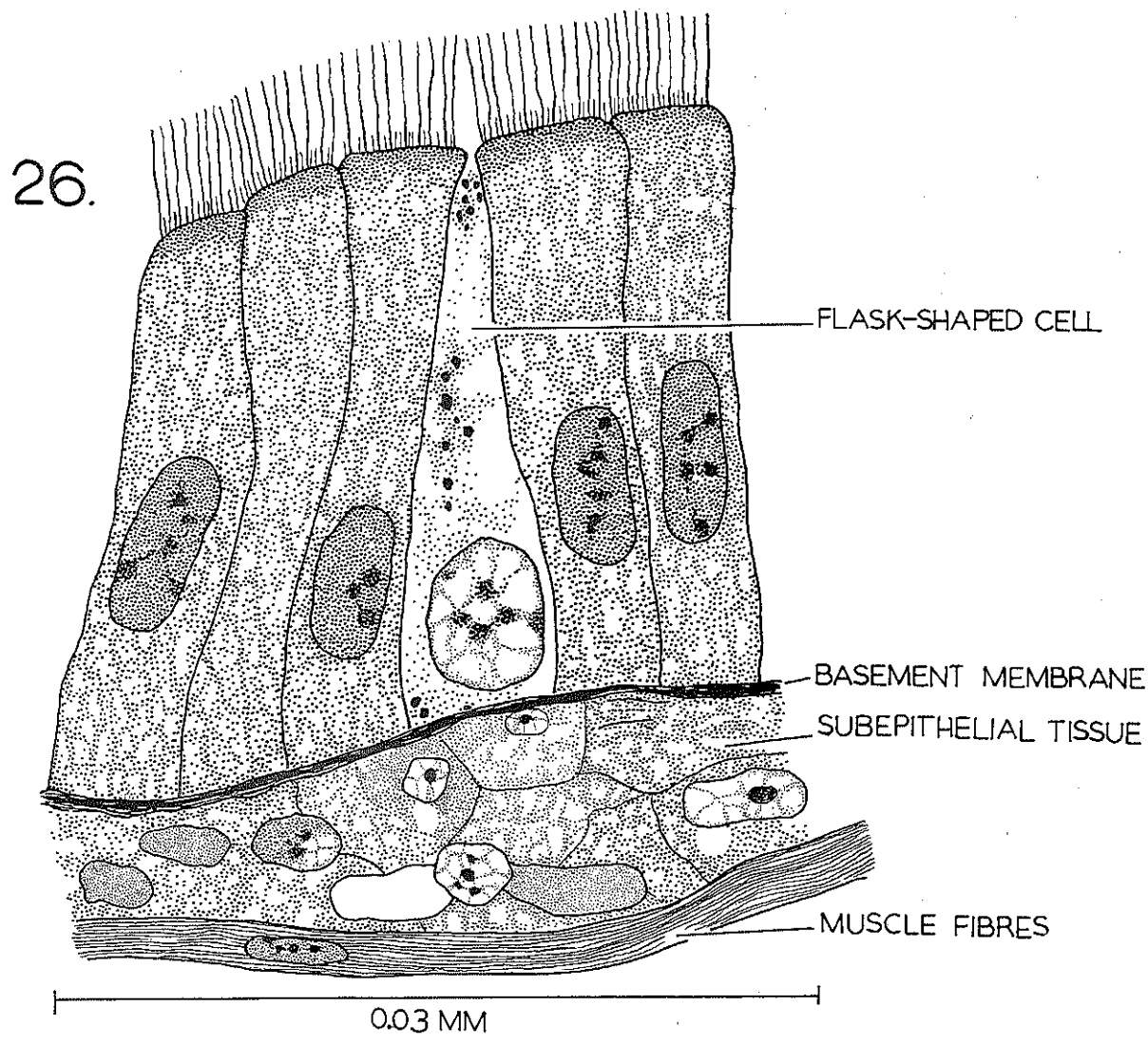
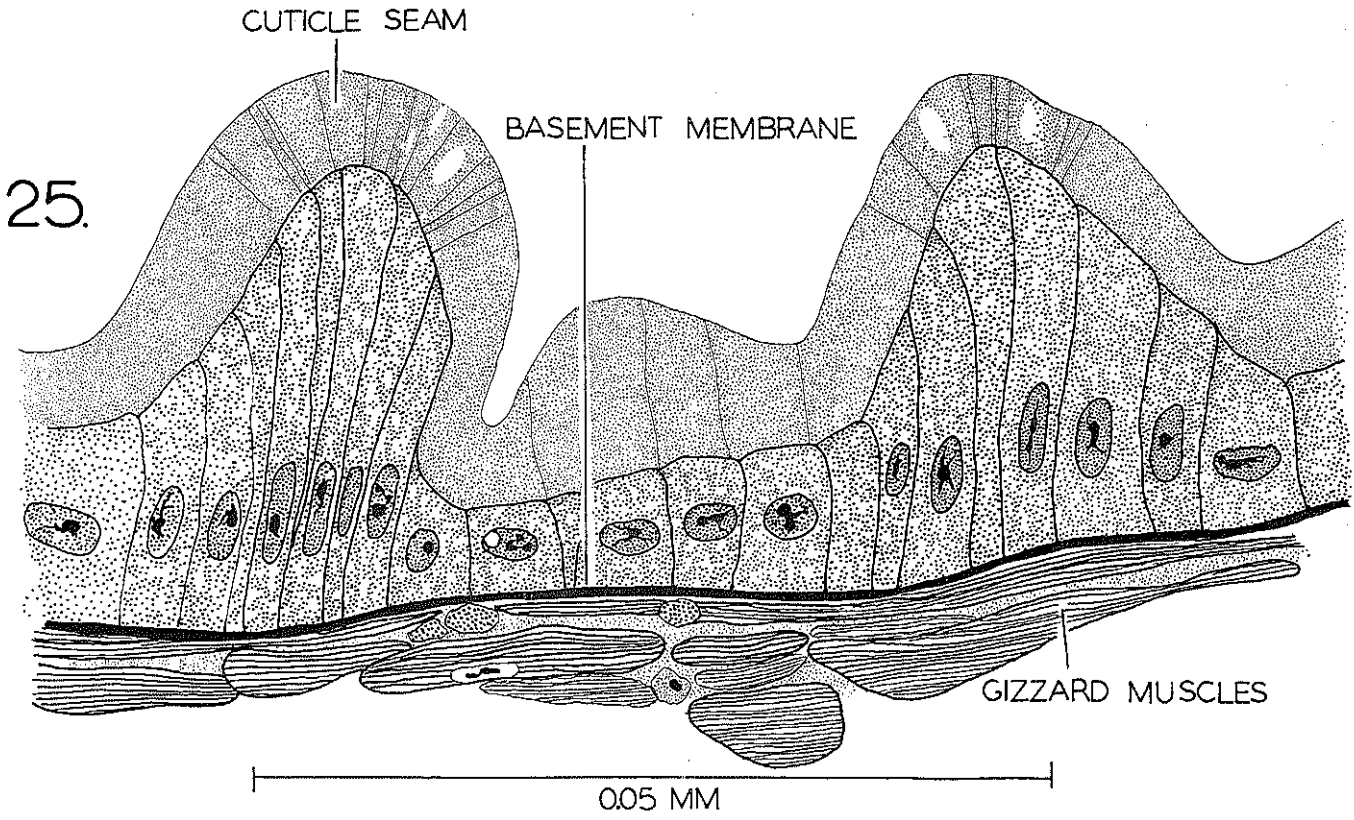
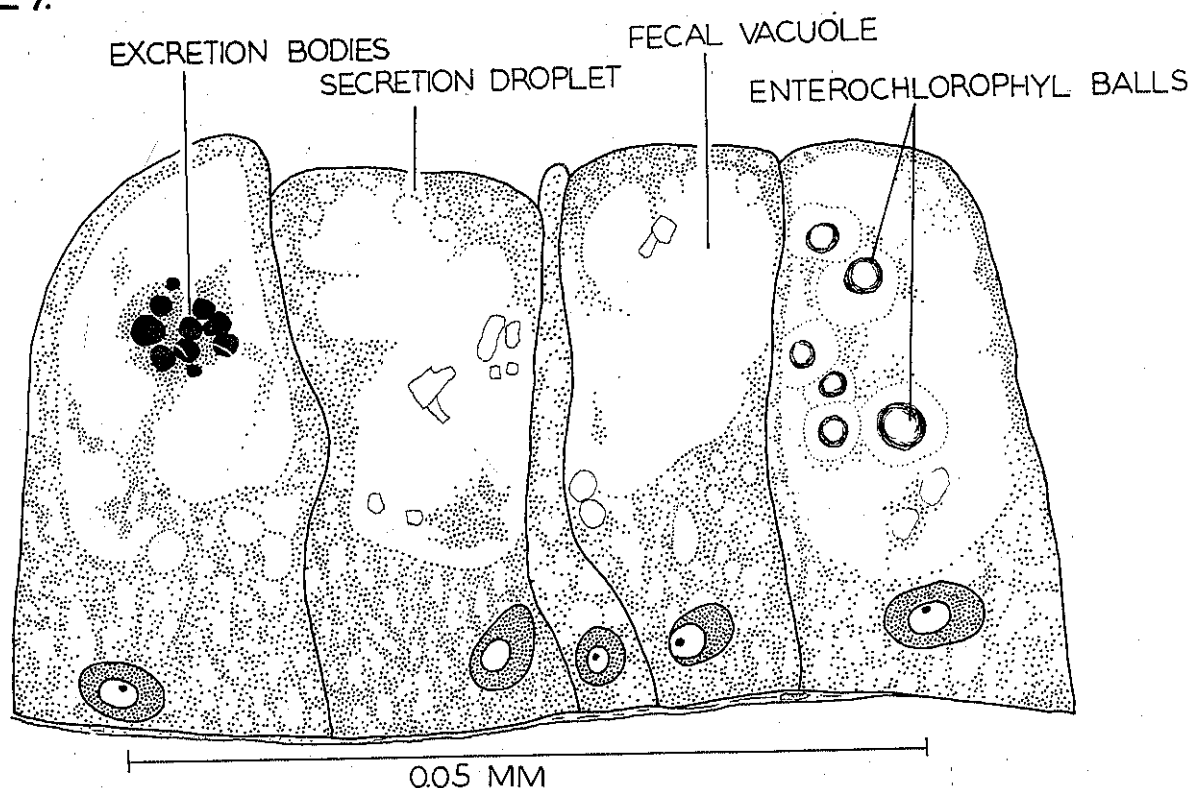


FIG. 25. EPITHELIAL LINING OF GIZZARD.
FIG. 26. EPITHELIAL LINING OF PYLORUS.

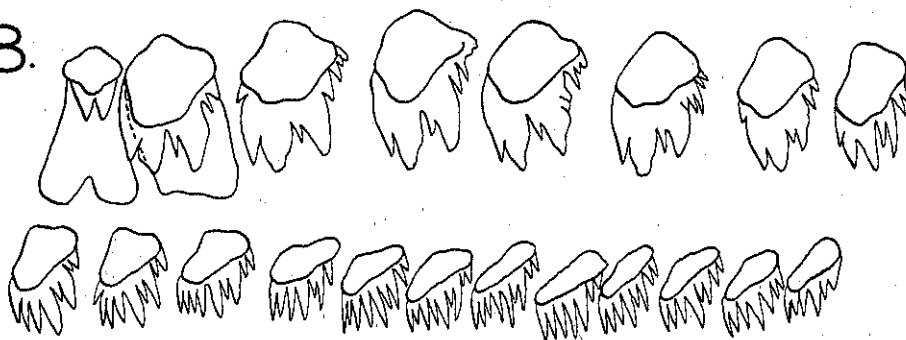
occurrence of cilia in the caecum.

The opening of the duct from the digestive gland is located laterally at the junction of the caecum with the pylorus (figs. 13, 21 & 24). This duct is not ciliated and is of considerable diameter but its lining is not folded as is claimed to be the case in F. tarda (Hoff, 1940). As in L. fuscus, the digestive gland (liver of authors) is a large lobulated sac whose central lumen is continuous with those of all the diverticula. It constitutes a considerable part of the visceral mass in the median and right regions of the animal from the posterior end of the right anterior shell muscle to the anterior margin of the posterior shell muscle (figs. 5 & 11). The cells composing the digestive gland (fig. 27) are large and two to three times as high as they are broad. They are bounded on the outside by an extremely thin layer of connective tissue elements that can be seen in well fixed specimens only. The cells of the digestive gland differ in appearance. Most of them possess a large vacuole and an elliptical, basally placed nucleus which contains a distinct nucleolus. In some the cytoplasm of the apical portions of the cell displays a fibroreticular texture, containing varying quantities of what could be secretion droplets which usually crowd underneath the apical membrane of the cell. In some cases it was observed that the apical membrane is erupted and that the contents of the cell is being passed into the lumen of the digestive gland diverticulum. This phenomenon was also observed in Lymnaea stagnalis ^Papressa (Carriker & Bilstad)

27.



28.



29.

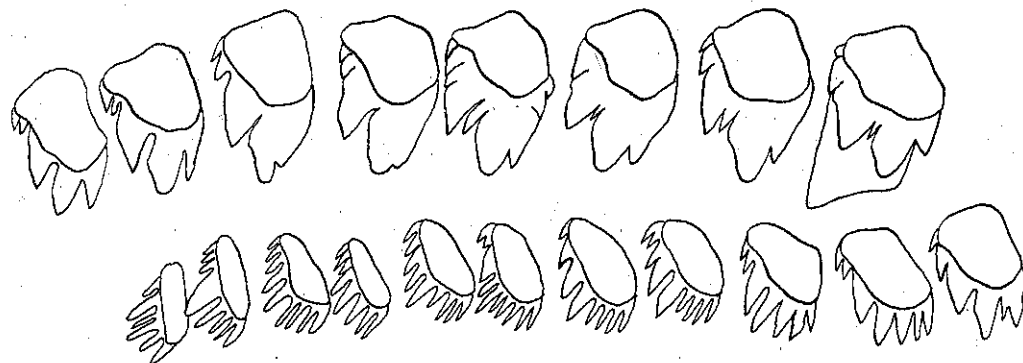


FIG.27. DIFFERENT CELL TYPES OF DIGESTIVE GLAND.
FIG.28-29. COMMONLY OCCURRING RADULAE IN SERIES EXAMINED.

1946). In addition to the secretion droplets, some cells contain small yellow green irregularly shaped bodies which do not seem to be affected by the staining method employed and which some authors (Enriques, 1901, quoted from Schneider, 1908) believe to be true chlorophyll which is accidentally taken up into the cell together with food material. In some cells these yellow green bodies are replaced by large bluish green balls, while still others contain rounded bluish green and brown bodies which differ from the former in being of a darker colour and by the fact that they seem to be affected by the staining method employed. These bodies probably represent what Carriker and Bilstad (1946) identified as excretion bodies in L. stagnalis compressa. Carriker and Bilstad maintain that the latter bodies are passed out of the liver in faecal strings. Although faecal strings were frequently seen in serial sections of B. mooiensis these bodies could not be detected in them. Carriker and Bilstad (1946) seem to support Krijgsman (1928), Peczenick (1925), Faust (1926) and Hurst (1927) (all quoted from Carriker & Bilstad, 1946) in the contention that the cells thus far described all represent digestive cells in different phases of the same process, viz, digestion.

Interspersed between the digestive cells, slender cells (fig. 27) occur with smaller nuclei than those of the digestive cells. Their apical portions project slightly above the surrounding cells. These probably represent mucous cells.

The lime cells referred to by Schneider (1908) and Carriker & Bilstad (1946) could not be identified in

B. mooiensis.

Large numbers of developing furcocercous cercariae, which were not identified, were frequently found in the digestive gland diverticula.

The general course of the intestine (fig. 13) agrees better with that of F. tarda (Hoff, 1940, Plate I, fig. 4) than with that of L. fuscus (Basch, 1959, fig. 4 A). Notably the two former species lack the two small loops displayed by the latter.

Four varieties of cells constitute the lining of the intestine. The first type agrees with the normal ciliated columnar cells. Interspersed between these are found large secretory cells (fig. 22) which agree with the description of the basal cell, a term which Carriker and Bilstad (1946) temporarily adopted for this kind of cell from a description of a similar cell by Howells (1942) in his work dealing with the histology of the intestinal epithelium of Aplysia (quoted from Carriker & Bilstad, 1946).

The third type of cell (fig. 23) conforms to the description of the basophilic flask cell described by Heidermans (1924, quoted from Carriker & Bilstad, 1946). The typical cell is flask-shaped while the nucleus is basally placed. The cytoplasm is granular and readily takes up the basic dye. Carriker and Bilstad (1946) maintain that these cells probably, in part, produce a mucoid material which envelopes the faecal residues. Carriker and Bilstad found these cells to be confined, among other structures, to the pro-intestine, but in B. mooiensis they were also found in the middle part of

the intestine.

Finally very large cells (fig. 17) sometimes with and sometimes without cilia, are frequently found between the rest of the cells constituting the lining of the intestine. They possess basally placed nuclei with distinct nucleoli. The most distinctive feature of these cells is that the greater part of the cell towards the lumen of the intestine is filled with a bluish-green substance which often cause it to bulge conspicuously. Sometimes a cavity separates this substance from the cytoplasm of the cell. Carriker and Bilstad (1946) distinguishes 2 kinds of ciliated cells, viz, the normal ciliated epithelium of the buccal cavity and the upper oesophagus and the secreting ciliated cells of the lower oesophagus, crop, pylorus and upper intestine. To these latter cells Heidermanns (1924), quoted from Carriker & Bilstad, 1946) attributes a cycle of secretion and ciliation during which the cilia may either be lost or regenerated. He also showed by experimental work that the secreting ciliated cells in L. stagnalis take up carbohydrate and fat. The carbohydrate is changed to glycogen and fat in the cell where it may be retained or is passed on to other cells; the fat may also be retained in the cytoplasm lumenward from the nucleus. Heidermanns thus attributed to the secreting ciliated cells the functions of ciliary action, secretion and resorption of fat and carbohydrates (quoted from Carriker & Bilstad, 1946). The varying presence and absence of the cilia on the particular cells of B. mooiensis under discussion seem to lend support to the above view of Heidermanns according

to which they might be regarded as representing secreting ciliated cells in the phase of resorption, in which case the cytological appearance of these could be explained by assuming the blue-green substance to represent absorbed carbohydrates which had been changed into glycogen while the cavity might have been produced by the fat having been dissolved by the xylol during preparation of the serial sections.

3.6 RADULA

The only structure other than the shell, which has thusfar been used for classification of the genus Burnupia, is the radula.

The original description of the radula as given by Walker (1923, p. 47) is as follows: "The central tooth of the radula has the cusps very small and close together and its base is very wide below, thus rendering the bases of the lateral teeth quite oblique; the cusps of the first four laterals are large and distinctly separated, the mesocone is slightly the largest, but it does not extend over the lower third of the base; an additional very small denticle is developed in the fifth lateral at the outer side of the ectocone; this gradually increases in size on the succeeding teeth and the original cusps diminish in size by the splitting up of these cusps, first the endocone, and then the mesocone; finally in the perfect marginals all the cusps become of the same size and the teeth are typically Ferrissia-like". The radula formula as given by Connolly (1939) is, "approximately 11 + 7 + 1 + 7 + 11."

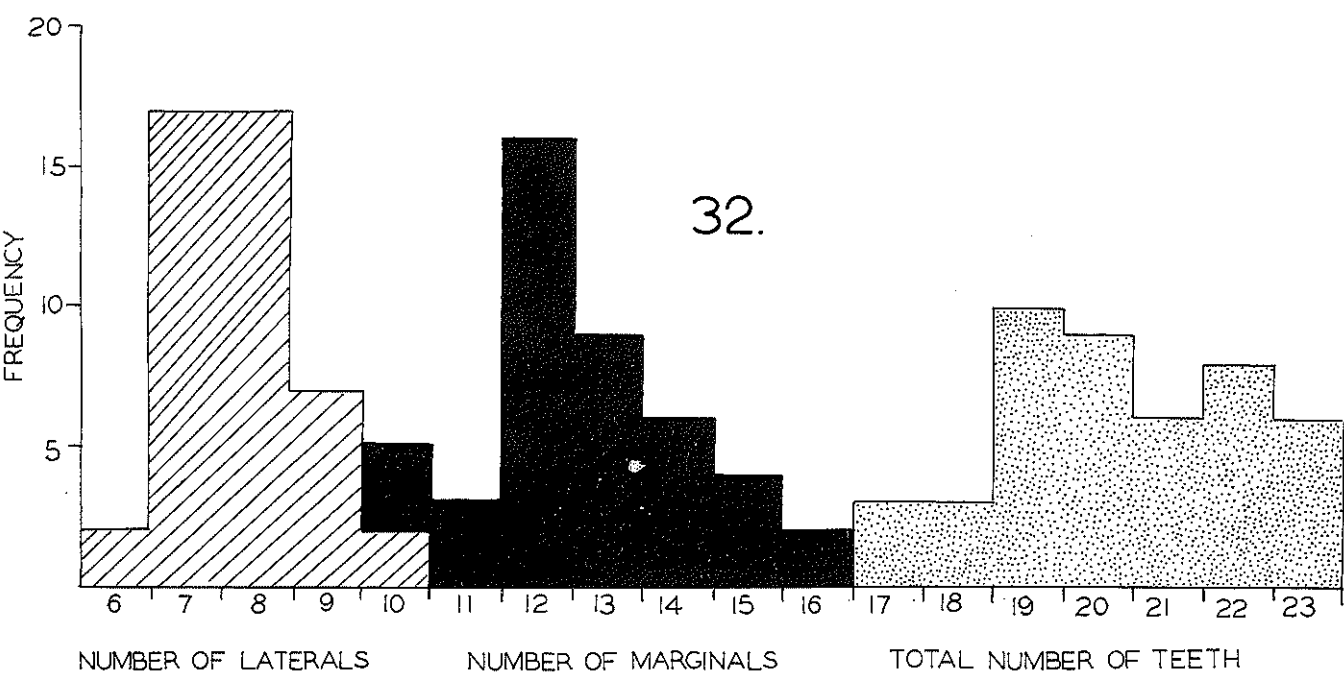
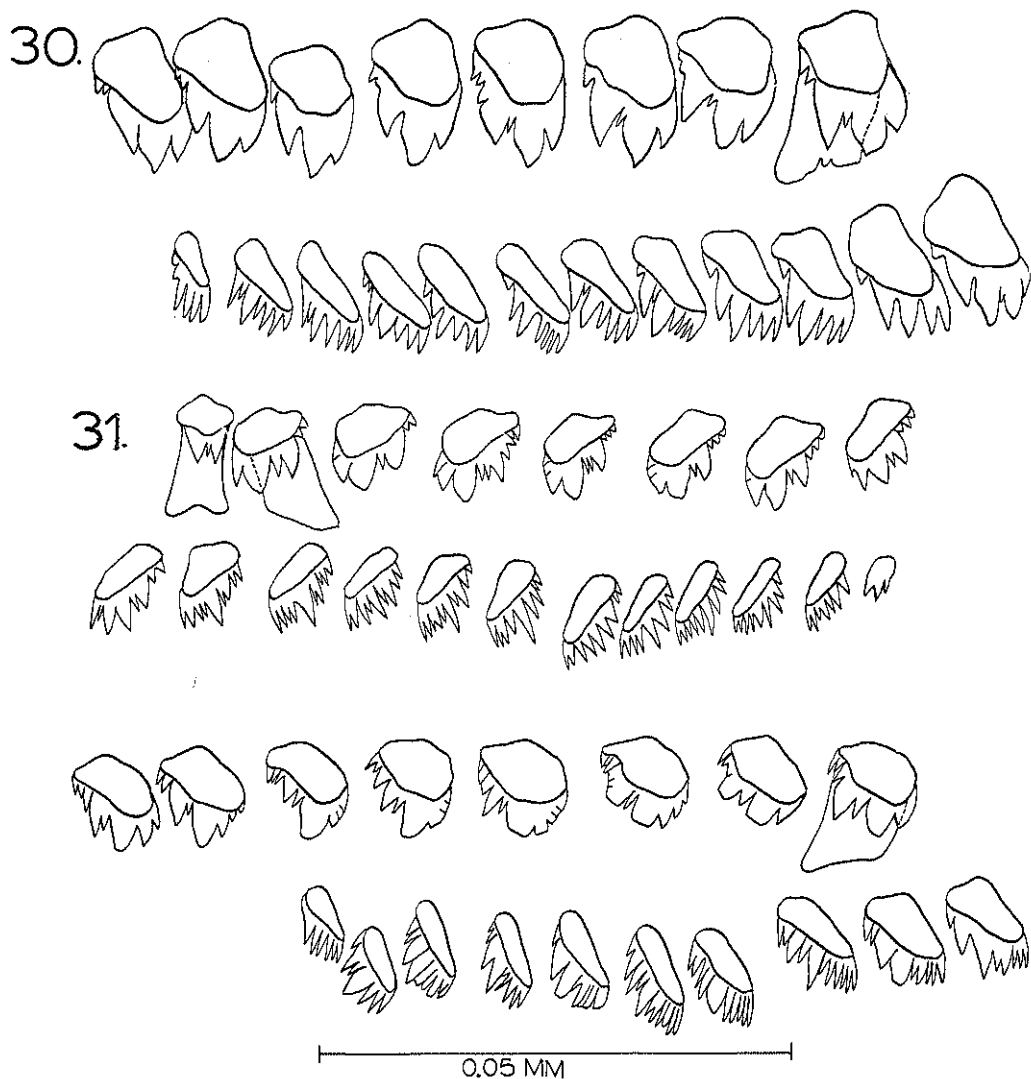


FIG. 30. COMMONLY OCCURRING RADULA IN SERIES EXAMINED.

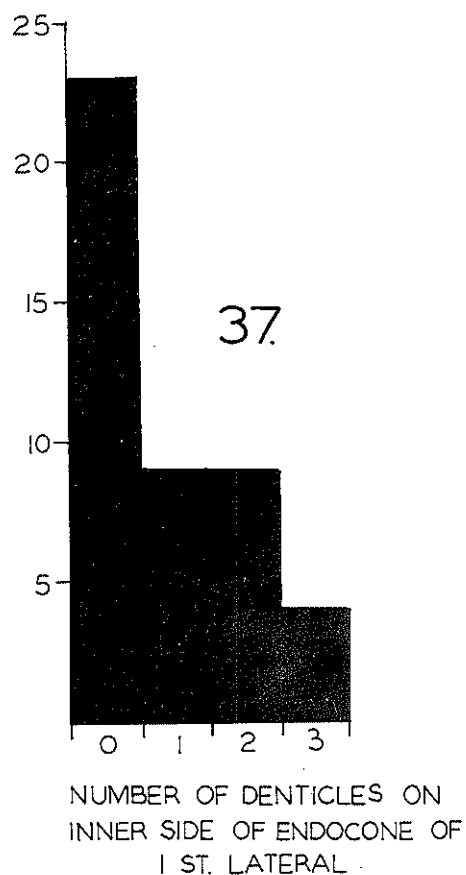
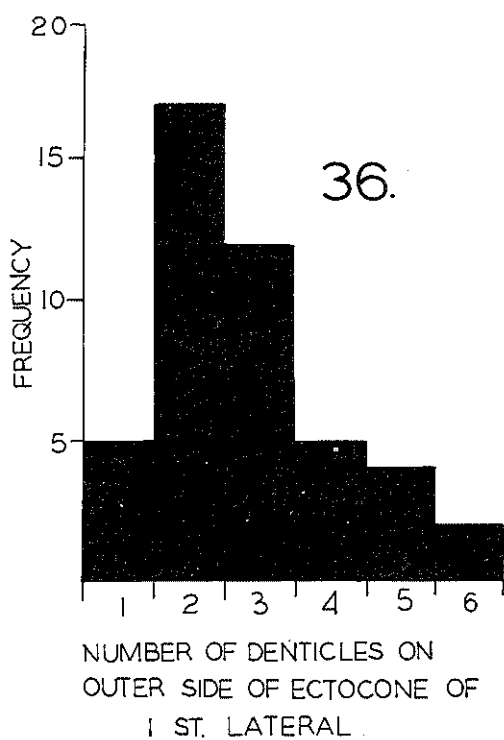
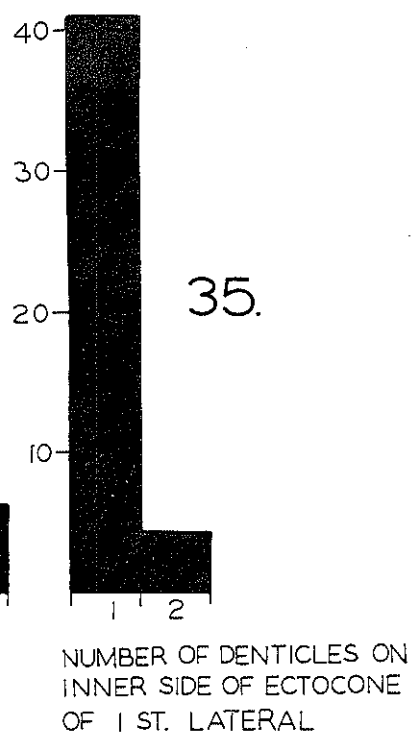
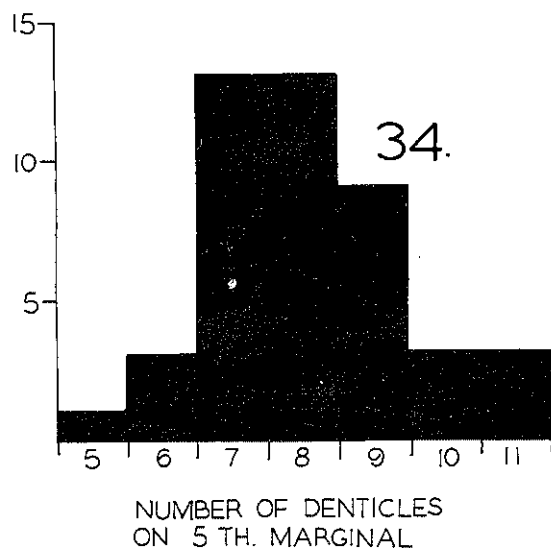
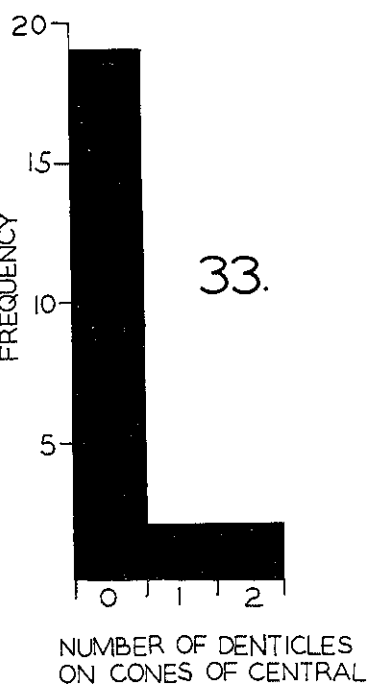
FIG. 31. RADULA OF ANIMAL FROM SHELL DEPICTED IN FIGURES 1-2.

FIG. 32. HISTOGRAMS SHOWING THE FREQUENCY OF OCCURRENCE OF VARIOUS ASPECTS OF THE RADULA AS DETERMINED IN 45 HALF TRANSVERSE ROWS FROM 23 RADULAE.

The above descriptions, however usefull, unfortunately are inadequate in as much as they do not reflect the degree of variability of different features of the radula and a more detailed description is therefore offered, based on 23 randomly selected radulae from specimens with shell lengths of not less than 4.4 mm and not more than 6.2 mm. In each of these radulae the thirteenth row from the posterior end of the radula, counted from the first row which took up the stain in such a way that the teeth can be definitely distinguished, was chosen for examination. In this region the radula teeth are already fully formed but not subject to deterioration. The features attended to and the results of the examination are summarised in figs. 32, 33, 34, 35, 36 & 37 which, coupled with other observations, the following conclusions may be drawn.

None of the features examined seem to be obviously correlated with increasing shell size. The number of teeth per half transverse row ranges from 17 to 23, with 19 and 20 slightly predominating. Likewise, the numbers of the laterals and marginals per half transverse row range from 6 to 10 and from 10 to 16 with 7 or 8 and 12 predominating in each case respectively. For this size range and transverse row the radula formula should therefore either be 10 to 16 : 6 to 10: 1 : 6 to 10: 10 to 16, if the entire range of variation be taken into account, or 12 : 7 or 8 : 1 : 7 or 8: 12 if only the predominating numbers are considered.

With respect to the numbers of different teeth to one half of a transverse row and the number and



FIGS. 33-37. HISTOGRAMS SHOWING THE FREQUENCY OF OCCURRENCE OF VARIOUS ASPECTS OF THE RADULA AS DETERMINED IN 45 HALF TRANSVERSE ROWS FROM 23 RADULAE.

arrangement of the denticles on the first lateral, figs. 28, 29 and 30 depict the most commonly occurring radulae in the specimens examined.

3.6 1 THE CENTRAL

As described by Walker (1923), this tooth has 2 well developed cusps, moderately separated from each other. Denticles are occasionally found either on the median or the lateral sides of either cones.

3. 6 2 THE LATERALS

The cones of the tricuspid laterals are well separated, the mesocone being slightly the largest. The cones are more or less of constant size and shape up to the seventh or eighth lateral, but directly on the next tooth the endocone splits into 2 or 3, or, in rarer cases into 4 or 5 denticles (table 1). This point is considered to mark the transition from laterals to marginals.

3.6 3 THE MARGINALS

The number of denticles on the fifth marginal varies between 5 and 11 with 7 or 8 as the most commonly occurring number.

TABLE 1				
Number of cones into which endocone splits	2	3	4	5
Frequency out of 45	34	8	2	1

In the rest of the marginals still further splitting and reduction in size of the original cusps take place, thus producing rake-like teeth in which the central denticles are slightly larger than those on the sides (figs. 28, 29 & 30).

The position and length of the base of the tooth relative to its crown, is, in my opinion, of minor importance because this can vary according to the manual pressure applied in the finishing stage of the process of mounting the radula.

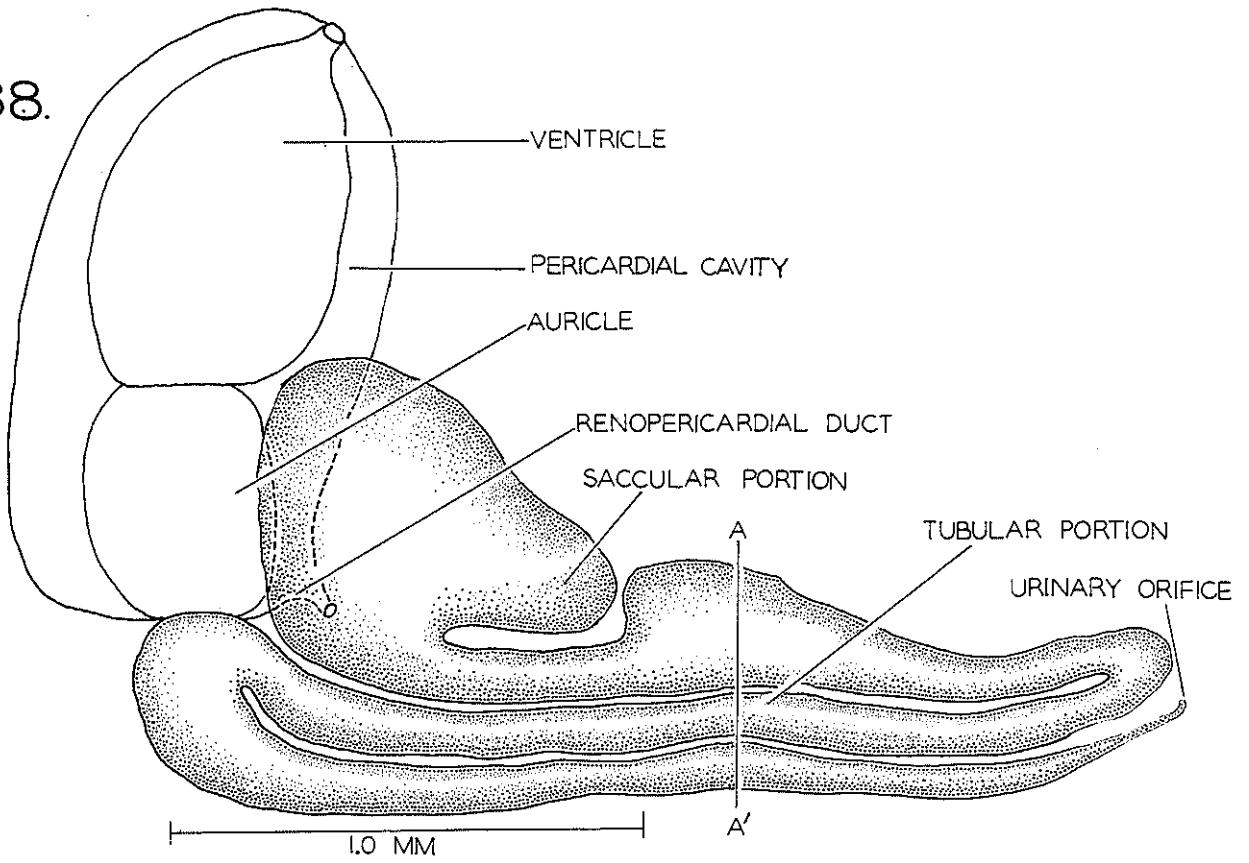
3. 7 EXCRETORY SYSTEM

The single kidney lies entirely within the blood sinus of the mantle on the left side of the body (fig. 44). In some specimens, freshly killed with nembutal and boiling water, the kidney can be seen as a rather bright yellow structure underlying the mantle surface. In other specimens however, the mantle may be so densely pigmented in this area as to obscure the kidney.

In order to observe this organ, the dorsal mantle covering was removed very carefully with a pair of forceps, thus leaving the heart as well as the entire kidney complex exposed. The distal region of the kidney is exceptionally delicate and renders removal of the mantle in this area, without tearing it, very difficult.

Basically the kidney is a single continuous tube (fig. 38) with only 2 sharp flexures in contrast to the 4 encountered in L. fuscus (Basch, 1959), F. tarda (Hoff, 1940) and A. fluviatilis (Sharp, 1883b). The

38.



39.

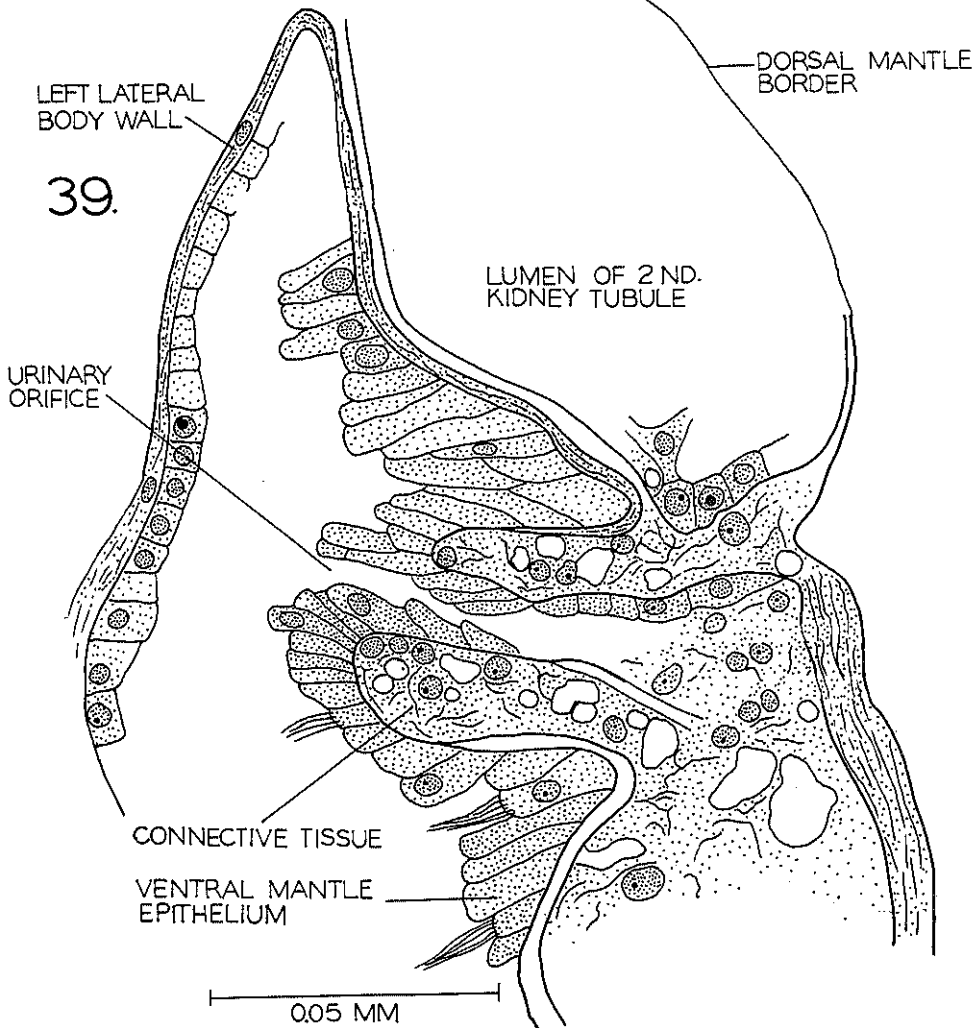


FIG.38.EXCRETORY SYSTEM OF A FRESHLY KILLED SPECIMEN.
FIG.39.TRANSVERSE SECTION THROUGH URINARY ORIFICE.

arrangement of the convolutions of the tube, apart from their number, is basically similar to those of L. fuscus (Basch, 1959).

Macroscopically, only a saccular and tubular region can be identified. A very small renopericardial duct connects the anterior left lateral wall of the pericardial cavity with the anterior right latero-ventral wall of the saccular region (fig. 38). This duct runs more or less at right angles to the longitudinal axis of the animal and close to the ventral mantle epithelium. Histologically its wall consists of small cuboidal cells with long massive cilia extending into the lumen of the duct and directed towards the lumen of the saccular region (fig. 40).

Immediately around the opening of the renopericardial duct into the saccular region of the kidney, and for a short distance backwards on its right lateral wall, the epithelial lining of the latter is slightly elevated by being composed of two or more layers of cells. This is annotated as elevated epithelium in fig. 40. Apart from this area, the saccular region is lined throughout by a single layer of columnar epithelium. The cell structure of the epithelium is essentially similar to that described for L. fuscus (Basch, 1959). The vacuole, situated between the nucleus and the apical cell membrane, almost invariably contains an irregularly-shaped blue staining body (fig. 41), also represented in Bulinus tropicus (Stiglingh et al., 1962) and certain Stylommatophora (Simroth, 1928). In sections where the cell membranes are indistinct or have a

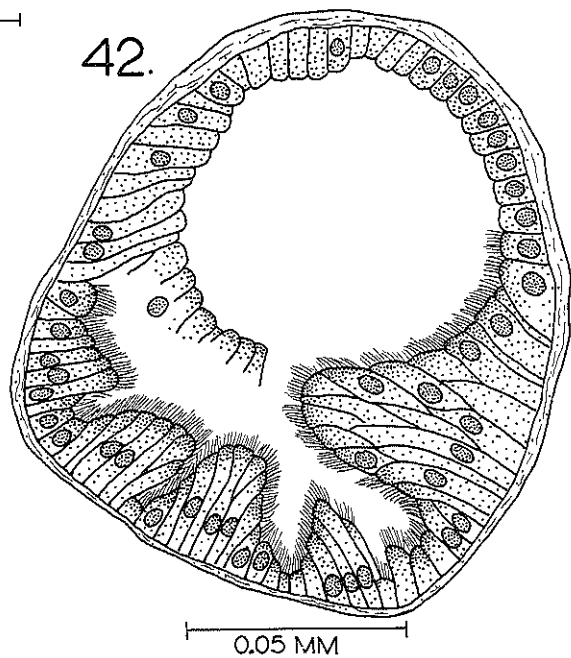
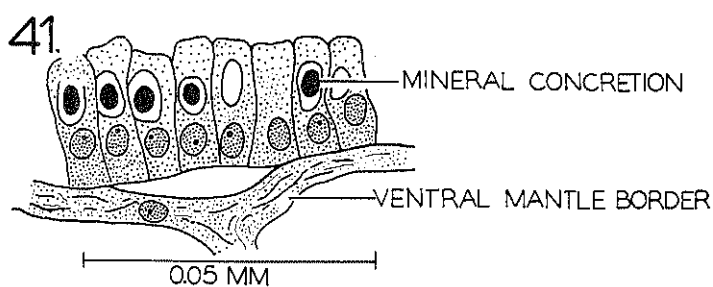
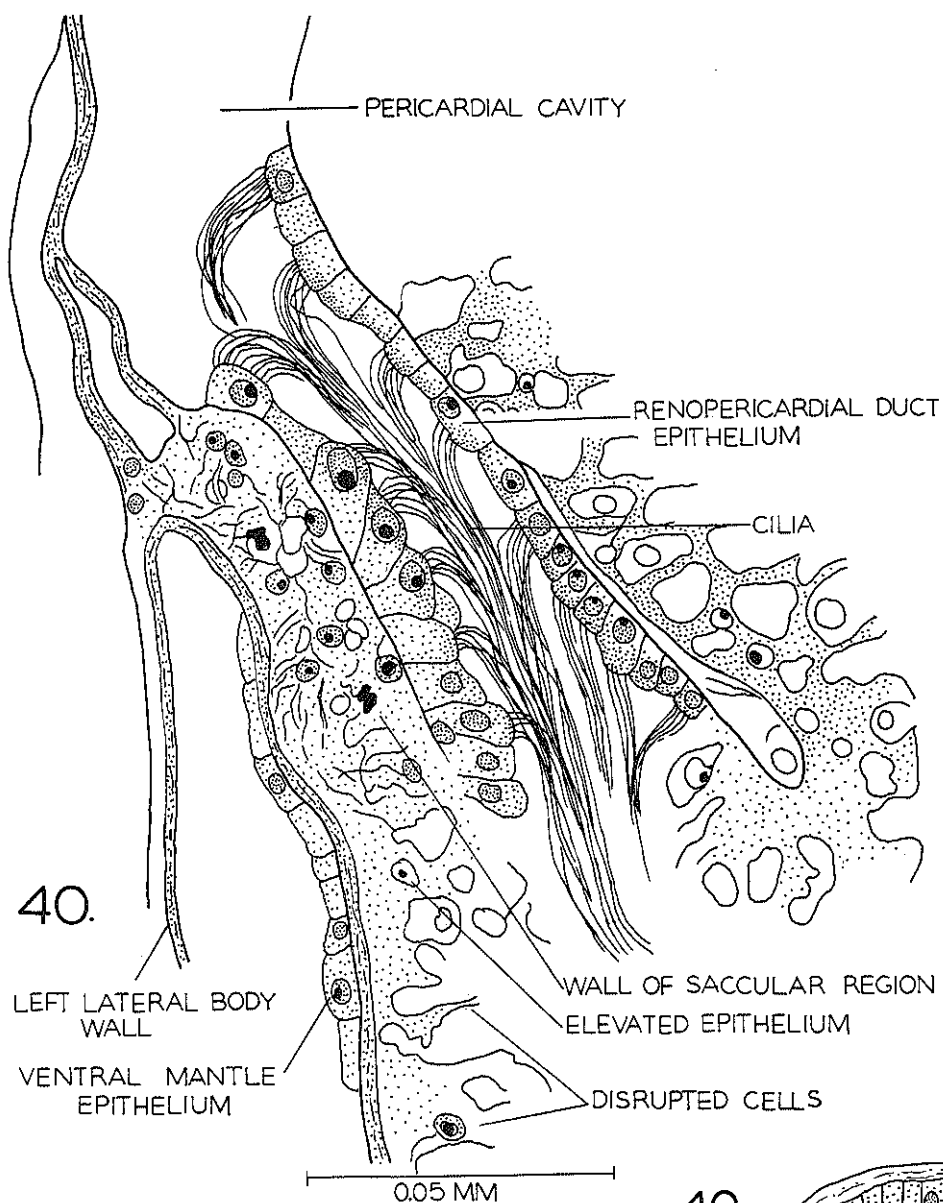


FIG.40. SECTION THROUGH RENOPERICARDIAL DUCT WHERE IT OPENS INTO SACCULAR PORTION OF KIDNEY.

FIG.41. EPITHELIAL LINING OF SACCULAR PORTION OF KIDNEY.

FIG.42. CROSS SECTION THROUGH DISTAL END OF CAECUM.

definite disrupted appearance (fig. 40), similar bodies are found in the lumen of the kidney. This may be due to disruption caused by the killing method employed. The saccular portion of the kidney gradually decreases in diameter and then merges into the tubular region.

The tubular region, which may either be circular or oval in cross section, is lined with cells which differ from those lining the saccular region in lacking the irregularly-shaped, blue staining bodies, by the greater affinity for the stain in their basal regions and by the indistinctness of their apical membranes. The nuclei are centrally placed.

The epithelium surrounding the small urinary opening, situated between the mantle and the left body wall, is slightly elevated by the underlying connective tissue (fig. 39). As in L. fuscus (Basch, 1959) the entire kidney, except the renopericardial duct, is devoid of cilia.

3.8 SENSE ORGANS.

3.81 THE EYE

Figure 43, which depicts a sagittal section through the eye of B. mooiensis, renders a detailed verbal description of this organ superfluous. Suffice it to add only the following minor details.

As in the case of L. fuscus (Basch, 1959) the eye is only weakly supplied by muscles. The strongly flattened cells forming the cornea, give the impression of representing a syncytium, for no cell membranes could be identified between the nuclei. The lens is

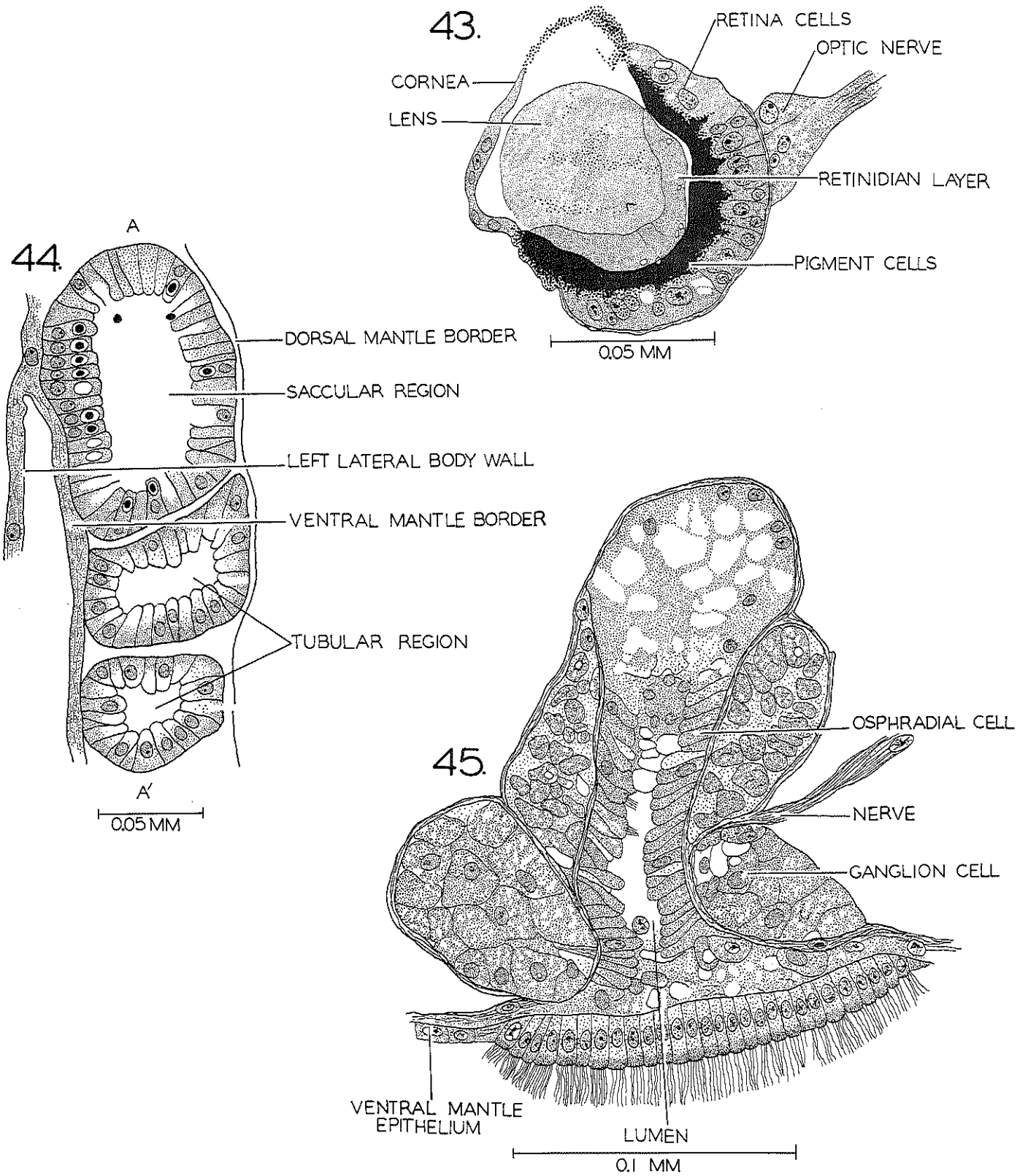


FIG.43.SAGITTAL SECTION THROUGH EYE.
 FIG.44.CROSS SECTION THROUGH KIDNEY AT LEVEL AA' IN FIGURE 38.
 FIG.45.LONGITUDINAL SECTION THROUGH OSPHRADIUM.

spherical and takes up the orange stain. No distinction can be drawn between retina cells and pigment cells as was possible in the case of Physa acuta (Simroth, 1928) and, unlike this species, the pigment reaches only half-way towards the base of the cells which seem to broaden out instead of tapering to a point as the pigment cells of P. acuta do. Occasionally cells were seen which, in general appearance, remind of Beck's cells, but which, by reason of their irregular distribution throughout the retina and their smaller nuclei, cannot, to my mind, be regarded as such.

3.82 THE OSPHRADIUM

The small osphradium is situated on the ventral mantle surface almost in line with the pneumostome (fig. 4). This organ is a blind tubular, dorsally directed invagination of the ventral mantle epithelium (fig. 45). In B. mooiensis it varies considerably from those described for other ancyliids (Basch, 1959, Hoff, 1940). In both L. fuscus and F. tarda the lining cells of the sac are ciliated throughout, and, according to Hoff, serve to create a current of water in and out of the sac. The only obviously ciliated cells connected with the osphradium of B. mooiensis are the columnar cells which border the opening, and continue into the neck for a short distance. The sac itself is lined by columnar cells some of which bear structures which could be tufts of cilia (fig. 45). Interspersed between these cells are transparent structures which might represent mucous cells. The osphradium

is not capped by a cup of ganglion cells as in the case of L. fuscus (Basch, 1959) and F. tarda (Hoff, 1940), but instead these cells are arranged like a collar round it's neck (fig. 45).

3.83 THE STATOCYST

These organs (fig. 49) are dorso-laterally and equatorially situated, one on each pedal ganglion, and are covered by the same fibrous sheath that covers the ganglion. The dimensions correspond well with those given by Basch (1959) for L. fuscus viz. 45 to 50 μ long and approximately 20 μ broad. The statoliths are single, oval-shaped and show up to two faint concentric layers. They can reach a size of up to 7.5 μ long and 4.0 μ broad thus being considerably larger than those of L. fuscus (Basch, 1959) which are 3.5 μ long and 1 to 2 μ broad. The number of statoliths present in each statocyst seems to increase with the age of the animal. Only very rarely were structures found on the inside wall of the statocyst that remind of a single cilium projecting into its lumen.

3.9 CIRCULATORY SYSTEM

The investigation of this system which, of necessity, had to be done microscopically, was greatly curtailed by the unsuitability of the serial sections at my disposal. Some aspects of it, therefore, had to be left unattended to.

The heart lies between the two shell muscles on the left side of the body. The pericardial cavity

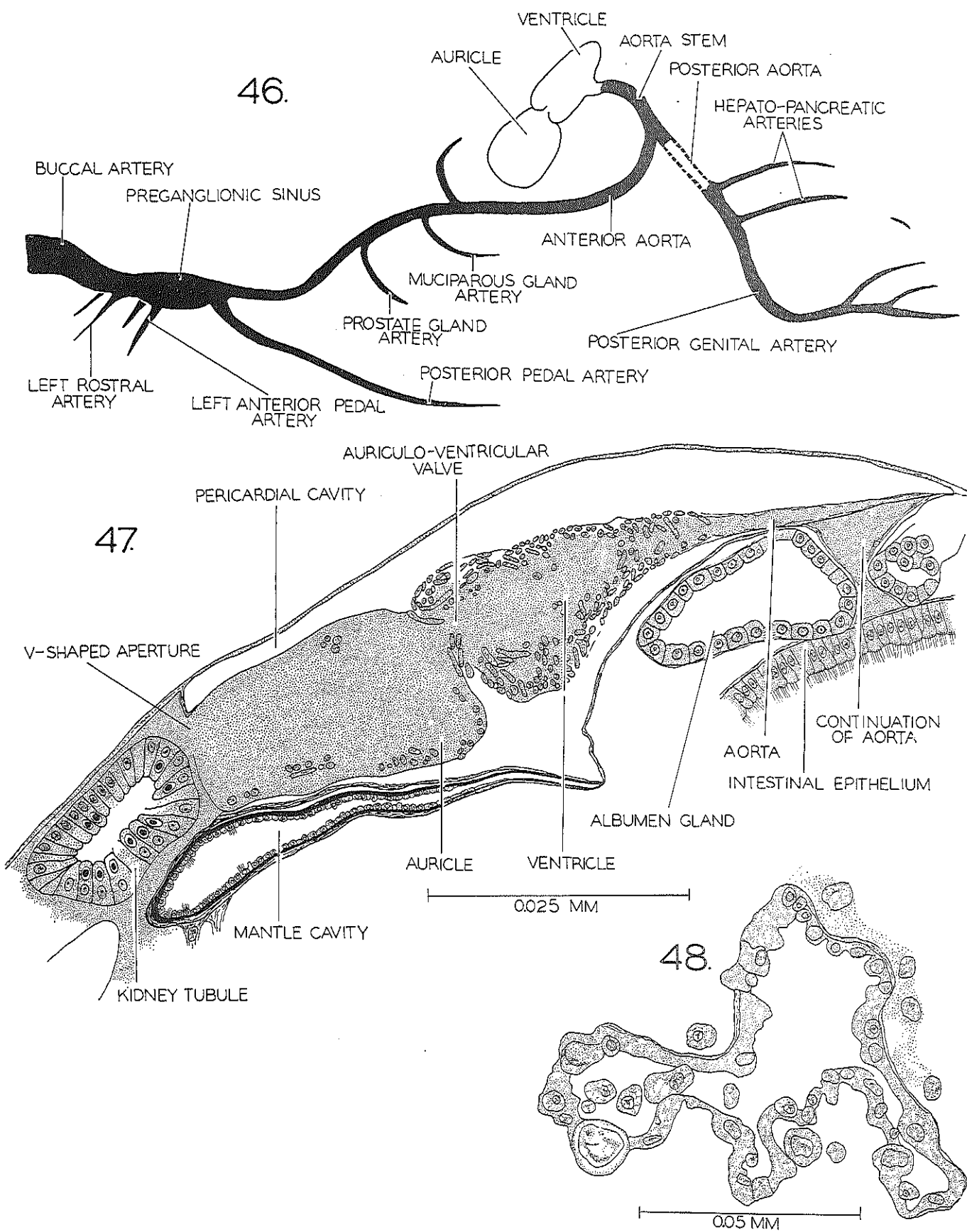


FIG. 46. ARTERIAL SYSTEM, LATERAL VIEW.
 FIG. 47. SECTION THROUGH HEART.
 FIG. 48. SECTION THROUGH PREGANGLIONIC SINUS.

is bounded ventrally by the fine membrane which also forms the roof of the mantle cavity, and dorsally by the mantle. It opens into the kidney via the small renopericardial duct already described elsewhere.

The heart (fig. 47) roughly lies at right angles to the sagittal axis of the animal. Whereas the wall of the auricle consists of a very delicate, transparent membrane with only here and there ribbon-like muscle cells containing scattered nuclei, that of the ventricle is composed of numerous muscular cells similar to those of the auricle. The general arrangement of the arterial blood vessels is depicted in fig. 46.

In B. mooiensis the aorta leaves the ventricle from its posterior left lateral wall and not from the posterior end of the ventricle as in F. shimekii (Boer and Lever, 1959) or from its right posterior side as in F. tarda (Hoff, 1940). It extends backwards between lobes of the albumen gland for a short distance and then passes over the intestine where it bifurcates, giving rise to the anterior aorta and the posterior aorta.

As in the case of F. shimekii (Boer and Lever, 1959), the main direction of the posterior aorta is ventro-caudad. Unfortunately, however, the posterior aorta in my serial sections disappears very close to the left side of the stomach and is only picked up again where it traverses the liver where it gives off at least two branches to the liver. Beyond this point it gives off 3 branches which supply the ovotestis.

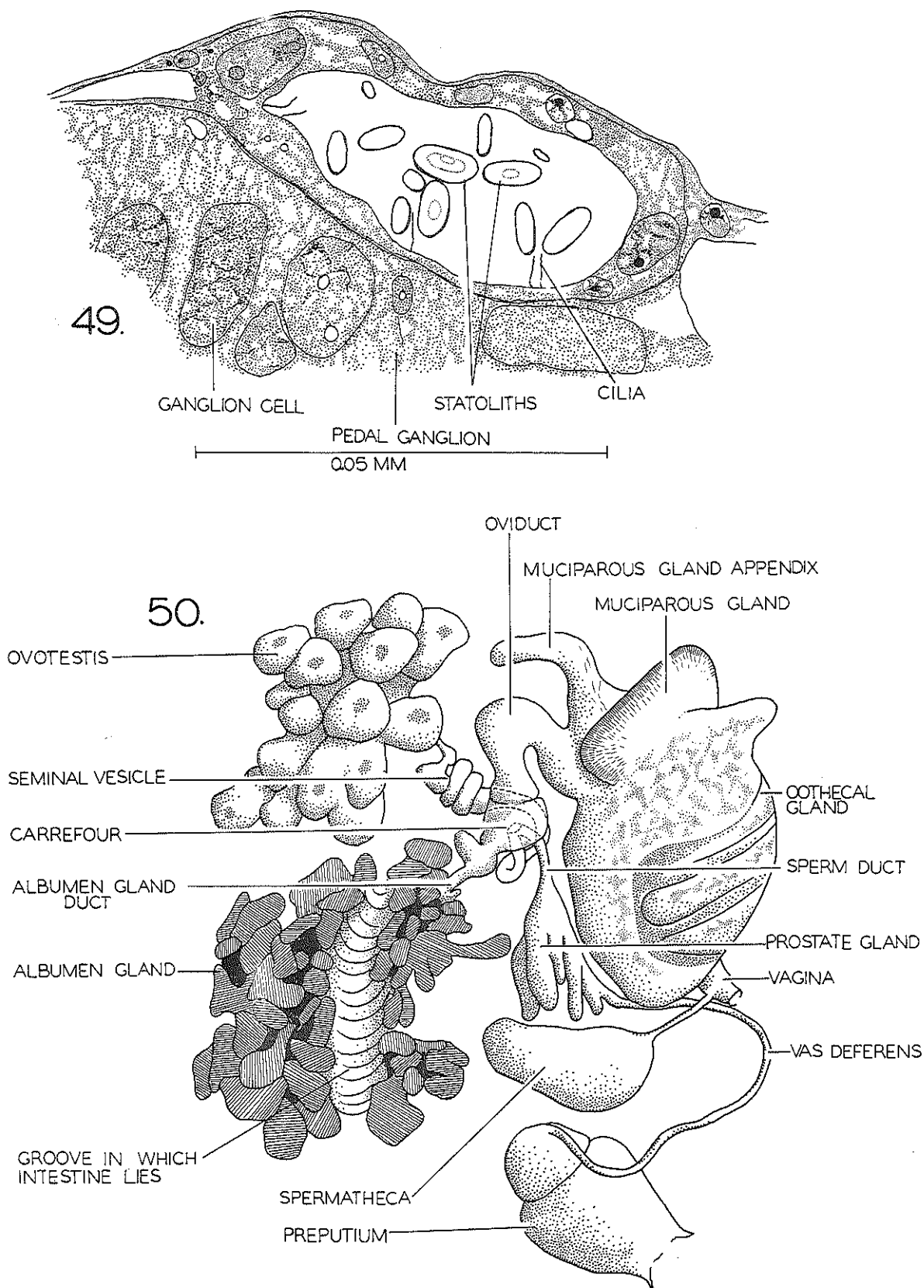


FIG. 49. SECTION THROUGH STATOCYST.
FIG. 50. GENITAL ORGANS, SLIGHTLY PUSHED APART

The anterior aorta passes forwards in a ventro-rostral direction. The first blood vessel to arise from the anterior aorta could not, unfortunately, be traced to its ultimate ramifications but it could represent either the pyloric artery or the albumen artery or it could supply the caecum. The second artery arising from the anterior aorta supplies the muciparous gland, while the third vessel supplies the prostate gland. The anterior aorta now proceeds forwards more or less to the immediate left side of the mid-ventral line of the body and finally reaches the left parietal ganglion. Its route through the central ganglia is exactly similar to that in F. shimekii (Boer and Lever, 1959). It runs alongside the ventral surface of the left parietal ganglion, following the right lateral aspect of the parieto-pedal connective and then crosses over the dorsal side of the left statocyst where it turns to the right, crossing still further over the left pedal ganglion. Anteriorly and medially to the pedal ganglia the aorta widens considerably to form the preganglionic sinus (Boer and Lever, 1959), a cross section of which is presented in fig. 48. The shape of the sinus is rather variable like a tube indented on the sides to various extents. The wall of the sinus (fig. 48) is composed of a number of cells in which no definite cell membranes could be identified. These are underlain by an extremely delicate connective tissue layer. Frequently some of the cells are found lying free in the lumen of the sinus. This description seems to apply to all the

arteries found in the body.

A number of blood vessels arise from the pre-ganglionic sinus. In caudo-rostral sequence these are, firstly the posterior pedal artery which proceeds ventrally and runs backwards in the body cavity close to, but dorsally to the muscles of the foot. It enters the lacunae in the foot muscles just beyond the level of the transverse midline of the body.

Secondly, paired rostral arteries run laterally in front of the pedal ganglia. Their ultimate ramifications could not be observed.

Thirdly, there are paired pedal arteries which seem to open in the sinusses of the foremost part of the foot.

The origin of the penial artery (not shown in fig. 46) could not be traced, but it runs on the ventral side of the penis and seems to enter the pigmented muscle fibres which envelope the ventral side of the penis.

Continuing forwards, the preganglionic sinus narrows down slightly towards the buccal mass where it comes to lie between the radula cartilages. Here it widens again considerably and is now called the buccal artery, which gives the impression of supporting the radula pouch.

No venous vascular system is present. The marginal sinus of the mantle is well developed, but that of the pseudobranch is not extensively developed. The latter communicates with the former in the region of the shell muscles on the left side of the body. In this area the sinus of the mantle surrounds the kidney. The blood finally re-enters the auricle through the

51.

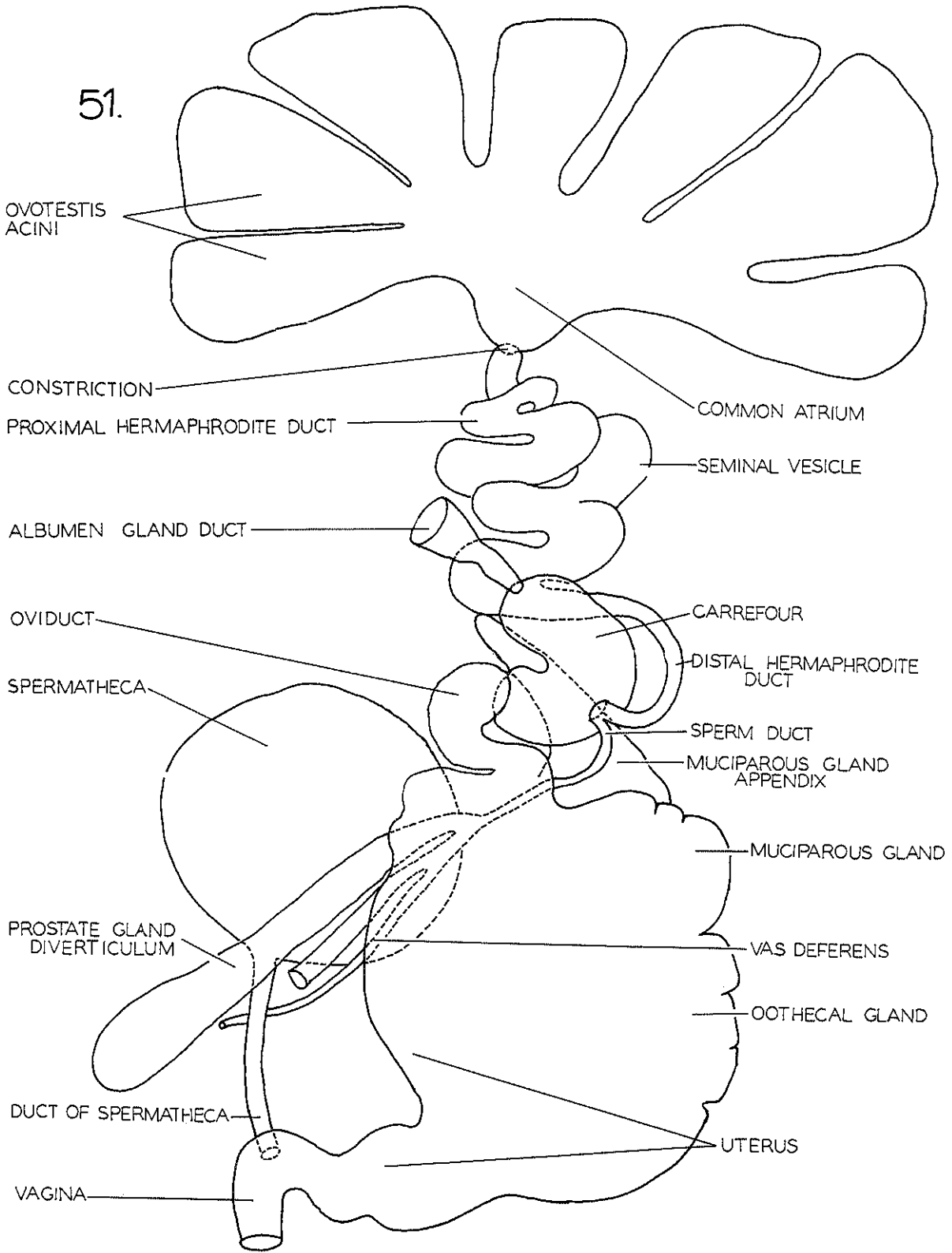


FIG. 51. DIAGRAM OF DORSAL VIEW OF GENITAL ORGANS IN SITU.
ALBUMEN GLAND AND PENIS COMPLEX OMITTED.

posteriorly placed, V-shaped aperture (fig. 47).

In 1893 André (quoted from Hoff, 1940) described a membrane in Ancylus lacustris and A. fluviatilis, subsequently called the membrane of André by Hoff (1940), which divides the body cavity into an antero-ventral cephalic cavity and a postero-dorsal visceral cavity. Although Basch (1959) found remnants of it in L. fuscus and Boer and Lever (1959) reports its occurrence behind the slime gland in F. shimekii, Hubendick (1960) denies its presence in the Ancyliidae investigated by him. My own sections, unfortunately, do not permit of an investigation as to its presence or otherwise in B. mooiensis.

3.10 MORPHOLOGY AND HISTOLOGY OF THE REPRODUCTIVE SYSTEM

The general topography and mutual relations of the different organs composing the genital system is depicted in figs. 11, 50 & 51.

The bulk of the genitalia are concentrated in the posterior half of the animal, while the penis complex and preputium lies in the left anterior half.

OVOTESTIS

The ovotestis, situated in the right posterior quadrant of the body, is completely covered dorsally by liver tissue and the stomach and the intestine covers part of it on the extreme right dorsal side. It is a roughly spherical gland composed of up to 28, elongated follicles or acini, more or less distinctly

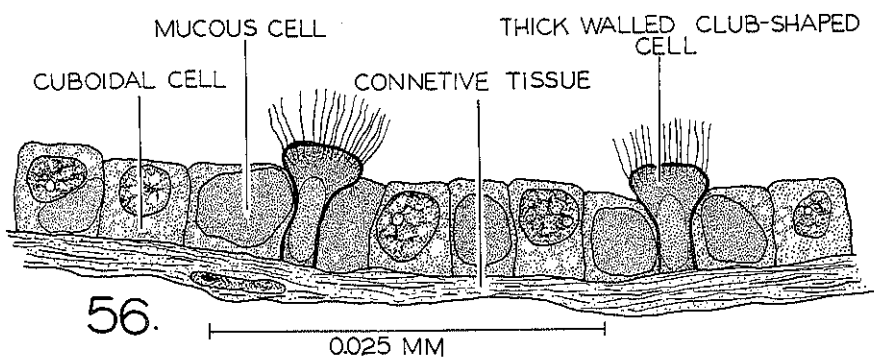
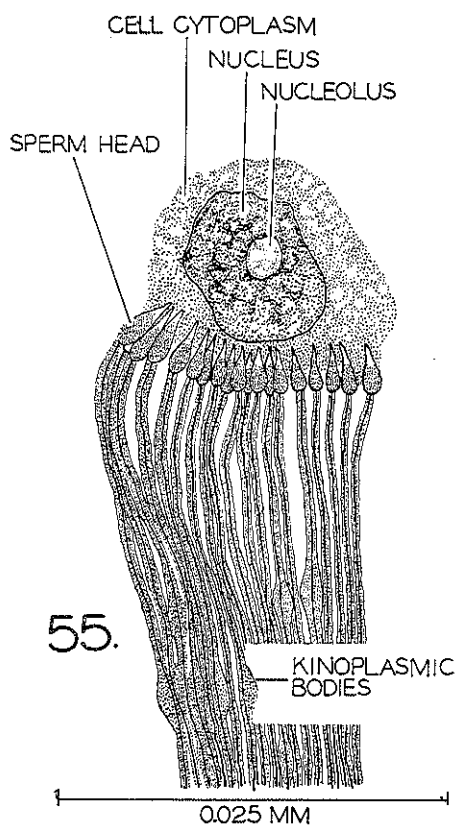
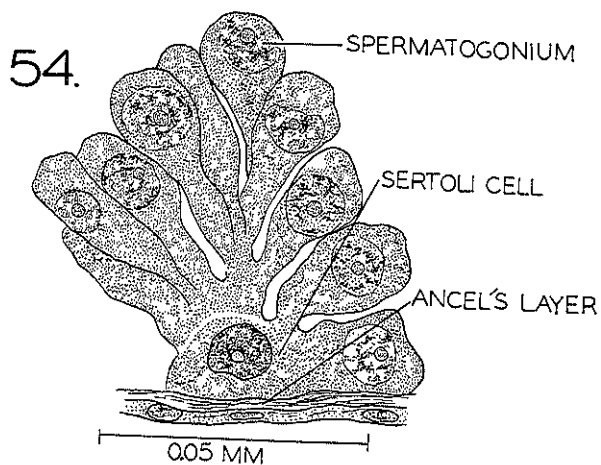
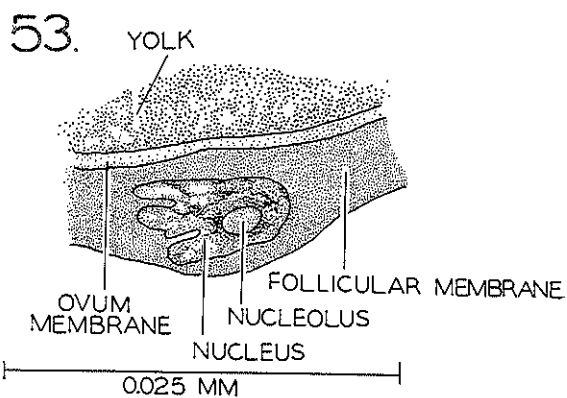
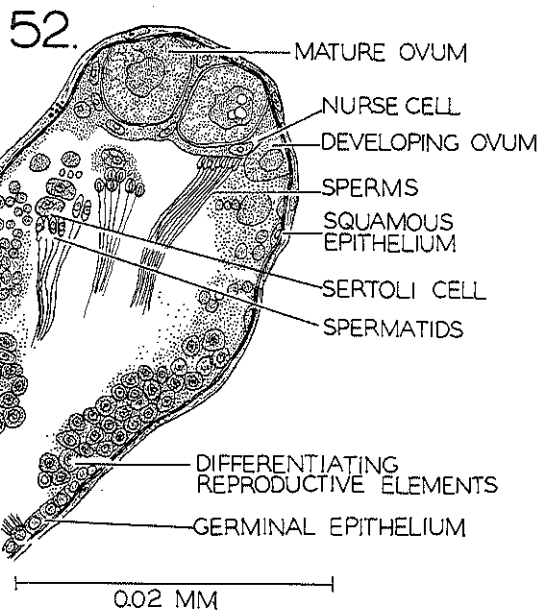


FIG.52. LONGITUDINAL SECTION THROUGH ACINUS FROM OVOTESTIS.

FIG.53. NURSE CELL.

FIG.54. SERTOLI CELL WITH ATTACHED SPERMATOGONIA.

FIG.55. SERTOLI CELL WITH ATTACHED SPERMATIDS.

FIG.56. EPITHELIUM LINING VENTRAL WALL OF COMMON ATRIUM OF OVOTESTIS.

separated from each other at their apices. These acini are also found behind the posterior shell muscle. As in other Planorbidae all the acini open into a common atrium which is marked off from the hermaphrodite duct by a poorly defined constriction (fig. 51).

The only constant feature of the wall of an acinus is the presence of a thin network of fibres (Ancel's layer figs. 54, 57, 58 & 60) reminding of a basement membrane covered externally by a slightly pigmented, connective tissue layer and lined internally by a variety of cell types. At the base of each acinus the lining consists of a single layer of cuboidal cells with oval to rounded nuclei. This constitutes the germinal epithelium which some authors claim to be a syncytium (Schneider, 1908, Simroth, 1928, Boettger, 1944, Van Aardt (unpublished thesis)), but which in B. mooiensis exhibit distinct cell membranes as maintained for Helisoma trivolvis (Say) by Abdel-Malek (1954). Proceeding from the base of the acinus towards the apex the germinal epithelium shows various stages in the production of male and female elements, such as oogonia, nurse cells, sperm cells and Sertoli cells. These stages are reflected in figs. 52, 53, 54 & 55 by reference to which the following may be emphasized. There is no differentiation between male and female zones in the acinus and both kinds of sexual elements occur intermingled (fig. 52). During the early stages of sperm development the Sertoli cells, to which the developing sperms are attached remain pressed up against the wall of the acinus (fig. 54). During the final stages of this

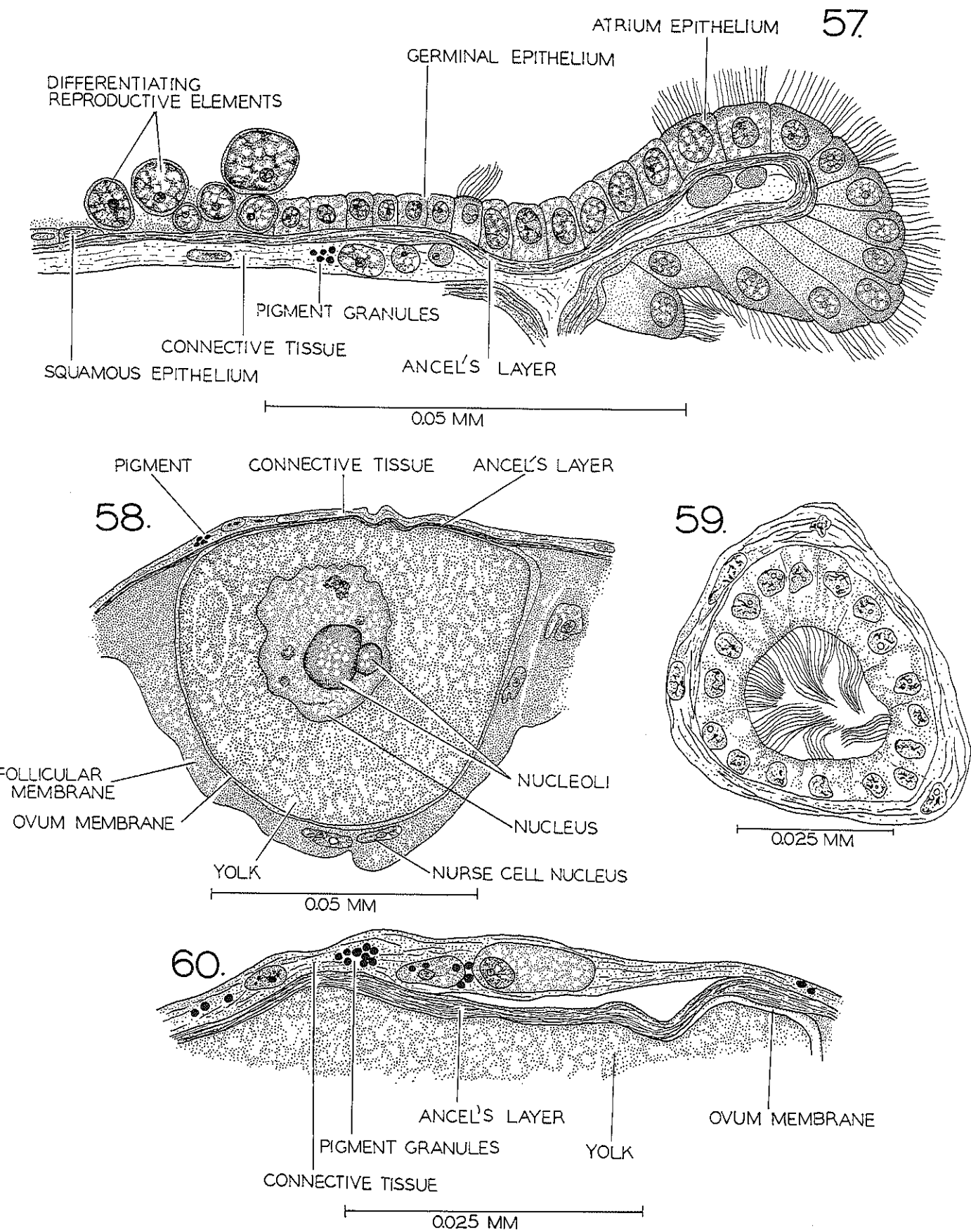


FIG.57. SECTION THROUGH BASAL PART OF OVOTESTIS ACINUS.

FIG.58. MATURE OVUM.

FIG.59. HERMAPHRODITE DUCT.CROSS SECTION THROUGH ITS DISTAL PART.

FIG.60. SECTION THROUGH WALL OF ACINUS FROM OVOTESTIS.

process, the Sertoli cells become freed from the wall of the acinus and float freely in the lumen (figs. 52 & 55) until they finally disintegrate thus liberating the mature sperms. This would therefore be in agreement with the findings of Simroth (1928) and Abdel-Malek (1954a).

The kinoplasmic bodies (fig. 55) on the axis of the spermatids, observed in Planorbis planorbis (Merton, 1930, quoted from Boettger, 1944), Lymnaea natalensis natalensis (Krs.) (Pretorius, unpublished thesis) and Bulinus (Physopsis) africanus (Krs.) (Van Aardt, unpublished thesis) could also be recognised in B. mooiensis. As in the case of the two last mentioned species, more than one kinoplasmic body of varying sizes can be seen on the same spermatid.

The ova also originate from the germinal epithelium at the base of the acinus which, in the course of their differentiation, migrate towards the apex of the latter so that mature ova are found only in this position (fig. 52). The nurse cells likewise originate from germinal epithelial cells which come to cut off the oogonium from the lumen of the acinus, thus constituting the follicular membrane. In the course of their differentiation they lose their membranes, as happens in H. trivolvis (Abdel-Malek, 1954a), so that, in the case of the mature ovum, the follicular membrane simulates a syncytium (fig. 58). The nucleus of a nurse cell is polymorphic and bears a distinct nucleolus (fig. 53).

In a mature ovum the nucleus may contain either

two distinct nucleoli or one double nucleolus. In the case of the immature ova one portion of the nucleolus usually takes up the orange stain whereas the other stains light to dark blue. No follicular cavity could be detected. Instead, clear patches of cytoplasm, creating the impression of vacuoles, are scattered throughout the cytoplasm of the ovum. This very much reminds of the condition obtaining in L. stagnalis (Archie, 1942, quoted from Abdel-Malek, 1954a). An ovum membrane immediately surrounds the cytoplasm of the ovum although it is less clear where the latter abuts on Ancel's layer (figs. 58 & 60).

Squamous epithelium which, according to Abdel-Malek (1954a), forms part of Ancel's layer, could be detected approximately at the equator of the acinus (fig. 57) where, moreover, the cells are extremely low and very poorly defined.

The common atrium is characteristically lined by ciliated cuboidal epithelium interspersed with ciliated columnar cells. These gradually merge into the germinal epithelium lining the basal regions of the acini, losing their cilia as they do so. On the floor of the common atrium (fig. 56) thick-walled, deeply staining club-shaped ciliated cells and mucous cells occur interspersed between the cuboidal cells which, in this patch, is devoid of cilia. Similar club-shaped cells, distributed differently, are described for B.(P). africanus (Van Aardt, op. cit.).

HERMAPHRODITE DUCT

The hermaphrodite duct can be divided into three

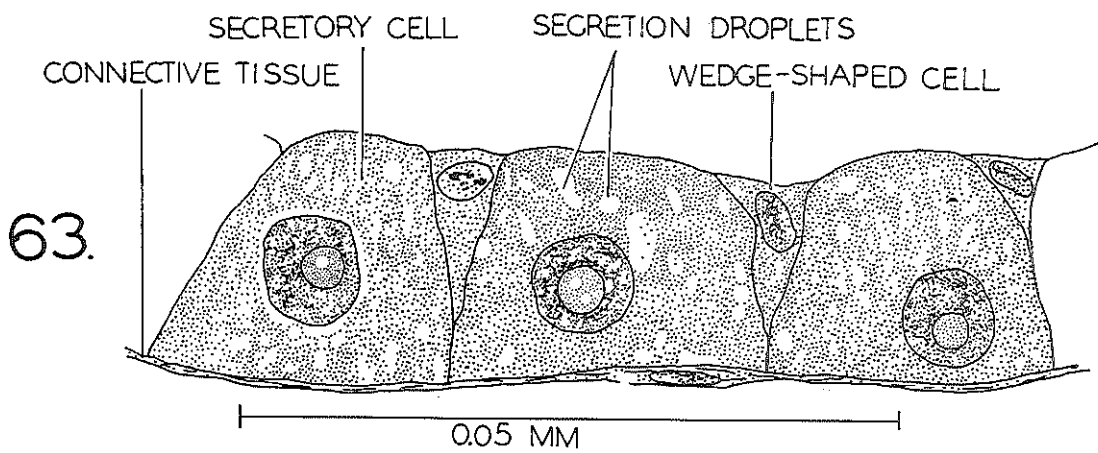
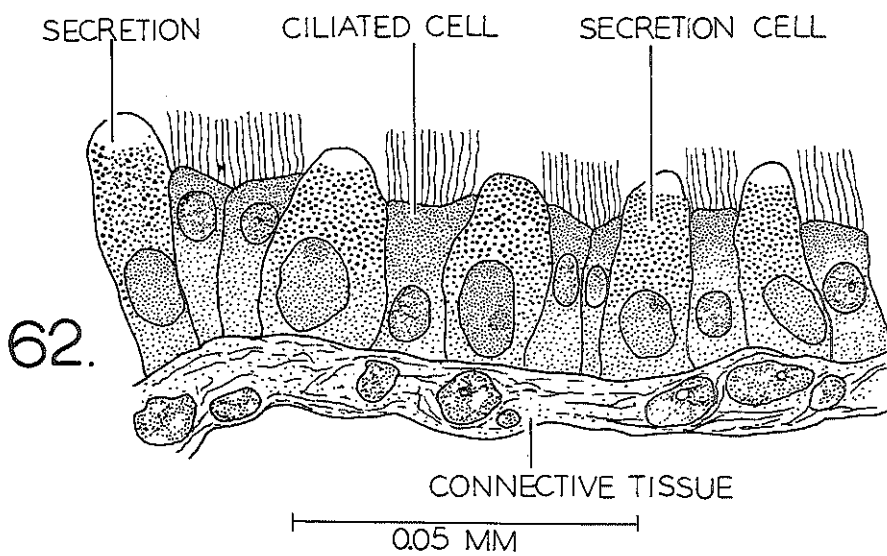
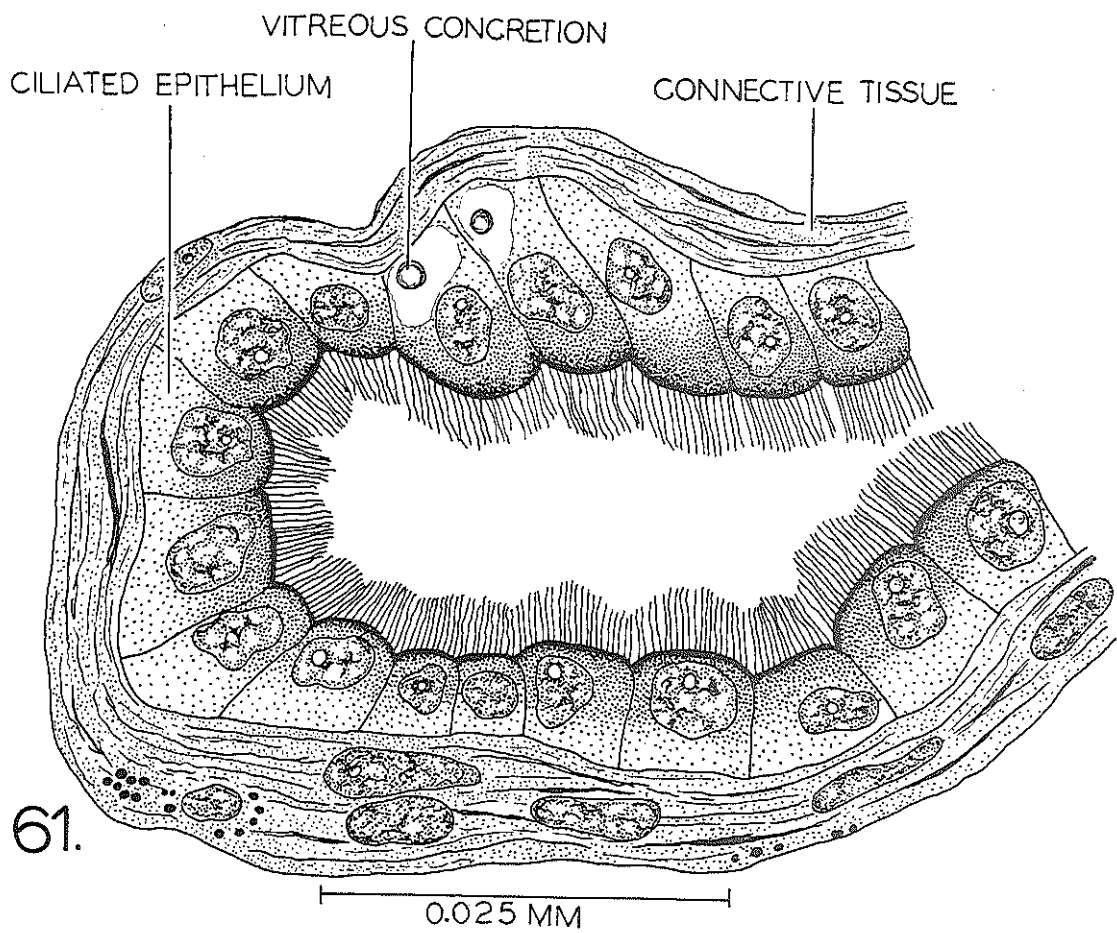


FIG. 61. HERMAPHRODITE DUCT. CROSS SECTION THROUGH ITS PROXIMAL PART.
 FIG. 62. EPITHELIAL LINING OF ALBUMEN GLAND DUCT.
 FIG. 63. ALBUMEN GLAND CELLS.

portions, viz. a narrow proximal portion leading from the common atrium, a dilated portion constituting the seminal vesicle which, in turn, narrows down to the distal portion opening into the carrefour. The relative lengths of these portions vary with different snails. In sexually mature animals all three regions are filled with masses of sperms, the seminal vesicle being considerably distended.

The proximal portion of the hermaphrodite duct is lined by heavily ciliated cuboidal epithelium (fig. 61). The apices of the cells are dome-shaped and stain much darker than the bases. Vacuoles which seem to contain a homogenous substance staining light blue are frequently found in the bases of these cells. These vacuoles sometimes also contain small rounded objects with a vitreous appearance. The epithelium is underlain by a rather thick connective tissue layer interspersed with numerous muscle fibres.

Histologically the seminal vesicle is exactly similar to the proximal part of the hermaphrodite duct of which it is a mere dilation.

The cells lining the distal portion of the hermaphrodite duct are slightly taller (fig. 59) and the nuclei are basally placed while the cell membranes are not easily distinguishable. Where its distal part opens into the carrefour, it narrows down to about three quarters of the diameter of the proximal part.

ALBUMEN GLAND

The albumen gland is composed of a large number of irregularly oval-shaped follicles concentrated in the left dorsal side of the animal next to the digestive gland. It partly embraces the left side of the stomach and enters the carrefour antero-ventrally via a short wide duct. The follicles of the albumen gland are lined with large secretory cuboidal cells interspersed with wedge-shaped cells (fig. 63). The nuclei of the former are large and possess distinct nucleoli, while secretion droplets can be seen within the cell. The wedge-shaped cells are not secretory.

The lumina of all the follicles of the albumen gland are continuous with each other, thus forming an irregular lumen from which the albumen gland duct leads to the carrefour. Where the albumen gland duct leaves the gland, the large follicle cells gradually merge into those lining the duct. In this duct two cell types can be distinguished viz, ciliated cells and large cells with a granular cytoplasm and large basally placed nuclei without nucleoli (fig. 62). The latter cells seem to have a secretory function, and their fluid filled apical portions project beyond the general surface of the ciliated epithelium. To my knowledge, cells of this nature have not yet been described in the albumen gland duct of any other freshwater mollusc. This epithelial lining is bounded externally by a connective tissue layer of varying thicknesses.

CARREFOUR

In gross dissection the carrefour of B. mooiensis appears bean-shaped (fig. 64) and therefore closely resembles this structure in the other basommatophoran species. It is extremely delicate and transparent and can only be seen when great care is exercised while removing the organs covering it dorsally.

By reference to its histology the carrefour complex can be divided into three parts (figs. 65 & 66). The stippled area in the diagrammatic sketch represents that part of the carrefour which is lined by cells similar to those which line the albumen gland duct. This is referred to as the proximal part of the carrefour. The part filled in with circles is lined by ciliated cuboidal to columnar cells, also similar to those lining the albumen gland duct, but lacking the secretion cells. The area shaded by the oblique lines is lined by tall columnar cells which are neutral to the stains employed. The nuclei of these cells are more or less basally placed. A rather thin connective tissue layer underlines the epithelial lining of the entire carrefour complex.

It is difficult, if not impossible, in the present state of our knowledge, to define the limits of the carrefour in B. mooiensis, because what morphologically seems to be a single structure, is histologically, composed of two distinct parts. The carrefour of this species may be regarded either as being represented by what is being referred to as its proximal part only, or it may be regarded as being of dual origin,

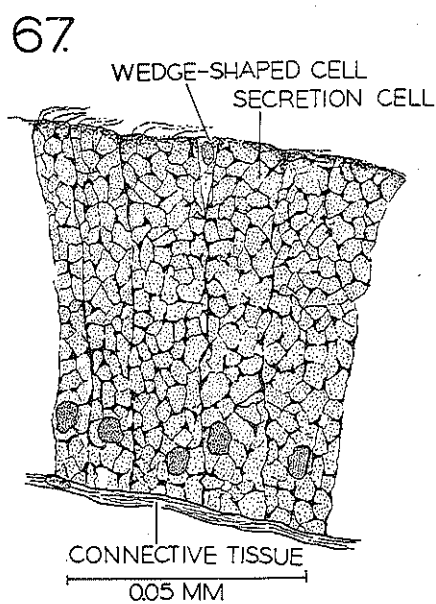
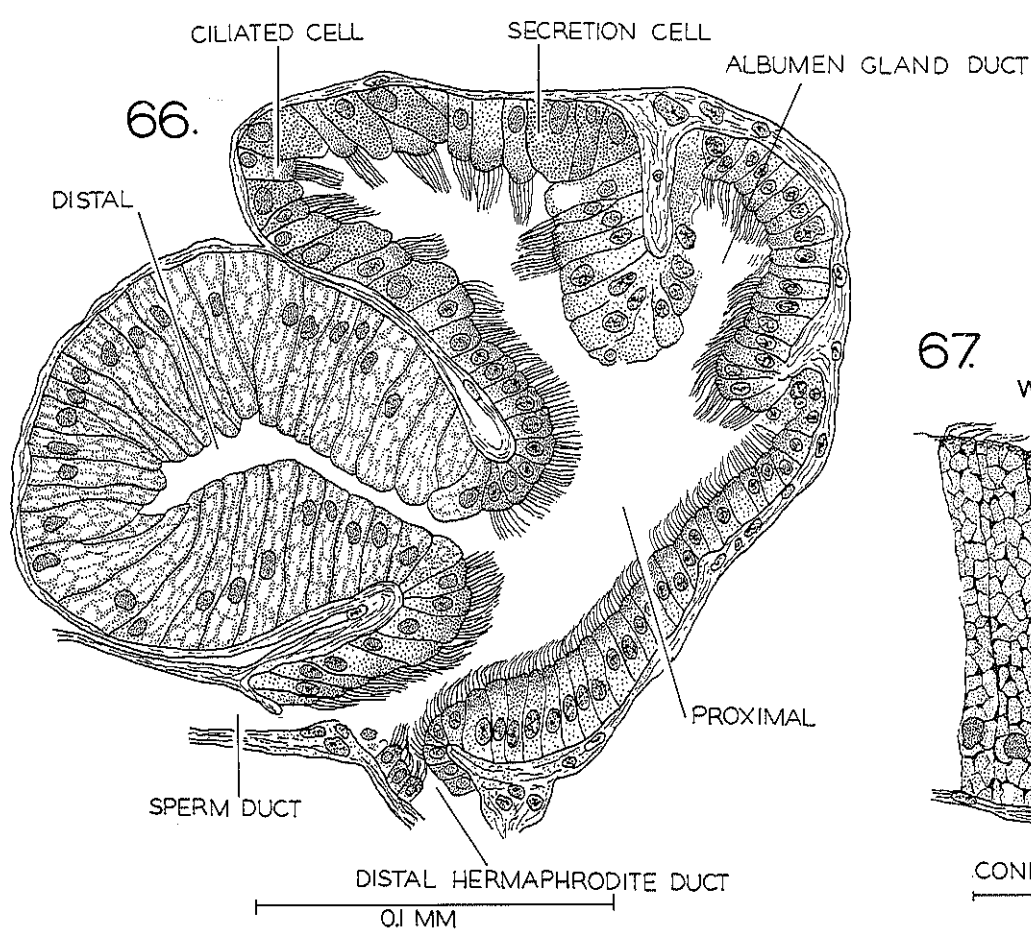
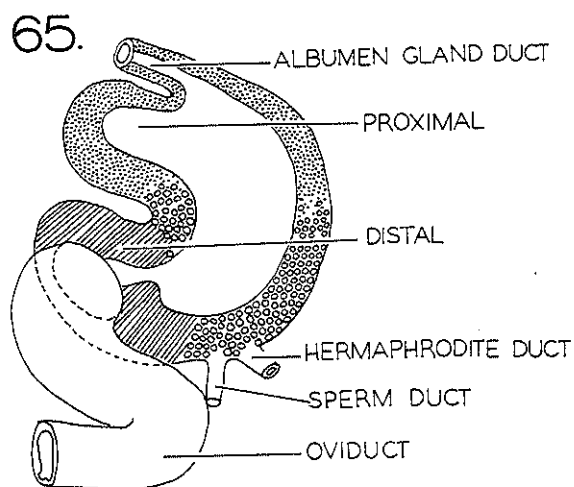
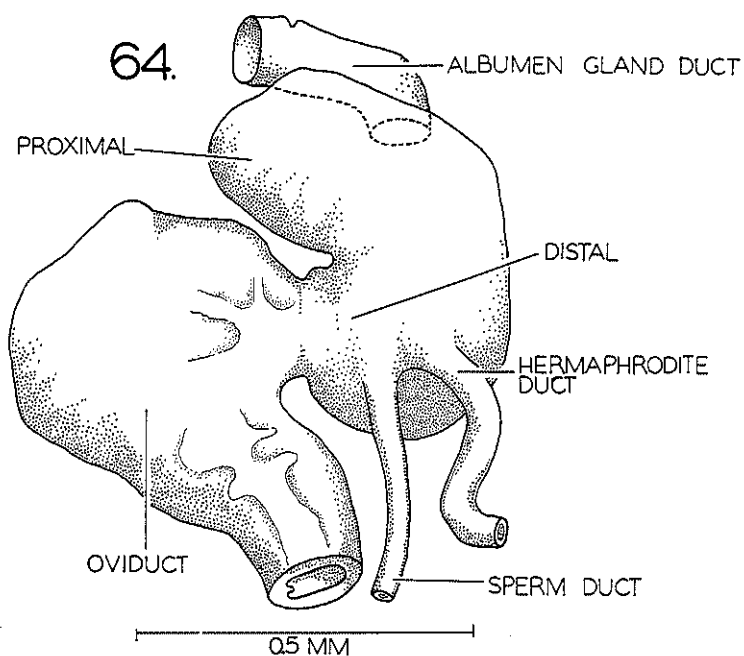


FIG. 64. CARREFOUR COMPLEX, VENTRAL VIEW.

FIG. 65. CARREFOUR COMPLEX. DIAGRAMMATIC SKETCH SHOWING DIFFERENT AREAS IN WHICH DIFFERENT CELLS ARE ENCOUNTERED.

FIG. 66. HORIZONTAL SECTION THROUGH CARREFOUR COMPLEX.

FIG. 67. MUCIPAROUS GLAND CELLS.

the formation of which both the albumen gland duct and the oviduct contribute. Superficially the situation in B. mooiensis is paralleled by the conditions obtaining in B. (P). africanus (Van Aardt, op cit.)

OVIDUCT

The oviduct leaves the carrefour at its posterior or distal dorsal side. Its topographical relations to the muciparous gland and uterus are illustrated in figs. 68 and 70. As already stated, a poorly defined constriction seems to mark the transition between the carrefour and the oviduct. In the region of this constriction the columnar cells of the distal part of the carrefour are replaced by cuboidal cells which are also neutral to the stain employed. Passing into the oviduct these cells become columnar and ciliated and their apical halves stain dark blue in contrast to their basal halves which either stain lilac or not at all (fig. 72). The nuclei are centrally placed. Interspersed between these, are cells of similar structure which, however, do not stain at all, except for their nuclei. These latter cells are probably identical to the former and may only reflect a different phase of activity. Along its right ventral aspect the ciliated columnar cells of the oviduct are replaced by a tract of ciliated cuboidal epithelium, more or less 10 cells wide, thus forming a groove or gutter (fig. 72) which extends from the proximal to the distal part of the oviduct where it opens into the ventral part of the lumen of the muciparous gland.

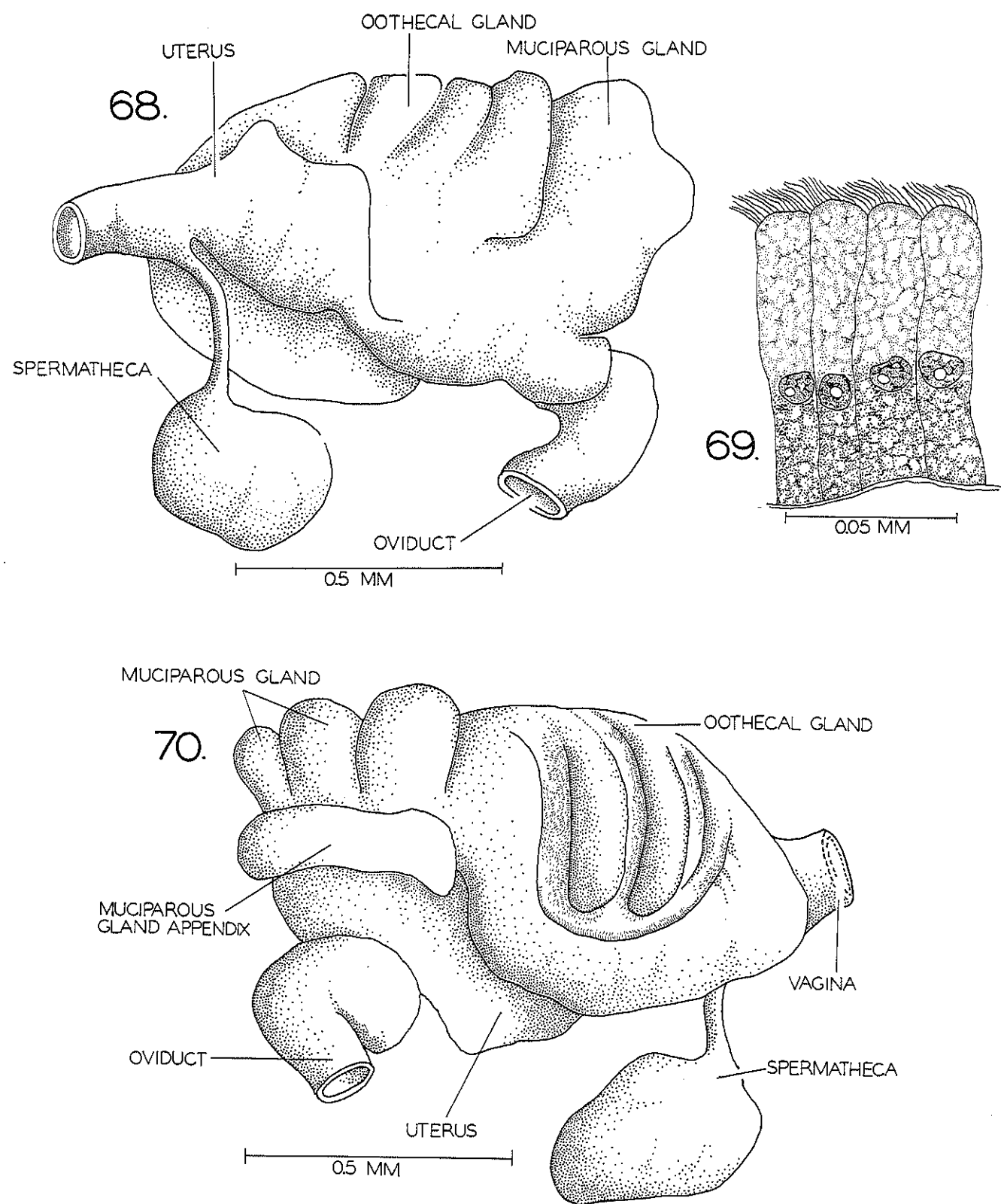


FIG. 68. OVIDUCAL COMPLEX, POSTERO-LATERAL VIEW.

FIG. 69. DETAIL OF CELLS LINING EXTREME DISTAL PART OF OOTHECAL GLAND.

FIG. 70. OVIDUCAL COMPLEX, ANTERO-LATERAL VIEW.

MUCIPAROUS GLAND

The anatomical relations of the large white muciparous gland to the oothecal gland and the uterus is depicted in figs. 68, 70, 71 & 78. It is characterized by its folded wall (fig. 70) which form simple acini (fig. 71). The transition from oviduct epithelium into muciparous gland epithelium is gradual and the lumina of the acini are almost obliterated by the extensive development of the tall, scantily ciliated glandular columnar cells. the membranes of these cells are delicate and the nuclei, which are only faintly outlined, stain bright orange. The fine threads and droplets of prosecretion within the cell do not seem to take up the stain used (fig. 67). Interspersed between the tall columnar cells, small wedge-shaped cells are found. The gland has no duct of its own and its secretion is poured directly into the main female duct system.

MUCIPAROUS GLAND APPENDIX

On its ventral side the muciparous gland gives off a finger-like appendix which projects slightly rostrad towards the right side of the animal (figs. 50 & 51). It passes underneath the carrefour-oviduct junction and comes to lie so close to the seminal vesicle, that, in gross dissection, the two structures cannot be distinguished from each other. Microscopical examination, however, reveals that only the connective tissue enveloping these structures are continuous. This appendix is completely filled with sperms which are orientated in such a way that their heads are embedded in the

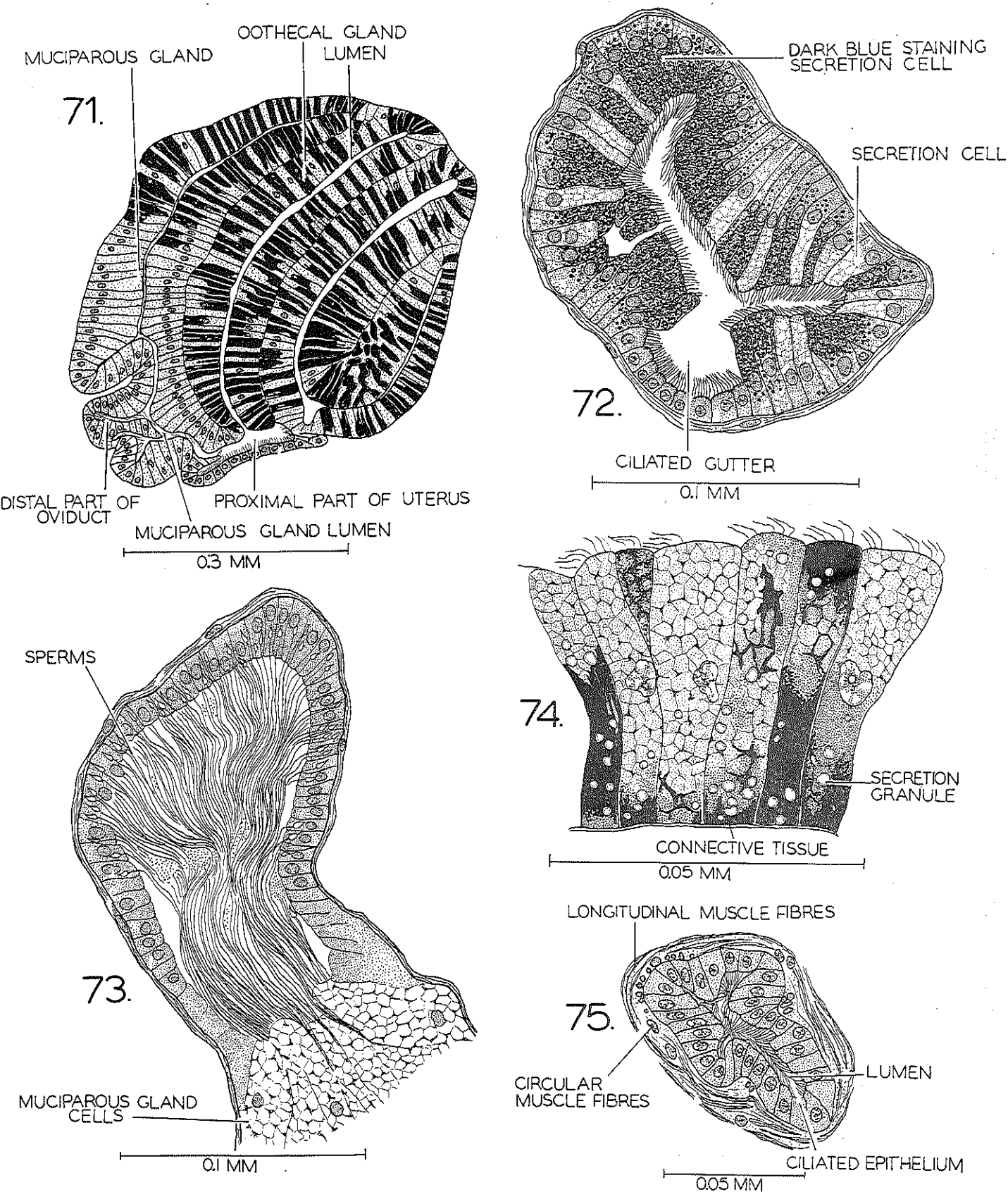


FIG. 71. CROSS SECTION THROUGH OVIDUCT, MUCIPAROUS GLAND, OOTHECAL GLAND, AND UTERUS, SHOWING FOLDS OF BOTH GLANDS AND THEIR OPENINGS INTO THE UTERUS.

FIG. 72. CROSS SECTION THROUGH OVIDUCT.

FIG. 73. HORIZONTAL SECTION THROUGH MUCIPAROUS GLAND APPENDIX, SHOWING SPERM HEADS EMBEDDED IN EPITHELIUM.

FIG. 74. CELLS FROM PROXIMAL REGION OF OOTHECAL GLAND

FIG. 75. VAGINA. CROSS SECTION THROUGH ITS TERMINAL REGION.

epithelial lining, whereas their tails, beautifully arranged one alongside the other, project towards the lumen of the muciparous gland (fig. 73).

The appendix is lined by cuboidal to columnar epithelium. Nuclei are easily detectable but the apical cell membranes are sometimes obscured due to the concentration of the sperm tails. The transition from the cells lining this structure to those lining the muciparous gland is abrupt.

To my knowledge no organ of similar structure and topographical relations has thusfar been described for any basommatophoran snail. Stiglingh et al. (1962) refers to an irregular sac extending from the left posterior margin of the uterus in Bulinus tropicus (Krauss) which serves the function of receiving the penis of a partner during copulation and into which sperms are liberated. Apart from the presence of sperms in both, these two sacs or diverticula of B. mooiensis and B. tropicus have nothing in common and this structure of the former cannot be accounted for by reference to that of the latter. Neither F. tarda (Hoff, 1940) nor L. fuscus (Basch, 1959) possess a muciparous gland and reference is made only to a nidamental gland (oothecal gland of authors, Abdel-Malek, 1952 and Wright, 1957) for both these species. Although the nidamental gland of F. tarda (Hoff, 1940) seems to be an entirely different structure, the nidamental gland of L. fuscus (Basch, 1959) seems to be quite comparable to the muciparous gland appendix of B. mooiensis as far as its shape and topographical relations are

concerned. Unfortunately, however, the histology of this structure is not described by Basch (1959), and obviously it does not agree with the nidamental gland of L. fuscus either.

The reason for the presence of sperms in this appendix as well as their origin cannot be accounted for. The circumstance that, quite often, sperms with their heads directed away from the external female genital opening were found in the uterus, might suggest that these had been received from another snail and were moving towards this appendix. This is supported by the observation that sperms were very seldomly found in the spermatheca.

OOTHECAL GLAND

The oothecal gland can be macroscopically distinguished from the muciparous gland, only by virtue of its pale yellow colour (in freshly dissected specimens only) and its characteristic folds (figs. 50, 68, 70 & 71). The lumen of the gland, which stands in open communication with that of the uterus, is crowded out by the enormous development of the columnar cells lining it and the plications of its wall. The transition from muciparous gland epithelium into that of the oothecal gland is gradual (fig. 71), both being scantily ciliated. In its proximal and dorsal part i.e. where it merges into the muciparous gland, the columnar cells of the oothecal gland stain dark red to orange or blue (fig. 74) from their basal up to either their middle or apical portions. In their basal

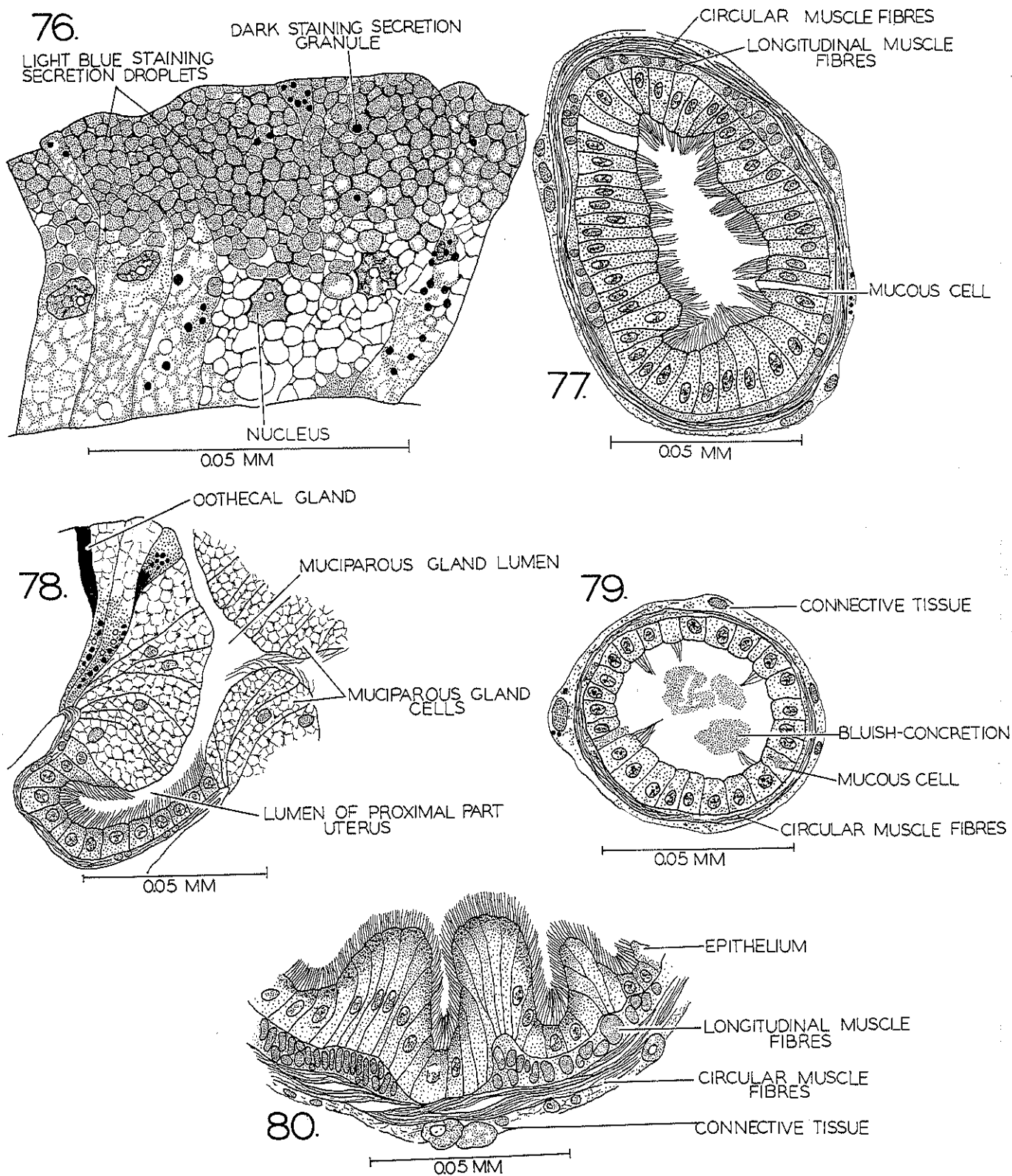


FIG. 76. CELLS LINING VENTRAL DISTAL PART OF OOTHECAL GLAND.
 FIG. 77. SPERMATHECA DUCT. CROSS SECTION THROUGH DISTAL REGION.
 FIG. 78. UTERUS, CROSS SECTION THROUGH PROXIMAL PART.
 FIG. 79. SPERMATHECA DUCT. CROSS SECTION THROUGH PROXIMAL REGION.
 FIG. 80. UTERUS. CROSS SECTION THROUGH MIDDLE PART.

regions, or dispersed in a lesser degree over the whole cell, acidophilic and basophilic granules are present. Some of these cells do not take up the stain so readily and appear to be in a different phase of its secretory activity. These cells strongly remind of the muciparous gland cells but are smaller. The rounded or irregularly shaped nuclei of the dark red staining cells are difficult to distinguish, but appear to be placed centrally or slightly towards the base.

Proceeding in the direction of the female genital opening, the cells (fig. 76) seem to become more active than those just described as composing the proximal part. In this region the secretion droplets stain light blue and become more pronounced throughout the cells. The basophilic and acidophilic secretion granules are less numerous than in the cells of the proximal region of the gland. The nuclei appear to be deformed by the pressure from the secretion droplets and contain pronounced nucleoli. The cell membranes are extremely delicate.

Proceeding still further in the direction of the female genital opening, a third variation of oothecal gland cell can be distinguished both by reference to their general appearance and staining affinities (fig. 69). The cells in this region are also tall and columnar, but gradually become smaller than those of the middle region of the gland. They are well ciliated and their nuclei are oval to rounded with pronounced nucleoli. In the basal halves the cytoplasm stains deeper than the rest of the cell and secretion droplets are sometimes found here.

UTERUS

The oviduct joins the uterus in such a way that its ciliated gutter cells (fig. 72) become continuous with a broad tract of ciliated columnar cells which constitute the floor of the uterus in this region where the roof of the latter is formed by the muciparous gland cells (fig. 78). The lumen of this part of the uterus is small but steadily increases in diameter. Simultaneously with this increase in diameter the ciliated floor of the uterus becomes thrown into folds (fig. 80) whereas the muciparous gland cells which constitute the first part of its roof gradually becomes replaced by oothecal gland cells in the sequence described for that structure. Where it emerges from underneath the oothecal gland, the uterus becomes a tube, more or less flattened dorso-ventrally and follows the course indicated in figs. 51 & 68. It is here lined throughout by ciliated columnar epithelium, thrown into folds (fig. 98) similar to but less marked than those described for its floor earlier on. In between the ciliated cells, mucous cells are frequently encountered. The epithelium of the uterus is underlain firstly by a layer each of longitudinal muscles, circular muscles and connective tissue elements in the sequence mentioned.

VAGINA

The vagina is lined by epithelium similar to that of the uterus (fig. 75).

SPERMATHECA

The spermatheca is situated immediately below the left side of the crop and the right side of the prostate gland. It is separated from the foot by liver lobules. Its general shape varies considerably, from club-shaped to oval to perfectly rounded. The spermatheca is lined by cuboidal to columnar epithelium with centrally placed nuclei bearing distinct nucleoli. In between these cells glandular cells occur, the secretion of which can be seen protruding as large rounded droplets above the general surface of the lining epithelium (fig. 95). The latter is bounded externally by a thin layer of muscle fibres followed by a thinner layer of connective tissue.

The duct of the spermatheca is lined by ciliated epithelium which, proceeding from the spermatheca to the vagina, changes from cuboidal (fig. 79) to columnar cells (fig. 77) and becomes progressively more ciliated. Their nuclei are basally placed and the cilia are deflected towards the spermatheca. Cells reminding of mucous cells are occasionally found in between the ciliated cells. The epithelial lining is bounded externally by a layer of longitudinal muscles, a layer of circular muscles and a layer of connective tissue in this order. Nearing the spermatheca, the longitudinal muscle layer disappears.

SPERM DUCT

From its origin at the bifurcation of the hermaprodite duct, the sperm duct continues in a latero-rostrad direction towards the prostate gland. Directly below the distal portion of the oviduct it receives the secretions from the diverticula of the prostate gland (fig. 50 & 51). Where it passes underneath the carrefour-muciparous-oothecal gland complex, it becomes a dorso-ventrally flattened tube. It is lined by low columnar epithelium (fig. 82), with oval to rounded moderately pronounced, more or less centrally or apically placed nuclei. The cytoplasm stains lightly and has a slight granular appearance. Occasionally a cell that reminds of a mucous cell is present. Two types of secretion cells can be distinguished. The first type is characterised by dark staining secretion granules crowded underneath the apical membrane of the cell which protrudes slightly above the general surface of the surrounding epithelium. The second type also protrudes above the surrounding cells, but its apical region is filled with a rounded, vitreous, blue staining body which might be identical to the bodies which van Aardt (op. cit.), in his study on B. (P) africanus, referred to as eosinophyl granules.

PROSTATE GLAND

Mandahl-Barth (1954) gives a general description of the prostate gland for the genus Burnupia, according to which it consists of three sets of single or bifurcate glandular tubes that are arranged fan-wise. In

81.

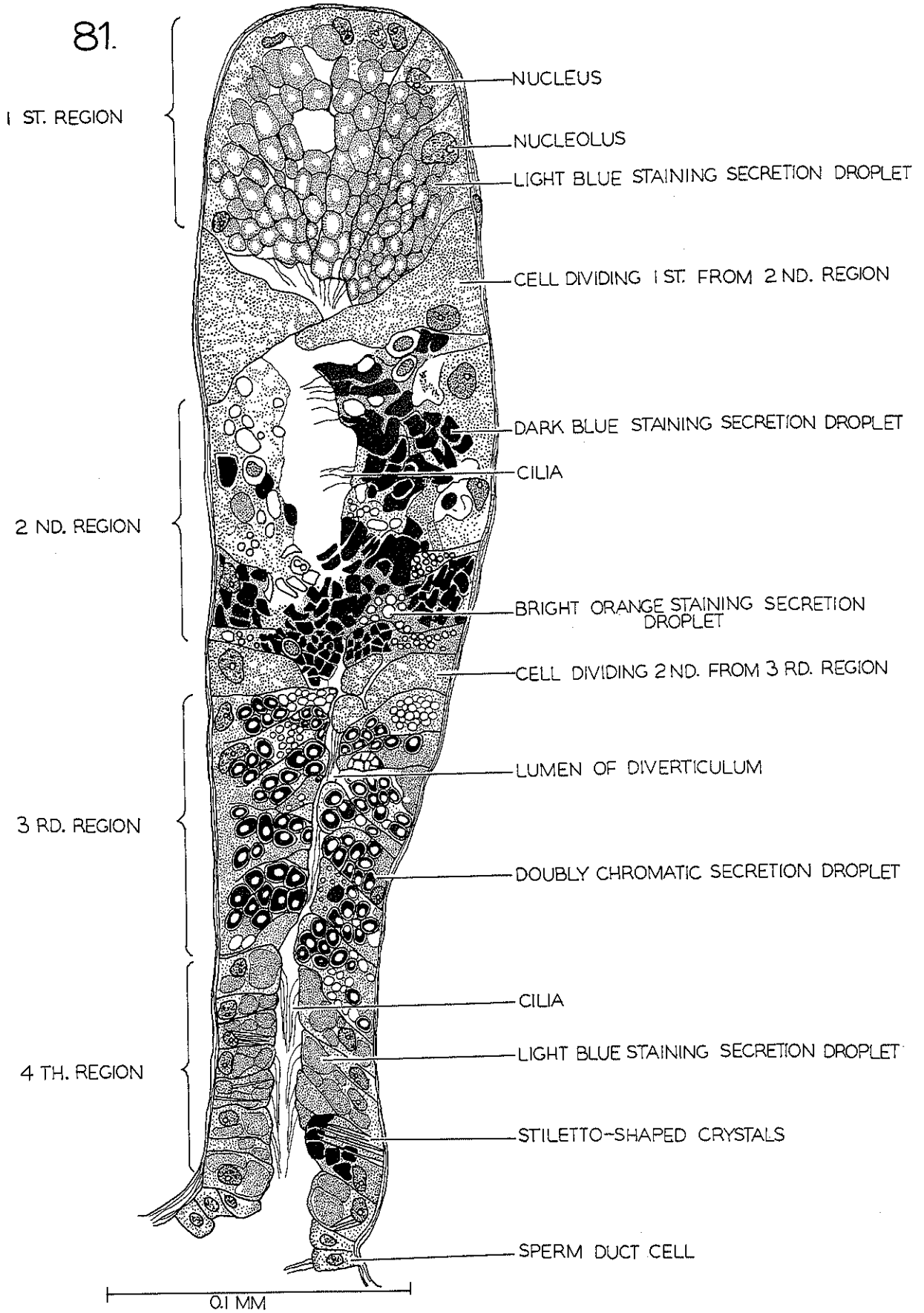


FIG. 81. LONGITUDINAL SECTION THROUGH DIVERTICULUM OF THE PROSTATE GLAND.

B. mooiensis approximately 8 finger-like diverticula (fig. 50) can be distinguished. These may be either separate or bifurcate. Basch (1959) records 7 to 9 of these diverticula in L. fuscus.

Histologically each diverticulum seems to be demarcated into four regions (fig. 81) which may be functionally different from each other. This reminds of the condition obtaining in L. stagnalis apressa where Holm (1946) claims to be able to recognise three functionally different regions although this author could not find histological support for his view. In B. mooiensis the apical region of each diverticulum is lined by large scantily ciliated columnar cells which taper towards the lumen. The nuclei of these cells are basally placed and are oval, rounded or slightly irregularly shaped, with one, two, or even three distinct nucleoli. The irregular shape of the nuclei is probably due to the pressure exerted upon them by the large amount of secretory material in the form of droplets which stain light blue and fills the greater part of the cell.

This first region is separated from the second by one or two rows of large columnar cells which also taper towards the lumen of the diverticulum. The nuclei of these cells are basally placed and the cytoplasm stains fairly deeply.

The second region is composed of scantily ciliated columnar cells slightly smaller than those found in the apical region. Their nuclei are basally placed with distinct nucleoli and the cells are filled with irregularly shaped secretion droplets which stain dark blue.

In the apical regions of the cells, perfectly round secretion droplets which stain bright orange are found interspersed between these secretion droplets.

Cells similar to those described as separating the first two regions of the diverticulum also separate the second from the third.

The third region is composed of columnar cells, slightly lower than those of the second region. The shape of the nuclei vary according to the pressure exerted upon them by the secretory droplets with which the cell is crowded. These droplets are doubly chromatic, staining blue with a red centre. In this region the lumen of the diverticulum is almost obliterated by the lining cells.

The third region gradually merges into the fourth, where the cells are of the low columnar type and are well ciliated. The nuclei are more or less rounded and basally placed. The secretory droplets are not so well defined as in the third region and stain light blue. In some of these cells, especially in the extreme basal part of the diverticulum, stiletto-shaped crystals can be seen reaching almost from the base to the apex. Where the diverticulum debouches into the sperm duct, the transition into sperm duct cells is abrupt.

VAS DEFERENS

From this level onwards the duct is known as the vas deferens which proceeds forwards free from the body wall, pierces the left anterior shell muscle from left to right and joins the penis after describing an open

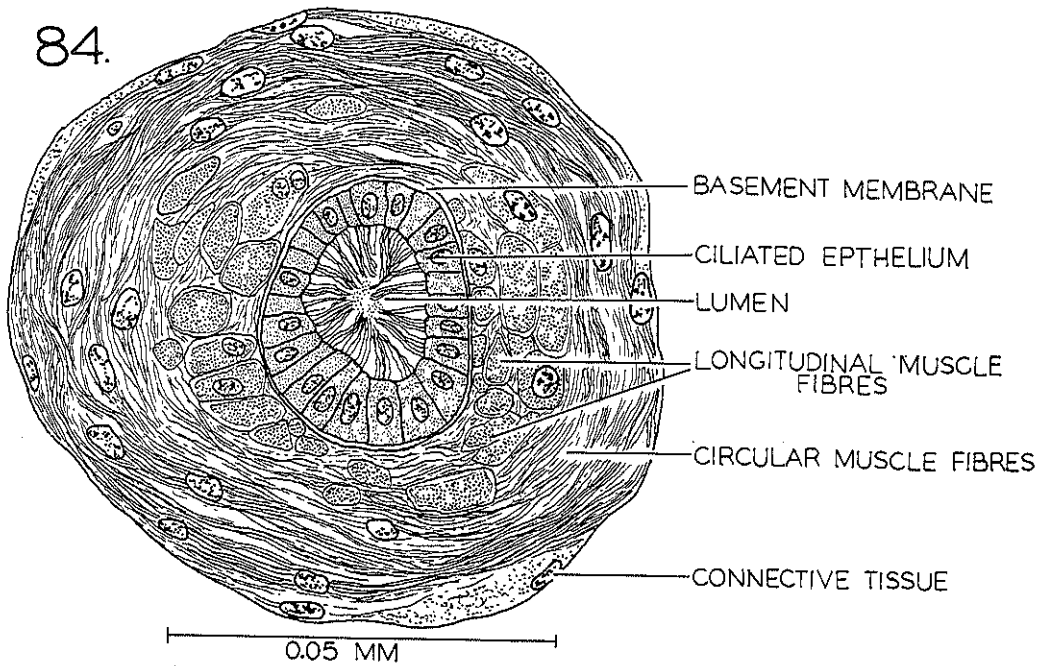
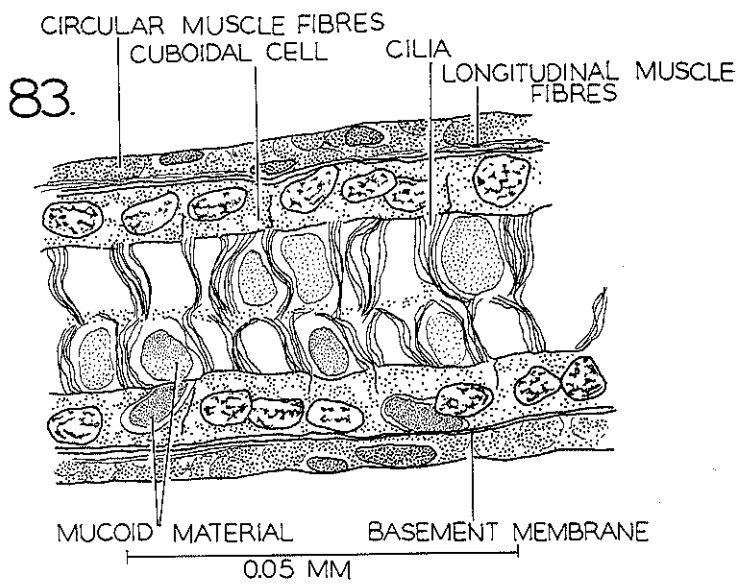
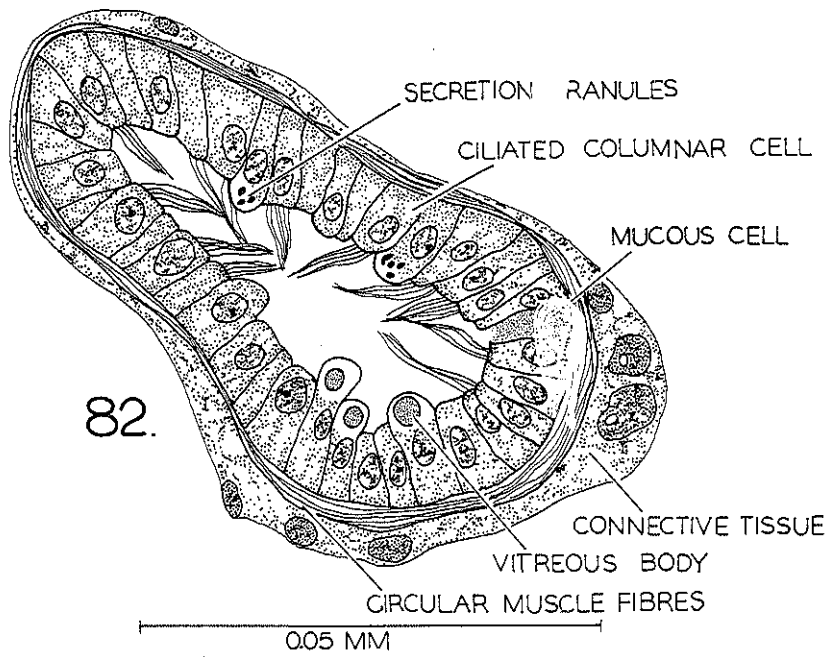


FIG. 82. SPERM DUCT. CROSS SECTION IMMEDIATELY BEFORE IT JOINS THE PROSTATE GLAND.
 FIG. 83. VAS DEFERENS. LONGITUDINAL SECTION IN REGION OF LEFT ANTERIOR SHELL MUSCLE.
 FIG. 84. VAS DEFERENS. CROSS SECTION THROUGH DISTAL PART.

loop. As far as present observations go there is no histological justification for distinguishing between sperm duct and vas deferens in B. mooiensis. The diameter of the vas deferens remains fairly constant, from the prostate gland up to a point just beyond the left anterior shell muscle, where it gradually decreases up to its junction with the penis complex.

The histology of the vas deferens very gradually changes as one proceeds from the prostate gland towards the penis complex. Near the prostate gland it is lined by ciliated cuboidal epithelium with indistinct cell membranes and extremely large oval to rounded nuclei in which the nucleoli are of infrequent occurrence. The cilia are about one and one half times as long as the cells are high and are clustered together in tufts (fig. 83) between which spaces are left which are occupied by masses of substance which stain light blue. This could be mucoid material and may originate from mucous cells which are interspersed between the ciliated cells. Towards the penis complex the epithelial lining of the vas deferens gradually changes from cuboidal to low columnar whose cilia are evenly distributed (fig. 84) and which contain distinct basally placed nuclei. The epithelial lining is underlain throughout by a distinct basement membrane. This is bounded externally by both circular and longitudinal muscle fibres which, in the region adjacent to the prostate gland, is not well developed and contain more circular than longitudinal fibres. Towards the penis complex the layer of muscle fibres becomes, by

comparison, extremely well developed and the two types of fibres tend to separate out into an inner layer of longitudinal and an outer layer of circular fibres.

PENIS COMPLEX

Although Mandahl-Barth (1954) characterises the penis of the genus Burnupia as being pear-shaped and as being retractile as in Bulinus, although it is much shorter, a comparison of my own findings on B. mooiensis (figs. 11, 50, 85, 86, 87 & 91) with those obtaining in the two bulinid species investigated in this Institute (B. tropicus, Stiglingh et al 1962, B.(P) africanus, Van Aardt, op. cit.) reveals that it is not easy to interpret the detailed structure of the penis complex in this species in terms of the structure of this complex in the Bulininae. The basic structure of the penis complex of B. mooiensis is best understood by referring to figures 85, 86, 87, 88, 89 & 90 which need very little supplementary description.

The copulatory organ is fairly large relative to the size of the body (more or less one fifth the length of the body) and almost invariably resembles that presented in fig. 86. The penis sheath is pear-shaped and is partly obscured by the large preputium which is always partly invaginated. The distal part of the preputium perforates the left anterior shell muscle on its way to the external male genital opening.

Numerous small muscles originating from the left body wall are inserted into the extreme distal tip of the preputium. Two sets of retractor muscle fibres

85.

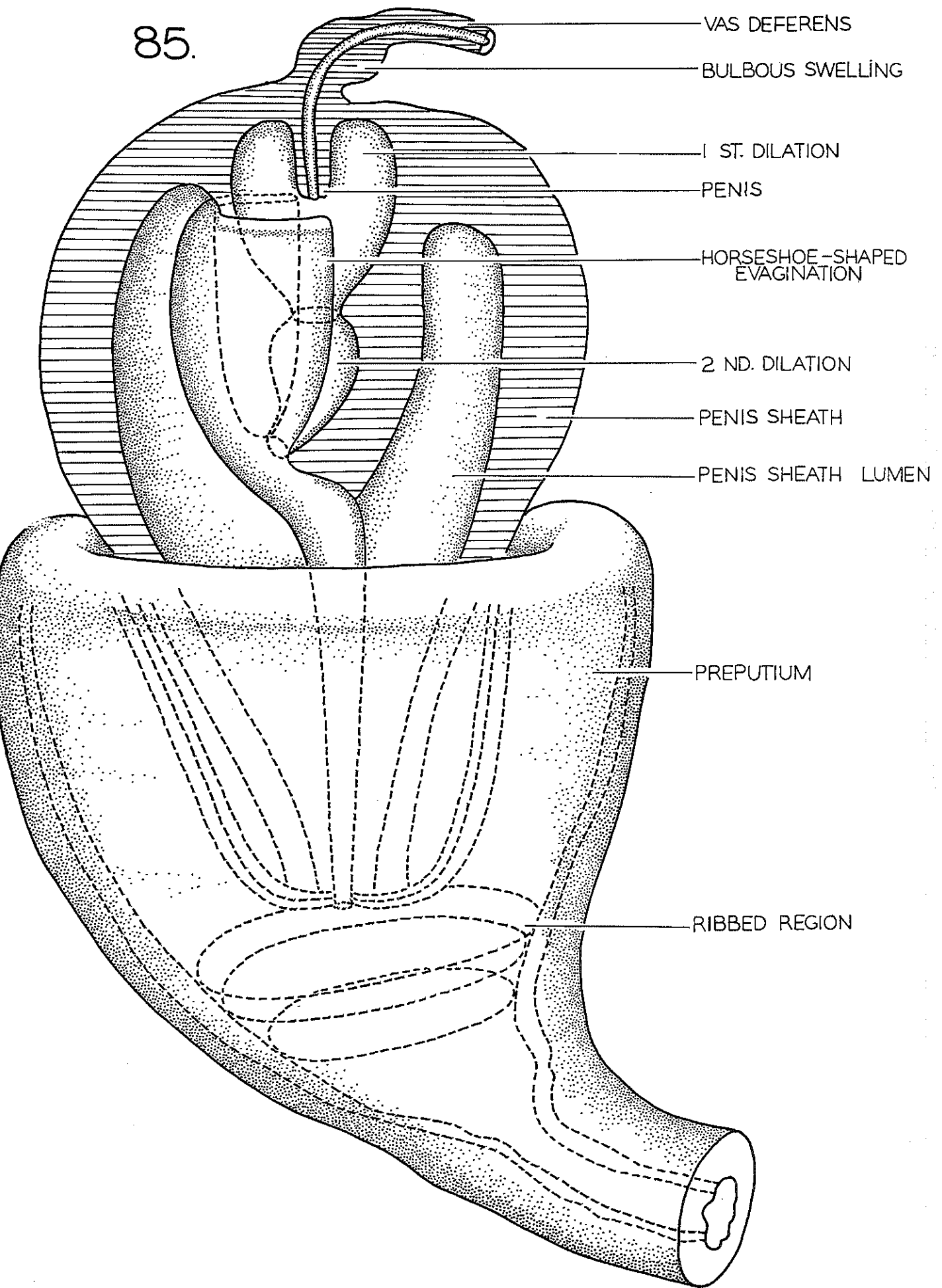


FIG.85.DIAGRAMMATIC PRESENTATION OF PENIS COMPLEX.

are inserted into the preputium as shown in fig. 86.

Those on the right side originate from the left anterior shell muscle where the latter inserts into the shell.

Those on the left side also originate from the left anterior shell muscle more or less on its right ventral side.

The vas deferens enters the penis sheath apically and slightly protrudes into the lumen of the latter. Purely morphologically, this protrusion seems to agree with the penis proper of B. pfeifferi (Schutte and Van Eeden, 1959b) and is considered to represent the penis which hardly seems capable of becoming everted. It is lined, to its tip, with ciliated cuboidal epithelium (fig. 93). The lumen of the penis sheath is tubular terminally and more complicated proximally where a backwardly directed, horseshoe-shaped evagination of its wall partly embraces one small and one larger laterally compressed dilation. The penis projects into the latter dilation which like the smaller one, is lined by lightly staining columnar epithelium with irregularly shaped, basally placed nuclei (fig. 93). The evagination is lined by ciliated cuboidal to low columnar epithelium which changes to distinctly ciliated columnar epithelium in that part of the tubular region adjacent to it (fig. 96). The terminal two thirds of the tubular portion of the lumen is lined by relatively large unciliated papillae depicted in figs. 92 and 94. In this region the lining of the lumen is folded in such a way that, in cross section, the lumen takes up the shape reflected in fig. 92. This figure also reveals two concentrations of longitudinal muscle fibres, one

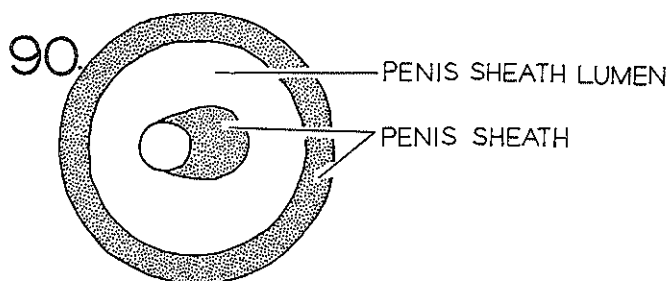
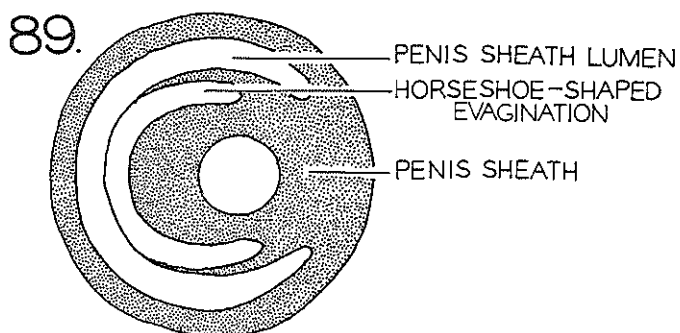
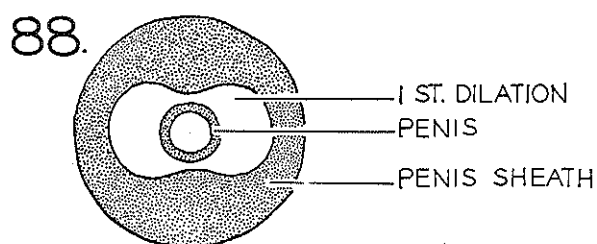
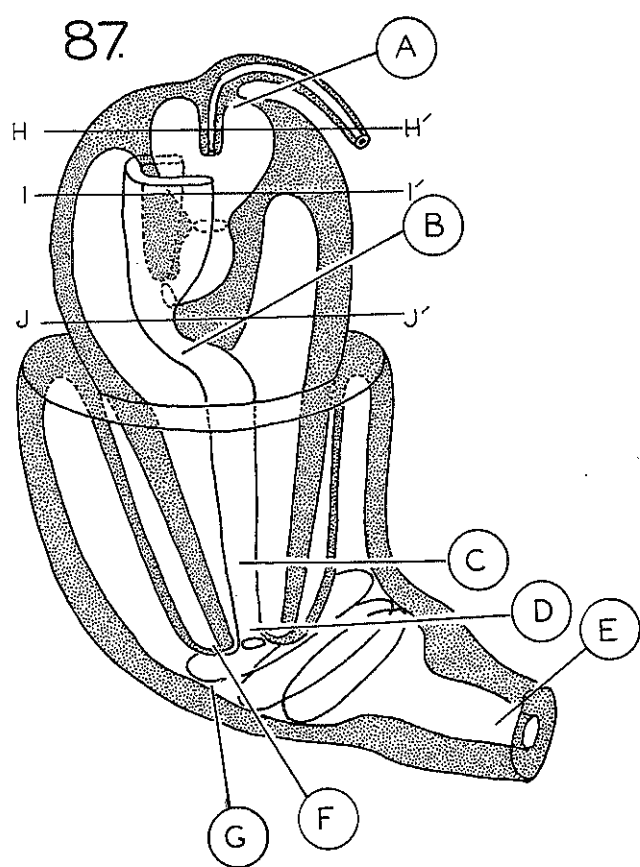
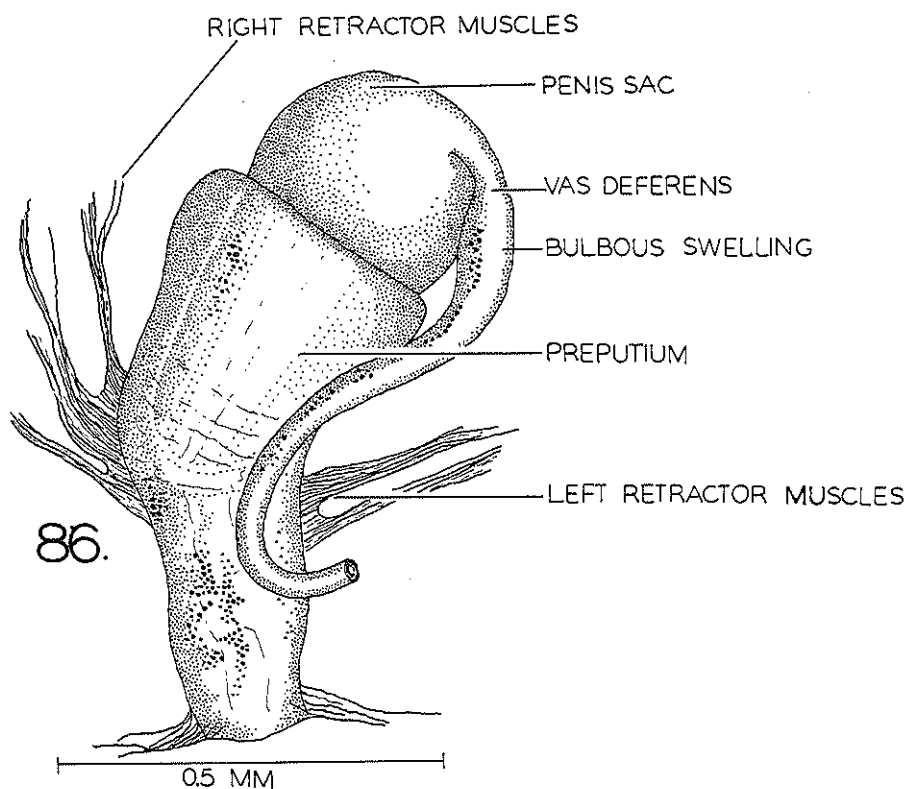


FIG.86. PENIS COMPLEX.
 FIG.87. PENIS COMPLEX; INDEX TO SECTION DRAWINGS.
 FIG.88. CROSS SECTION AT LEVEL HH' IN FIGURE 87.
 FIG.89. CROSS SECTION AT LEVEL II' IN FIGURE 87.
 FIG.90. CROSS SECTION AT LEVEL JJ' IN FIGURE 87.

lying immediately dorsal to and the other immediately ventral to the lumen. These relations are maintained throughout the terminal two thirds of the lumen where it is lined by the papillae described. The opening of this portion of the lumen in the preputium may or may not be elevated into a poorly defined papilla.

Apart from the epithelial lining of its lumen, the wall of the penis sheath is largely composed of intermingled longitudinal and circular muscle fibres which are not everywhere pressed up against the wall of the former, thus leaving, between itself and the lining of the lumen, a space of considerable size which is traversed by strands of muscle fibres as illustrated in fig. 91.

The preputium is a simple muscular tube the first two thirds of which, proceeding from the penis sheath, is lined by a more or less columnar epithelium, irregularly ciliated in patches which is covered by a thin homogeneous layer resembling a cuticle through which the cilia project where present (figs. 91 & 99). In the terminal third of the preputium the lining cells become cuboidal and are interspersed with mucous cells. In this region ciliation is limited to inconspicuous tufts on irregularly distributed cells.

Apart from the epithelial lining of its lumen, the wall of the preputium consists of a layer of variable thickness composed of connective tissue and longitudinal, circular and diagonal muscle fibres which more or less occur intermingled, although some may be more abundant in particular regions than others. The exact distri-

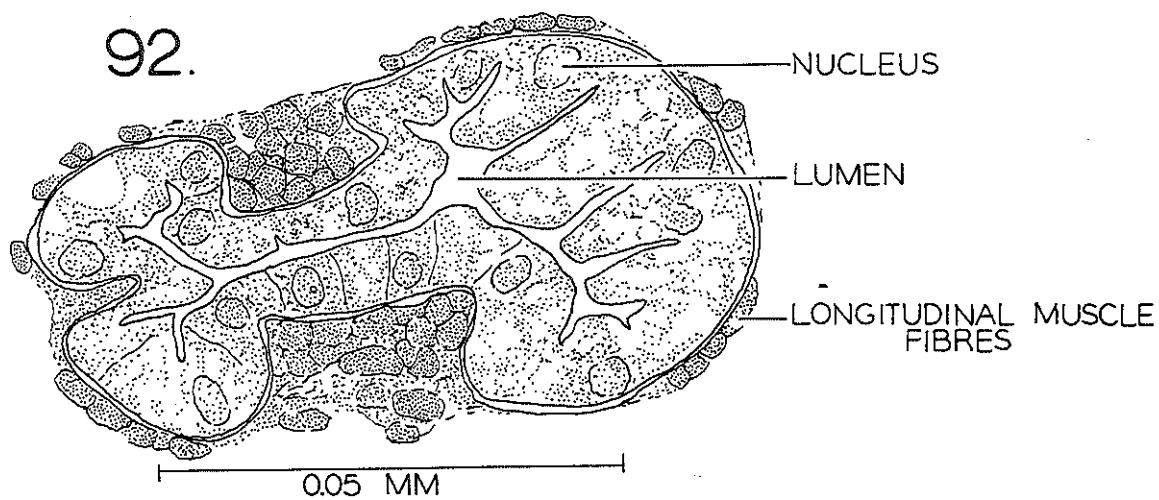
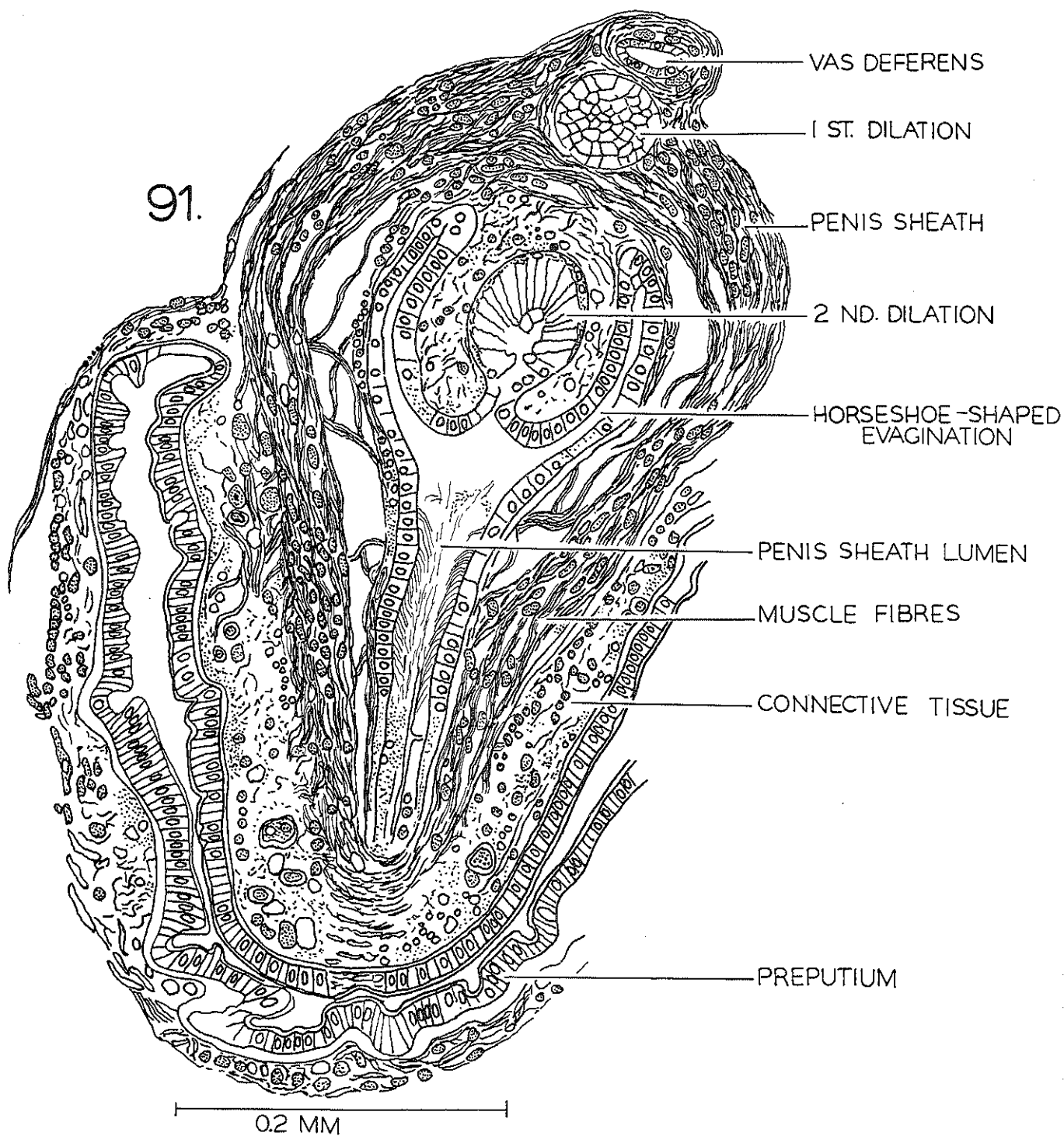


FIG.91.PENIS COMPLEX.LONGITUDINAL SECTION.

FIG.92.PENIS SHEATH.CROSS SECTION AT LEVEL D FIGURE 87.

bution of the muscle fibres has a profound effect on the appearance of the epithelial lining. In the proximal region the muscle fibres are not plentiful (fig. 91) but in the middle region the circular fibres predominate and seem to be arranged in such a way that the epithelium is thrown into a conspicuous series of folds which completely encircle the preputium in this region which may, for the sake of convenience, be referred to as its ribbed region (figs. 85 & 100). In the terminal region the longitudinal fibres predominate and are arranged in such a way as to cause the epithelial lining to display longitudinal ridges (fig. 97). It is impossible to homologise any two of these ridges with the pilasters which characterise the preputium in such species as B. pfeifferi (Schutte and Van Eeden, 1959b) and B.(E) africanus (Van Aardt, op. cit.).

Space F (fig. 87) formed between the penis sheath and the invaginated portion of the preputium wall, is filled up mainly by connective tissue. Imbedded in this connective tissue, right round the penis sheath, are found large secretory cells with distinct nuclei and well defined nucleoli, packed with orange staining secretory granules (fig. 99). These cells seem to communicate with a number of ducts which eventually penetrate the preputial wall just next to its junction with the penis sheath and may perhaps be designated as preputial glands.

It is to be regretted that Basch (1959), apart from his figure 11, p.45, gives a rather incomplete description of the male copulatory organ of L. fuscus, in which no

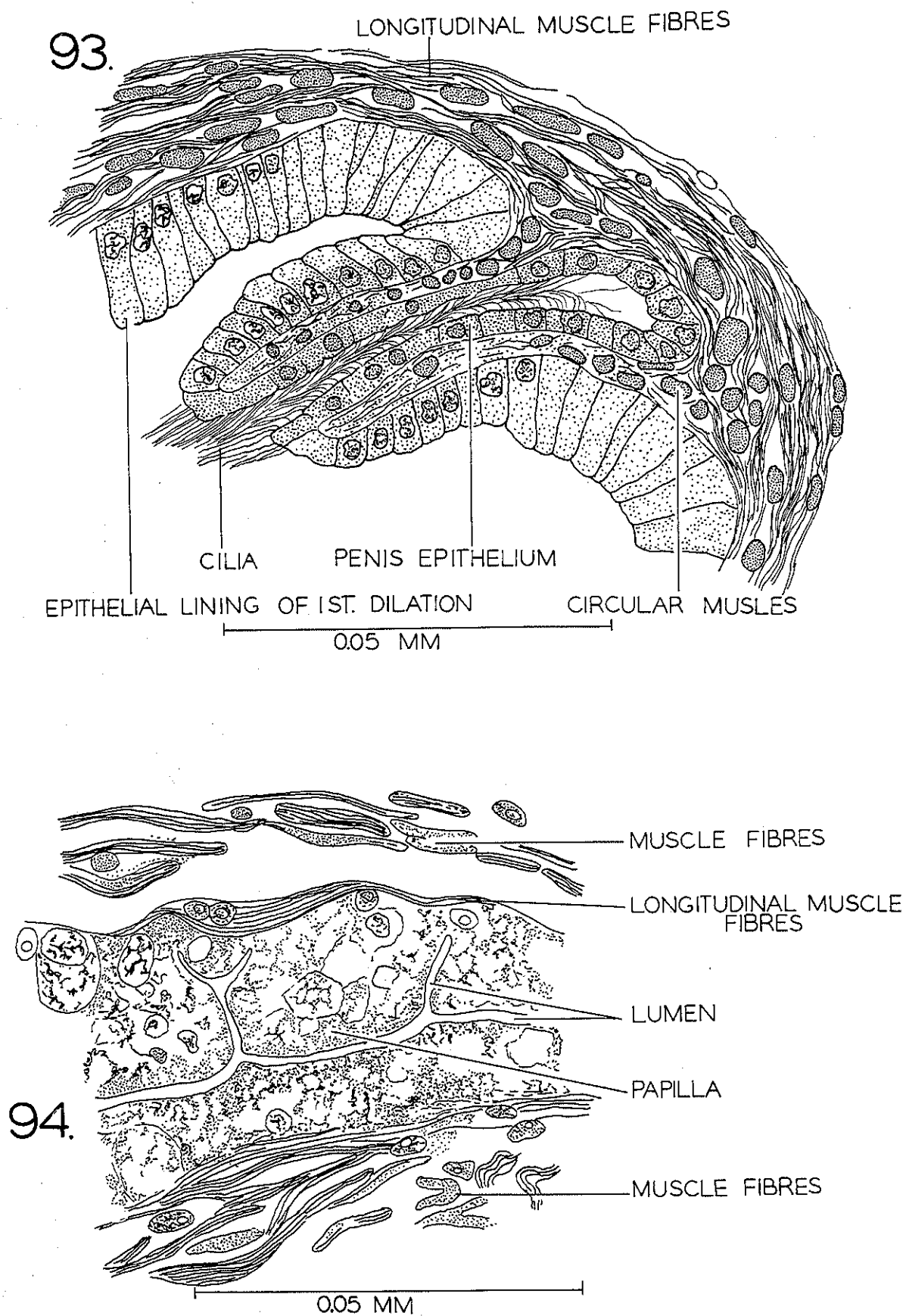


FIG.93. LONGITUDINAL SECTION THROUGH PENIS AT LEVEL A FIGURE 87.
 FIG.94. PENIS SHEATH. LONGITUDINAL SECTION AT LEVEL C FIGURE 87.

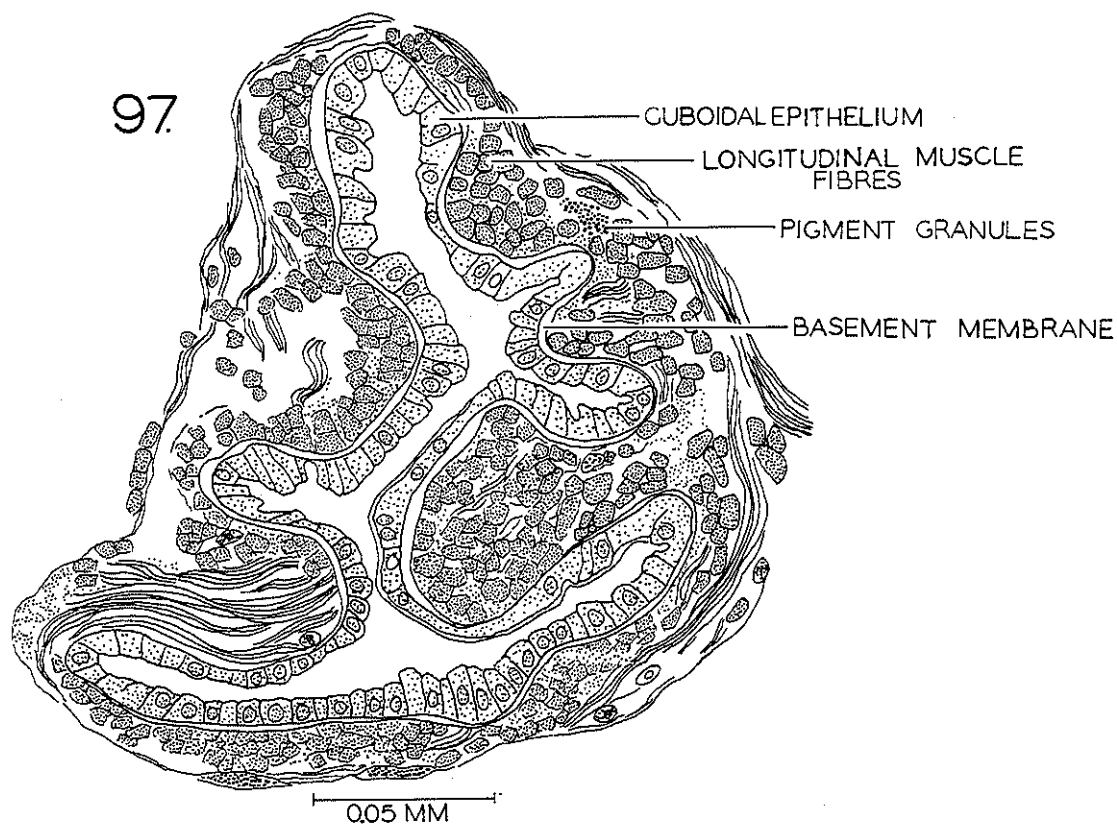
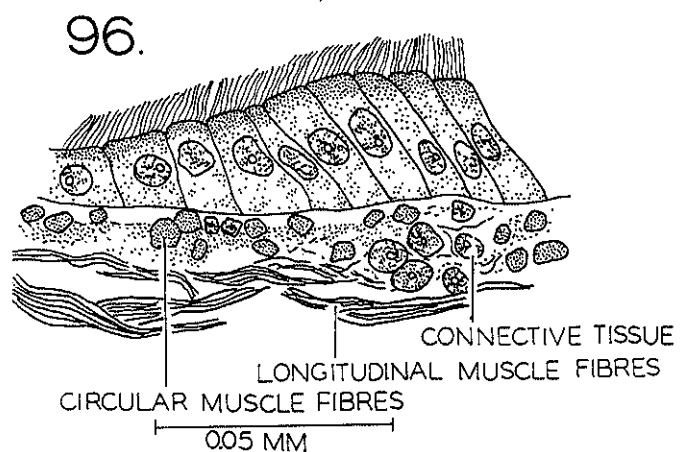
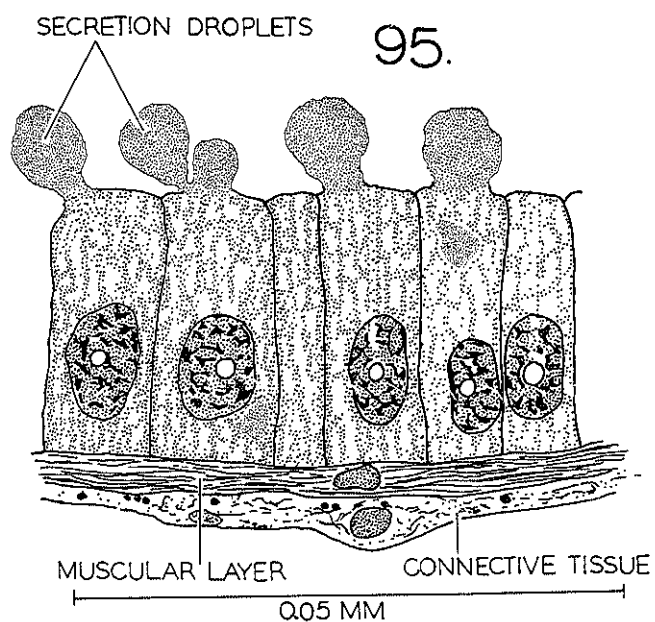


FIG. 95. CELLS LINING SPERMATHECA.

FIG. 96. PENIS SHEATH EPITHELIUM. LONGITUDINAL SECTION AT LEVEL B FIGURE 87

FIG. 97. PREPUTIUM EPITHELIUM. CROSS SECTION AT LEVEL E FIGURE 87

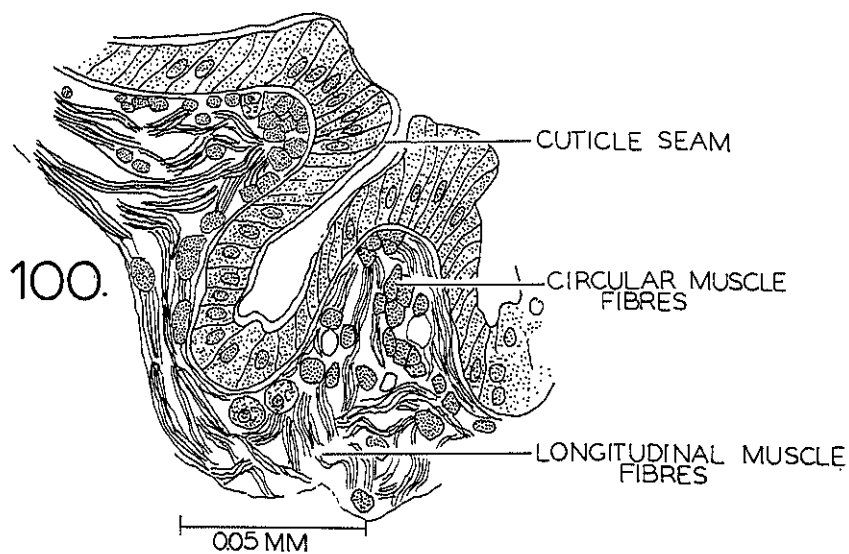
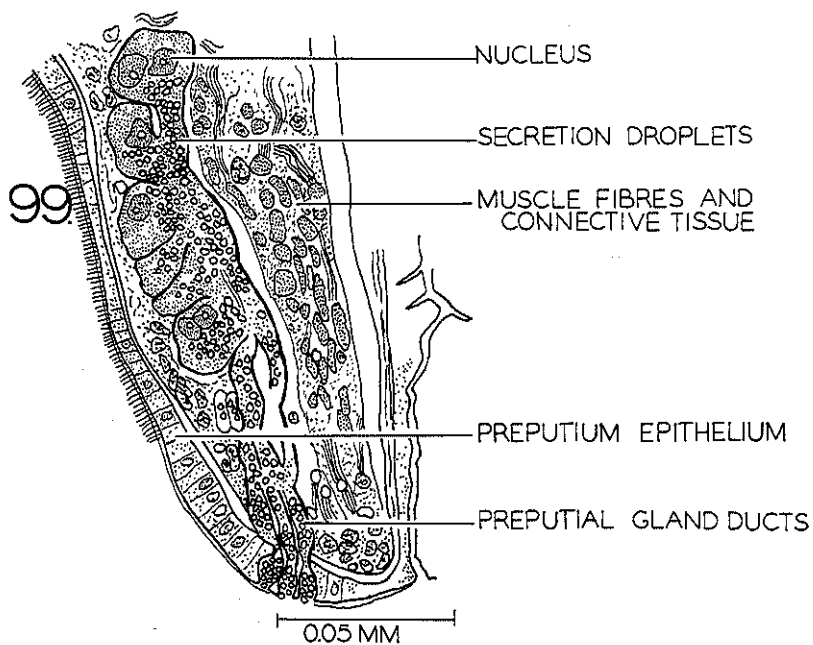
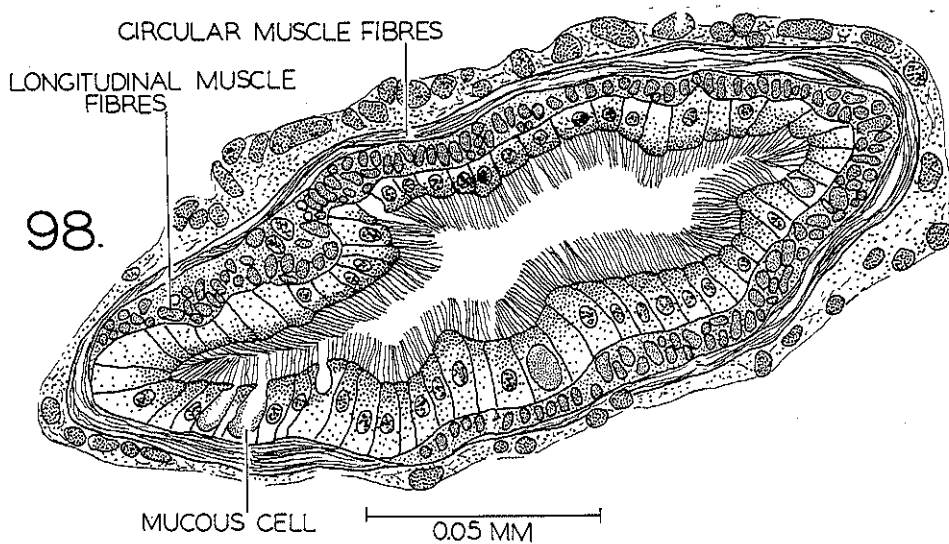


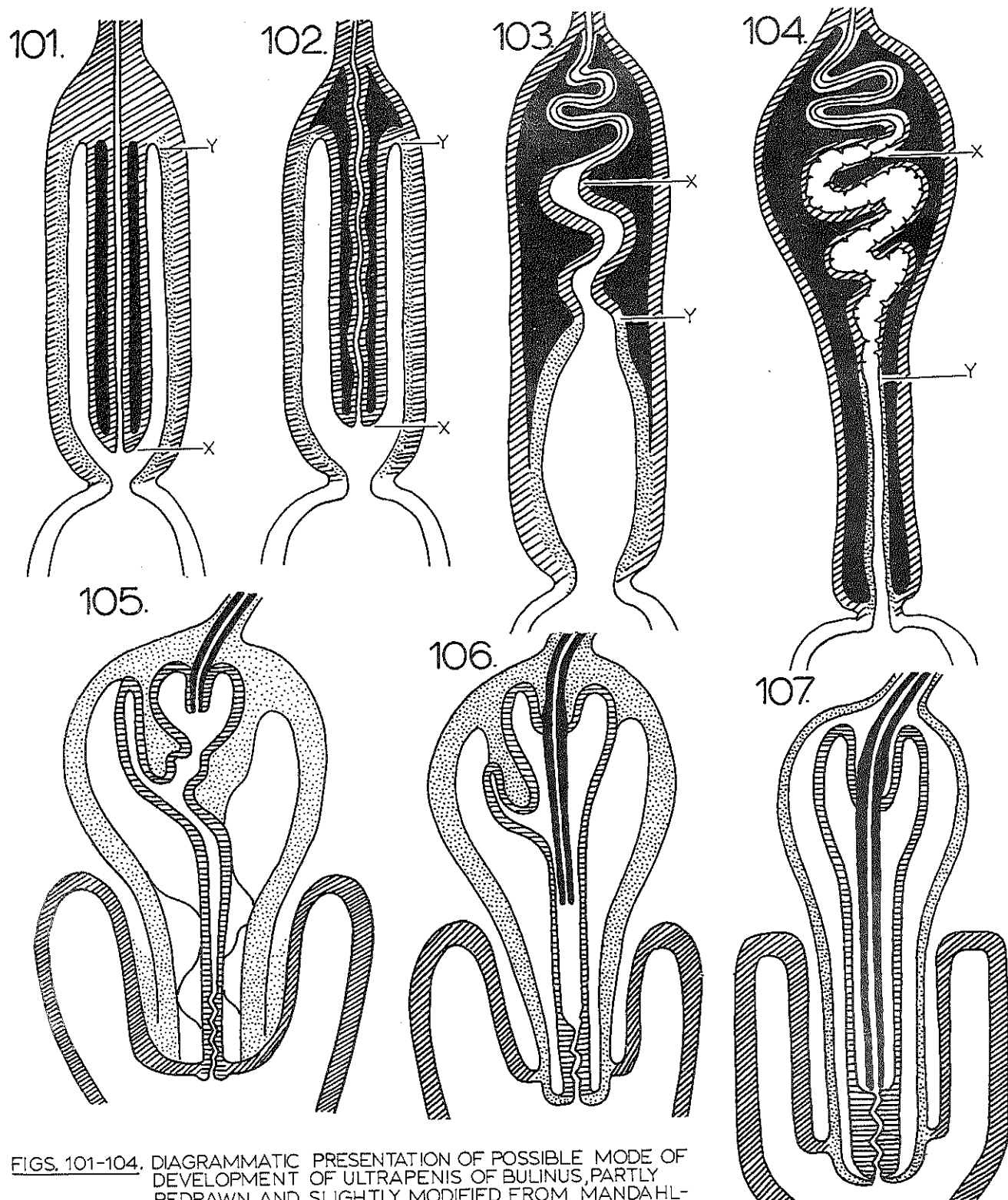
FIG. 98. UTERUS. CROSS SECTION THROUGH DISTAL PART.

FIG. 99. PREPUTIAL GLANDS. LONGITUDINAL SECTION AT LEVEL F FIGURE 87.

FIG. 100. PREPUTIUM EPITHELIUM. SECTION THROUGH RIBBED REGION AT LEVEL G FIGURE 87.

reference is made to the histology of this structure. In view of this it is most difficult to compare in detail, conditions obtaining in B. mooiensis with those reported for L. fuscus. Moreover, in his interpretation of the penis of L. fuscus, Basch (1959) is, in my opinion, guided by a misinterpretation of the views of Hubendick (1955) and Mandahl-Barth (1957) as to how the ultrapenis of Bulinus could have evolved, according to which the ultrapenis could have been produced not only by a longitudinal splitting of the wall of the penis proper but also by a similar splitting of the wall of the penis sheath (figs. 101 to 104). If this synthesis be accepted then the homologue of the penis proper of Biomphalaria must be sought in the epiphallus and middle portion of the ultrapenis of Bulinus whereas the terminal portion of the latter must have originated from the wall of the penis sheath. When this interpretation is applied to Basch's fig. 11, then what he annotates as penis must become ultrapenis, of which his so-called ultrapenis could, at most, represent either the epithelial lining of the lumen of the ultrapenis, such as that of Bulinus, with some surrounding tissue, or the vas deferens which extends down into the greatly dilated lumen of an ultrapenis type of organ such as that of Bulinus. The second of the latter two alternatives would be in line with Basch's inability to find any definite continuity between what he refers to as ultrapenis and penis.

Arguing along these lines, the condition obtaining in B. mooiensis could be interpreted as representing a stage in the process of development towards an ultra-



FIGS. 101-104. DIAGRAMMATIC PRESENTATION OF POSSIBLE MODE OF DEVELOPMENT OF ULTRAPENIS OF *BULINUS*, PARTLY REDRAWN AND SLIGHTLY MODIFIED FROM MANDAHL-BARTH, 1957.

FIG. 101. PENIS OF *BIOMPHALARIA PFEIFFERI* KRS, AFTER SCHUTTE & VAN EEDEN 1959 b.

FIG. 102. PENIS OF *BIOMPHALARIA*, AFTER MANDAHL-BARTH, 1957.

FIG. 103. HYPOTHETICAL INTERMEDIATE STAGE, AFTER MANDAHL-BARTH, 1957.

FIG. 104. PENIS OF *BULINUS*, AFTER MANDAHL-BARTH, 1957.

FIGS. 105-107. DIAGRAMMATIC PRESENTATION OF THE POSSIBLE MORPHOLOGICAL RELATIONSHIP BETWEEN THE PENIS COMPLEX OF *BURNUPIA MOOIENSIS* AND THAT OF *LAEVAPEX FUSCUS*.

FIG. 105. PENIS OF *BURNUPIA MOOIENSIS*.

FIG. 106. HYPOTHETICAL INTERMEDIATE STAGE.

FIG. 107. PENIS OF *LAEVAPEX FUSCUS*, AFTER BASCH, 1959.

penis at which the lumen of the penis sheath is being transformed into the lumen of an ultrapenis. Should this be acceptable, then a prolongation of the vas deferens, after the manner suggested in fig. 106 would produce a stage intermediate between B. mooiensis and L. fuscus (figs. 105 & 107).

It must be obvious that the penis of B. mooiensis, or even the ultrapenis of L. fuscus (Basch, 1959) as interpreted here, cannot be everted after the manner this takes place in Bulinus. In fact, on one occasion a specimen of B. mooiensis with an everted penis complex was narcotised and examined. The preputium was located outside the body, completely turned inside out and enclosing the penis sheath which remained unaffected. It would therefore seem that the penis complex of B. mooiensis cannot be employed as an intromittent organ but can, at the most, be pressed up against the female genital opening and thus serve as a bridge between two copulating animals.

3.11 SUMMARY

1. The morphology and histology of some systems of Burnupia mooiensis, a fresh water ancyliid, is described.
2. The circulatory system is almost similar to that of Ferrissia shimekii.
3. The pseudobranch is more or less similar to that obtaining in Laevapex fuscus. However, the position of the rectum and anus relative to the pseudobranch is essentially different from that of the latter species

and all other ancyliids yet described in not being situated anteriorly, but posteriorly.

4. The eye, osphradium and statocyst are described.

5. A study of the prostate gland reveals four histologically different regions within each diverticulum in contrast to the normal two or three described for other fresh water molluscs.

6. The osphradium differs basically from those described for other ancyliids.

7. There seems to be a considerable intraspecific variation as far as the characteristics investigated for the radula are concerned.

8. A structuarlly new organ, the muciparous gland appendix, is described in detail.

9. The penis complex differs basically from all others yet described.

LITERATURE CITED

- ABDEL-MALEK, E.T.
1954a. Morphological studies on the family Planorbidae (Mollusca: Pulmonata) I. Genital organs of Helisoma trivolvis (Say) (Subfamily Helisomatinae F.C. Baker 1945). Trans. Amer. micr. Soc., 93, 2: 103-124.
- BOER, H.H. & LEVER, J.
1959. On the anatomy of the circulatory system in Ferrissia shemeki (Ancyli-
dae, Pulmonata); especially on the blood supply of the central nervous system. Konink. Nederl. Akademie van Wetenschappen. Amsterdam Proc. Series C, 62, No. 1.
- BOETTGER, C.
1944. Tierwelt. Nord-und Ostsee, 35 Lieferung IX. b2, Basommatophora.
- BASCH, P.F.
1959. The anatomy of Laevapex fuscus, a freshwater limpet (Gastropoda: Pulmonata). Miscellaneous Publication Museum of Zoology, University of Michigan, No 108: 54 pp.
- CARRIKER, M & BILSTAD, N.
1946. Histology of the alimentary system of Lymnaea stagnalis appressa Say. Amer. Micr. Soc. 65: 250-275.
- CONNOLLY, M.
1925. The non marine mollusca of Portuguese East Africa. Trans. Roy. Soc. S. Africa. ; Xll, 200-2.
- CONNOLLY, M.
1939. A monographic survey of South African non-marine Mollusca. Ann. S. Afr. Mus., 33, 1 - 660.
- HOFF, C.C.
1940. Anatomy of the ancyliid snail, Ferrissia tarda (Say). Trans. Amer. Micros. Soc., 59 (2) : 224-42.
- HOLM, L.W.
1946. Histological and functional studies on the genital tract of Lymnaea stagnalis appressa Say.
- HUBENDICK, B.
1955. Phylogeny in the Planorbidae. Trans. Zool. Soc. Lond. 28, 6: 453 - 542.
- HUBENDICK, B.
1960. The Ancyliidae of lake Ochrid and their bearing on intralacustrine speciation. Proc. Zool. Soc. Lond. Vol. 133. Part. 4, pp. 497-529.

- JOOSSE, J & LEVER, J
1959
Techniques of narcotization and operation for experiments with Limnaea stagnalis (Gastropoda: Pulmonata). Koninkl. Nederl. Akademie van Wetenschappen Proc., Series C, 62, No. 2.
- MANDAHL-BARTH, G
1954
The freshwater mulluscs of Uganda and adjacent territories. Ann. Mus. Congo belge. Serie in 8 vò , 32.
- MANDAHL-BARTH, G
1957
Intermediate hosts of Schistosoma. African Biomphalaria and Bulinus: II. Bull. Wld. Hlth. Org. 17: 1-65.
- MORTON, J.E.
1958
Molluscs. An Introduction to their form and functions. Hutchinson & Co., Ltd., London.
- PRETORIUS, S.J.
Some aspects of the morphology of Lymnaea natalensis natalensis Krauss (Mollusca : Basommatophora) Unpublished thesis, Potch. Univ. for C.H.E. S. Africa.
- SCHNEIDER, K.C.
1908
Histologisches Practicum der Tiere für Studenten und Forscher. 615 pp. Gustav Fischer. Jena.
- SHARP, B.
1883b
On the anatomy of Ancylus fluviatilis O.F. Muller and Ancylus lacustris Geoffroy. Proc. Acad. Nat. Sci. Phila. (1883), 214-40.
- SCHUTTE, C.H.J. &
VAN EEDEN, J.A.
1959b
Contributions to the morphology of Biomphalaria pfeifferi (Krauss). II. Internal anatomy. Ann. Mag. nat. Hist., Ser. 13, 11: 136 - 156
- SIMROTH, H.
1928
Pulmonata in Bronns Klassen und Ordnungen des Tierreichs. 3 Bd. Mollusca. 2 Abteilung. 2 Buch. Leipzig. 1354 pp.
- STIGLINGH, I.,
VAN EEDEN, J.A. &
RYKE, P.A.J.
1962
Contributions to the morphology of Bulinus tropicus (Gastropoda: Basommatophora : Planorbidae) Malacologia, I(1) : 73 - 114.
- VAN AARDT, W.J.
1960
Bydraes tot die morfologie van Bulinus (Physopsis) africanus (Krauss) (Mollusca Basommatophora). Unpublished thesis, Potch. Univ. for C.H.E., S. Africa.
- VAN EEDEN, J.A.
1958
Two useful techniques in freshwater malacology. Proc. Malac. Soc. Lond., 33, 2 : 64-66.

VAN EEDEN, J.A.,
OBERHOLZER, G.
PRETORIUS, S.J.
1962

A method for preparing stained
whole mounts of freshwater snail
radulae. Separata de Revista de
Biologia, 3 (2-4) : 199-200.

WALKER, B.
1923

The Ancyliidae of South Africa,
London : Printed for the author,
82 pp.

3.13 ACKNOWLEDGEMENTS

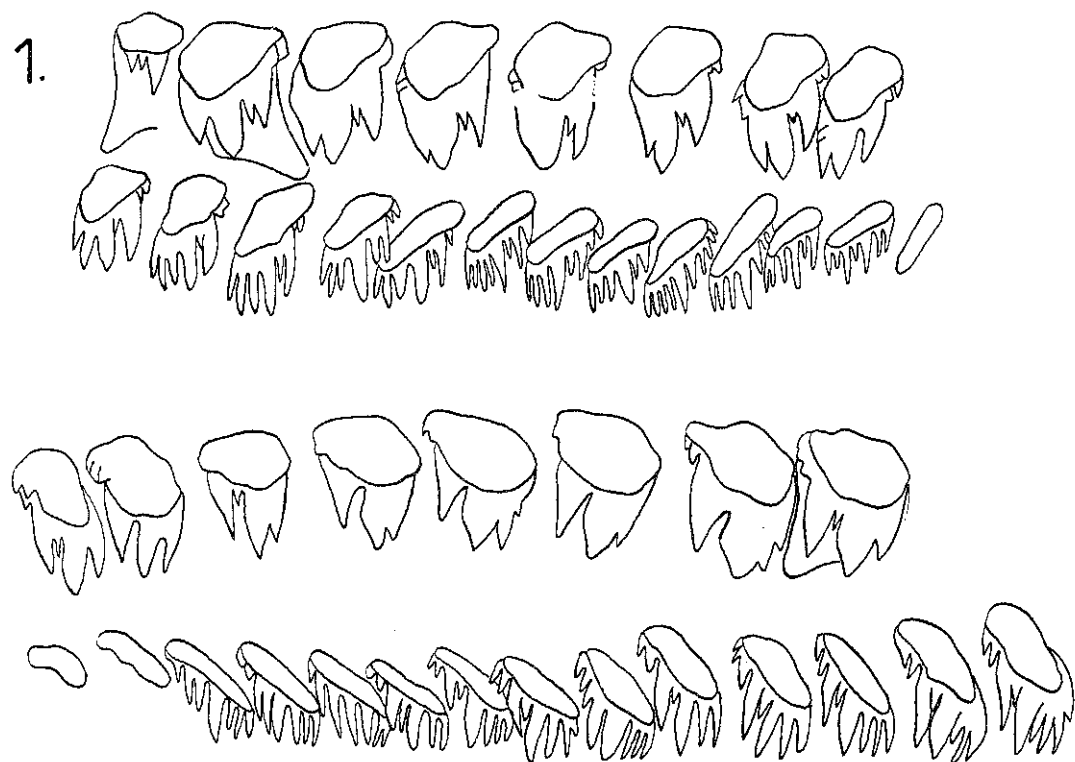
My sincere thanks are extended to Professor J.A. van Eeden for his guidance in this study. His unflagging interest was an inspiration. I also wish to express my gratitude to Professor P.A.J. Ryke for his guidance and highly valued suggestions. The help and suggestions of Mr. H.J. Schoonbee, Mr. S.J. Pretorius, Mr. V. Hamilton Attwell and Miss Ina Stiglingh are appreciated.

For permission to redraw Figure 23 a, b & c p.58 from Mandahl-Barth's "Intermediate Hosts of *Schistosoma*. African *Biomphalaria* and *Bulinus*." World Health Organization, Monograph Series No. 37, I am indebted to Dr. N. Howard-Jones, Director, Division of Editorial and Reference Services, World Health Organization, Palais des Nations, Geneva, Switzerland.

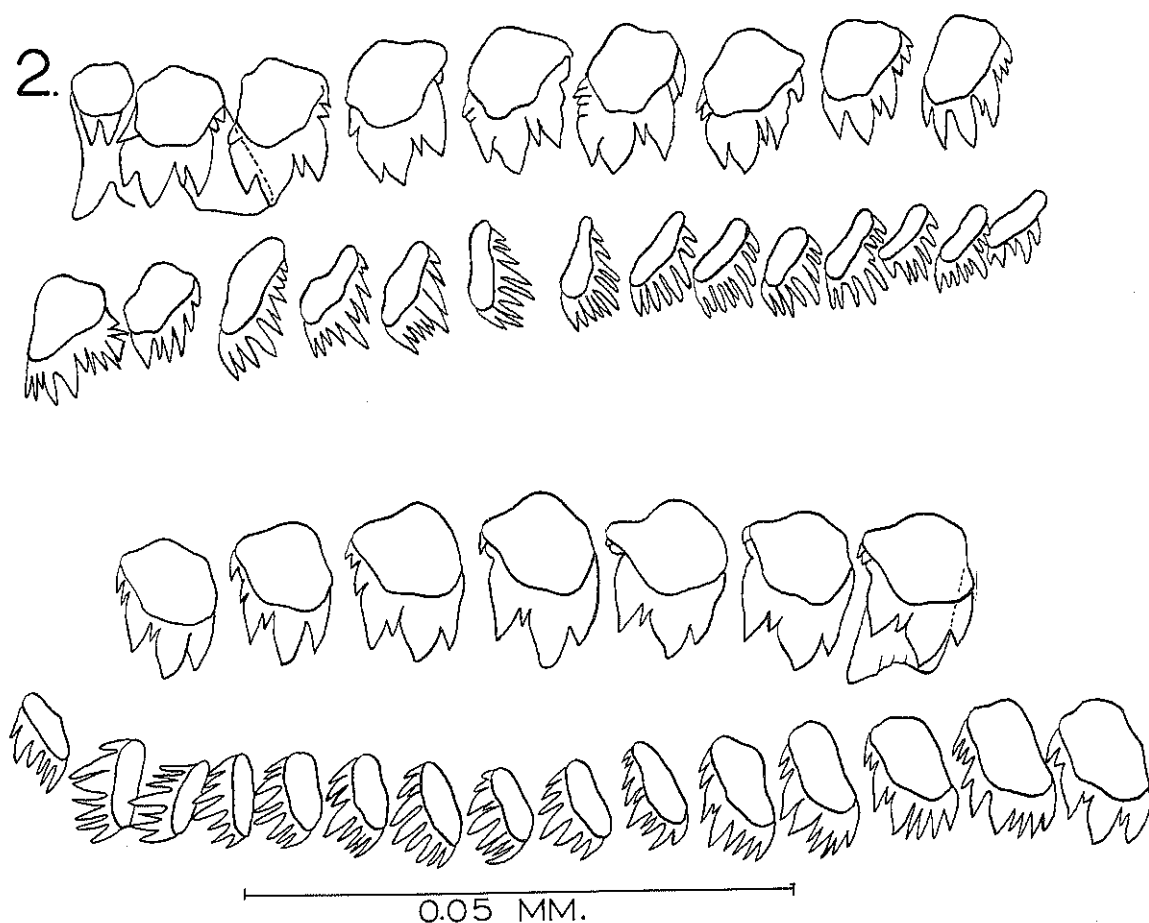
My sincere thanks are extended to the Executive Committee of the Museum of Zoology, University Museums, University of Michigan, U.S.A., for granting the permission to redraw figure 11 D, p.45, from Basch's "The anatomy of *Laevapex fuscus*, a freshwater limpet (Gastropoda: Pulmonata)". Miscellaneous Publications Museum of Zoology, University of Michigan, No. 108.

APPENDIX

1.

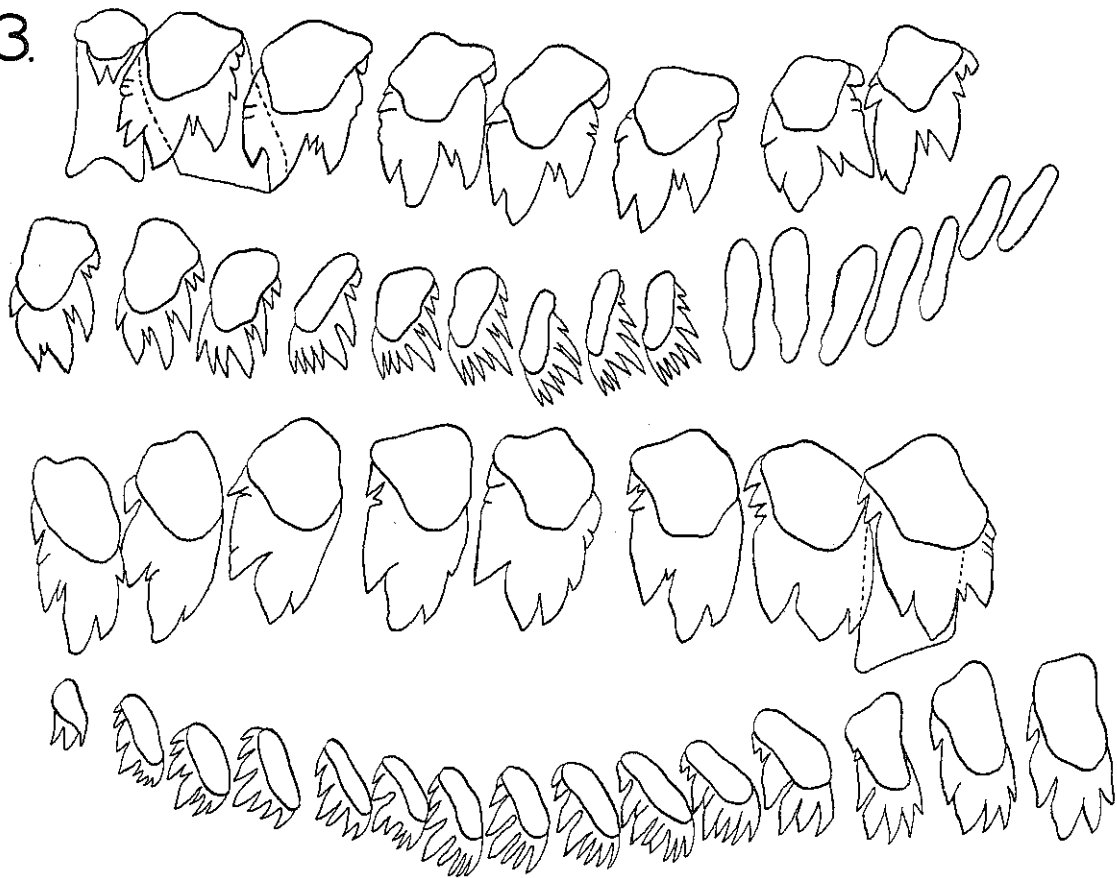


2.



FIGS. 1-22. REMAINDER OF SERIES OF LEFT AND RIGHT HALF TRANSVERSE ROWS OF RADULAE ON WHICH THE INVESTIGATION OF THE RADULA OF *BURNUPIA MOOIENSIS* IS BASED.

3.

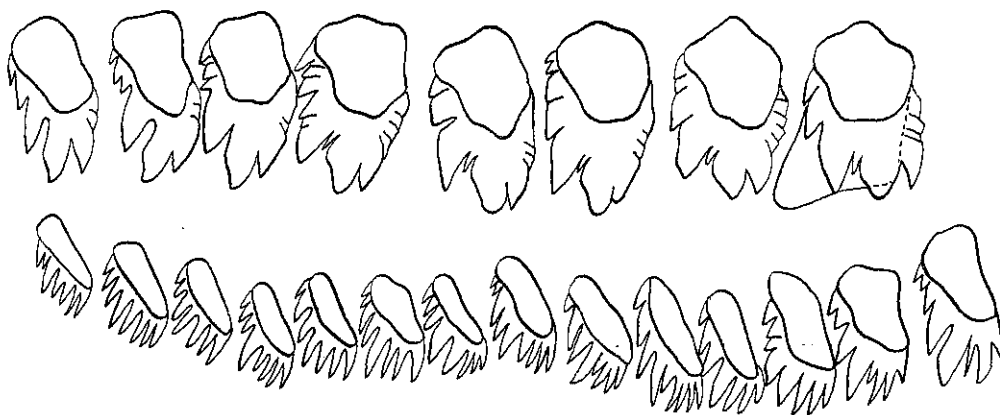
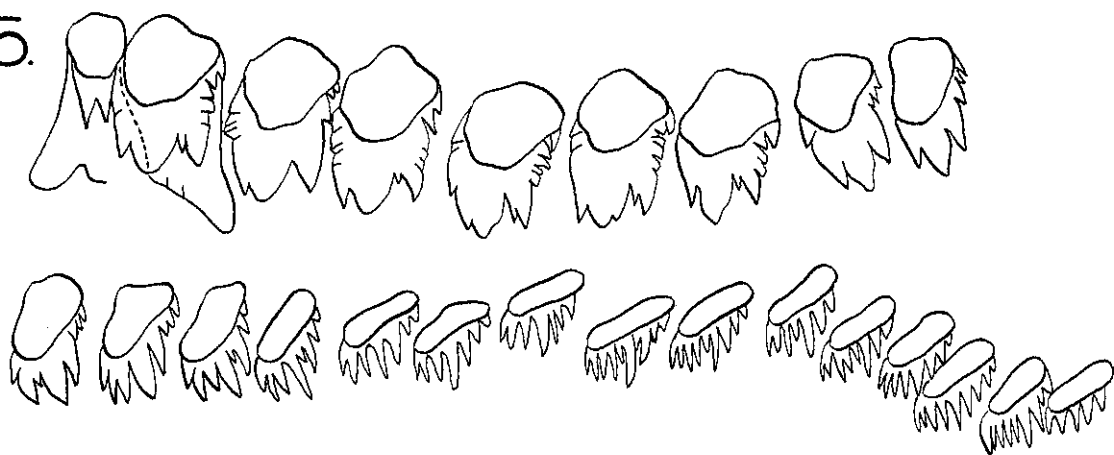


4.

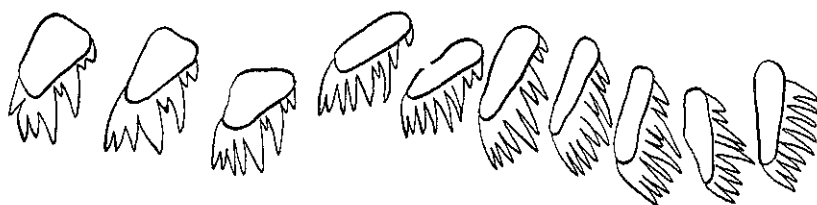
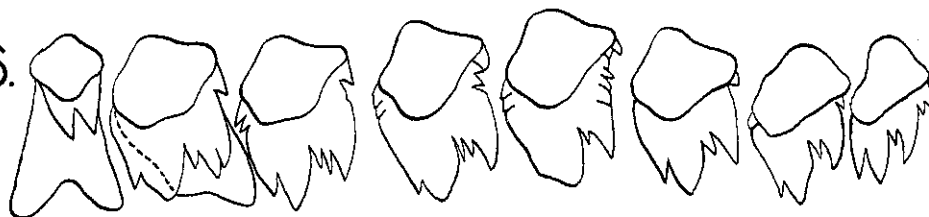


0.05 MM.

5.

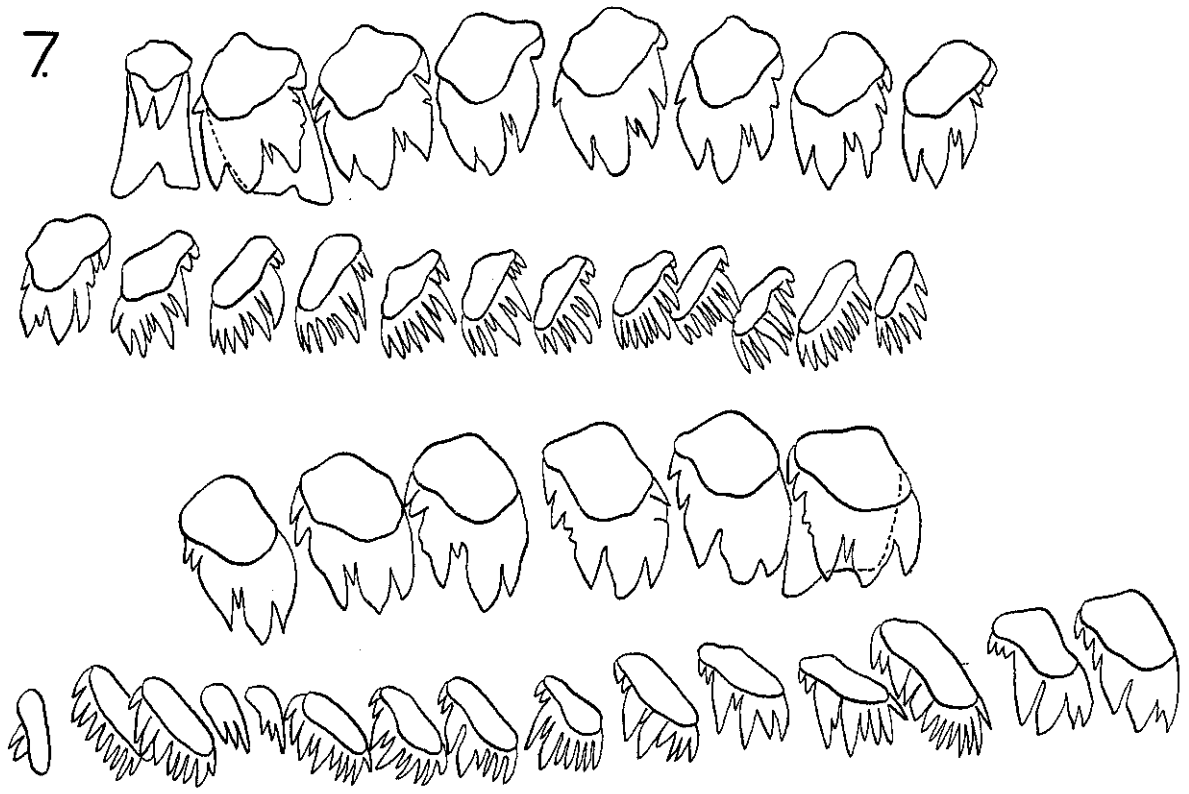


6.

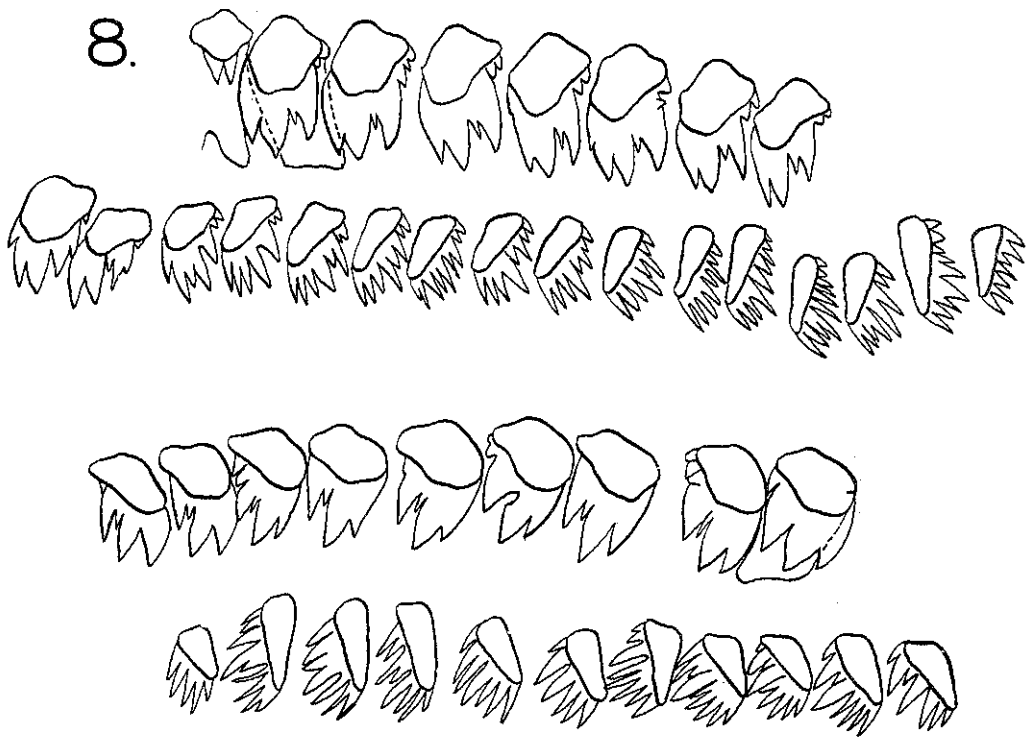


0.05 MM.

7.

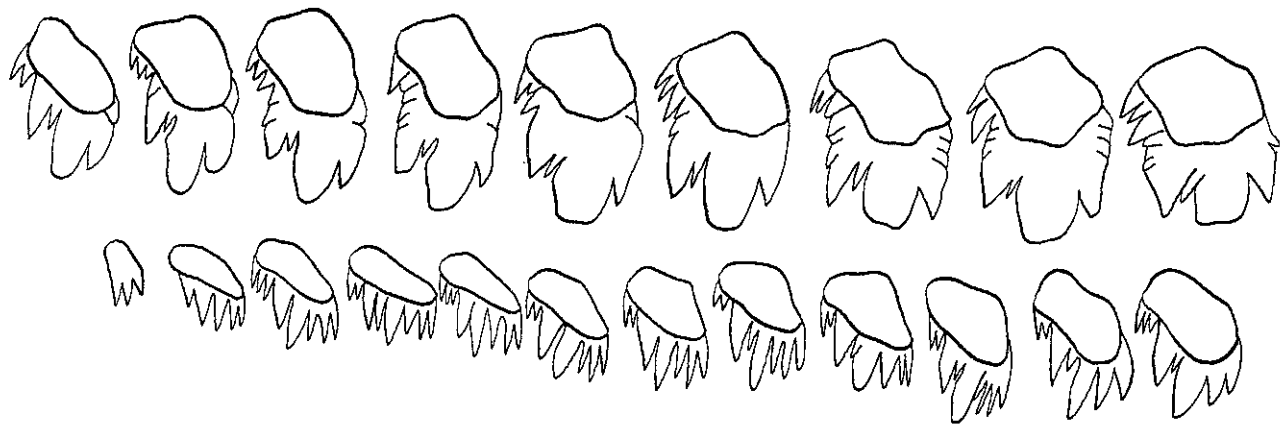
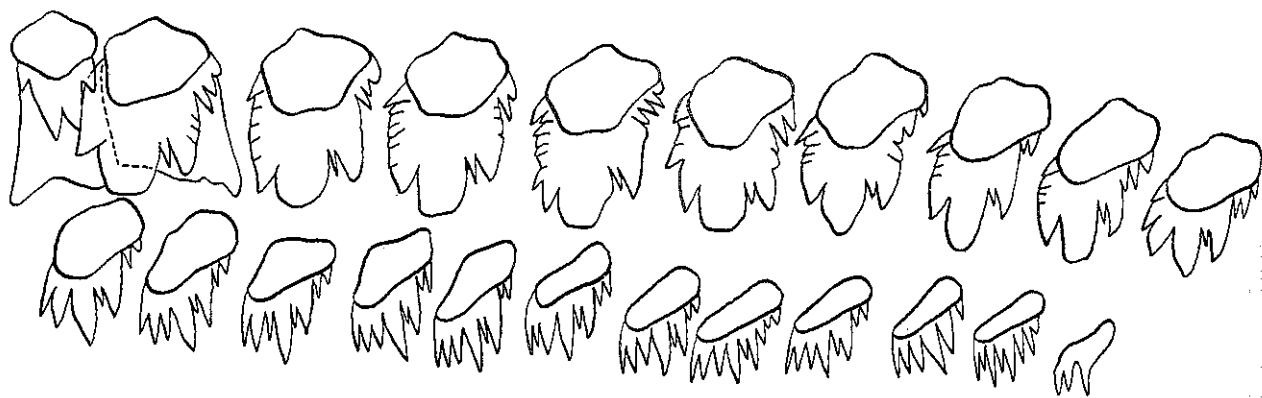


8.



0.05 MM.

9.

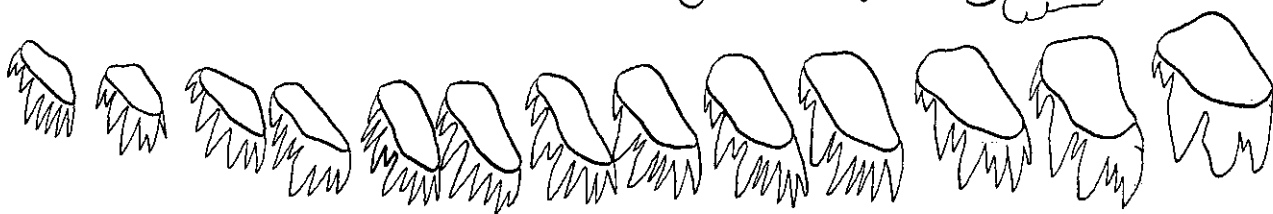
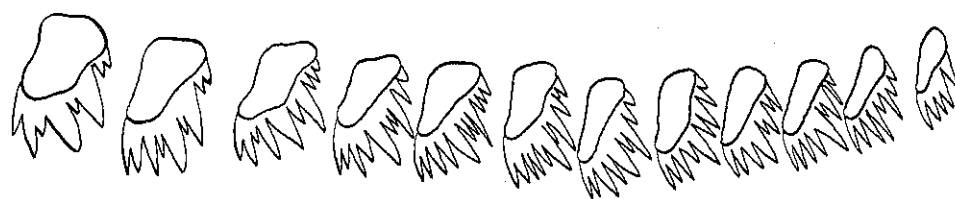


10.

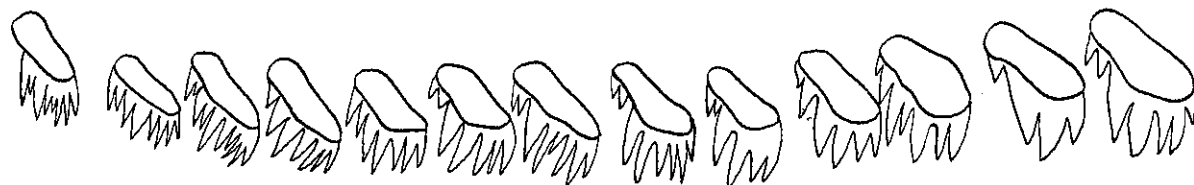
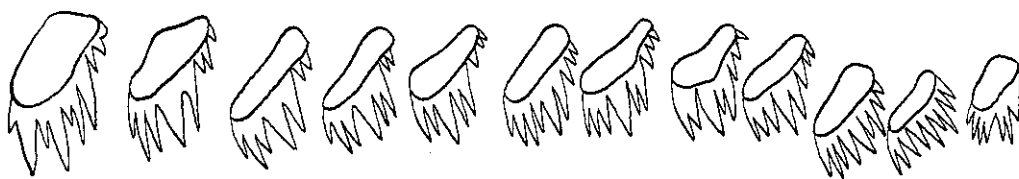


0.05 MM.

11.

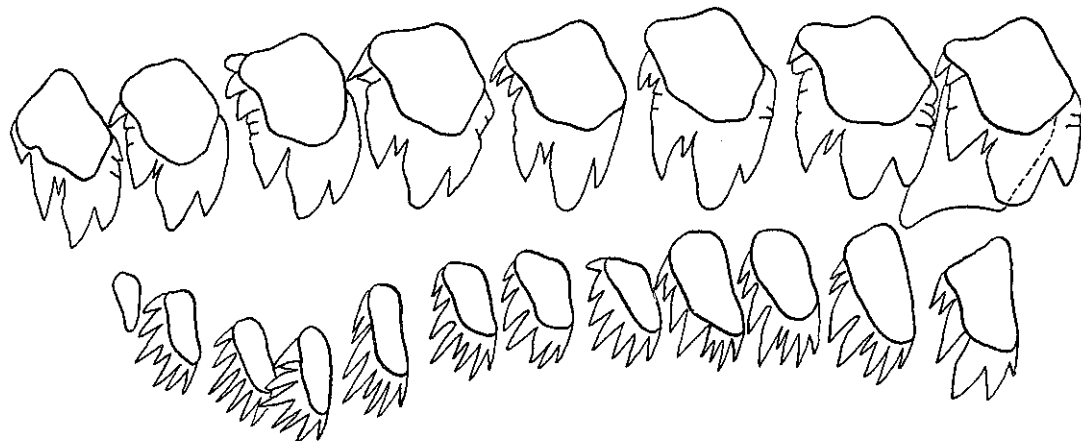
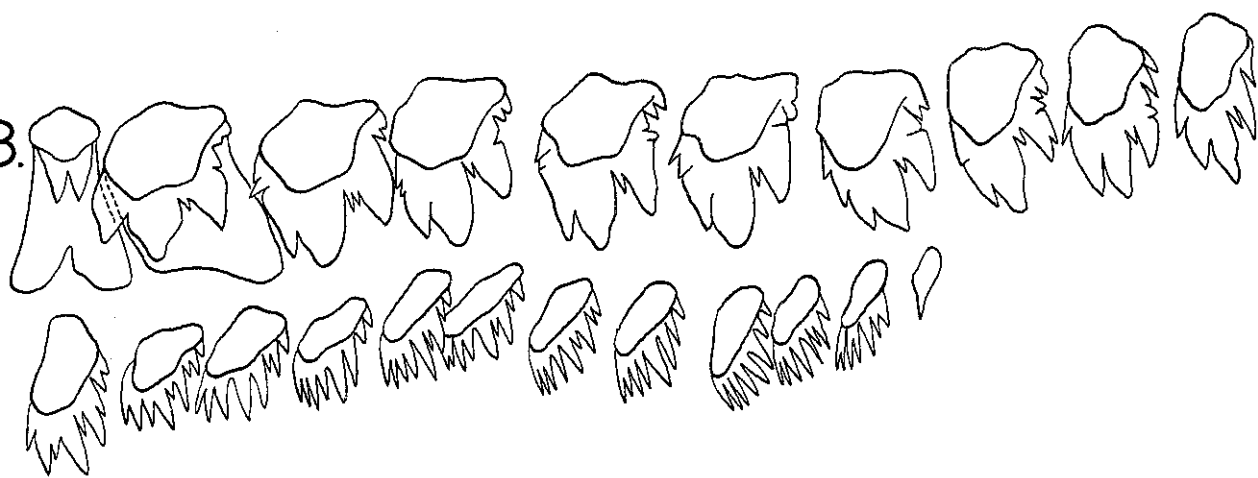


12.

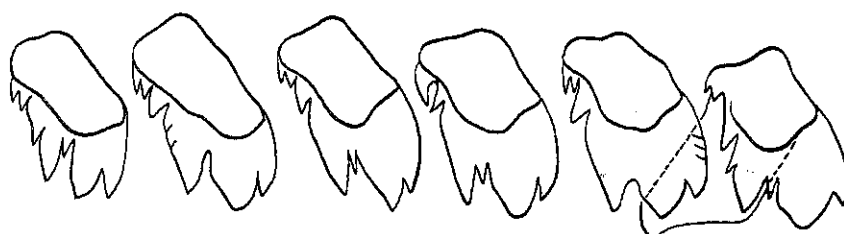
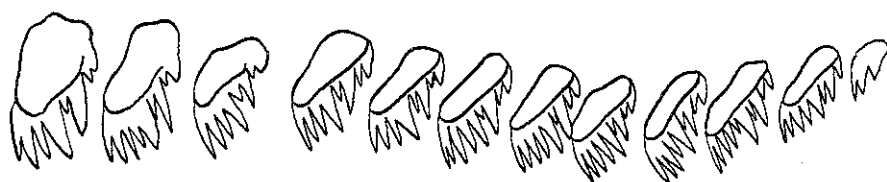


0.05 MM.

13.



14.

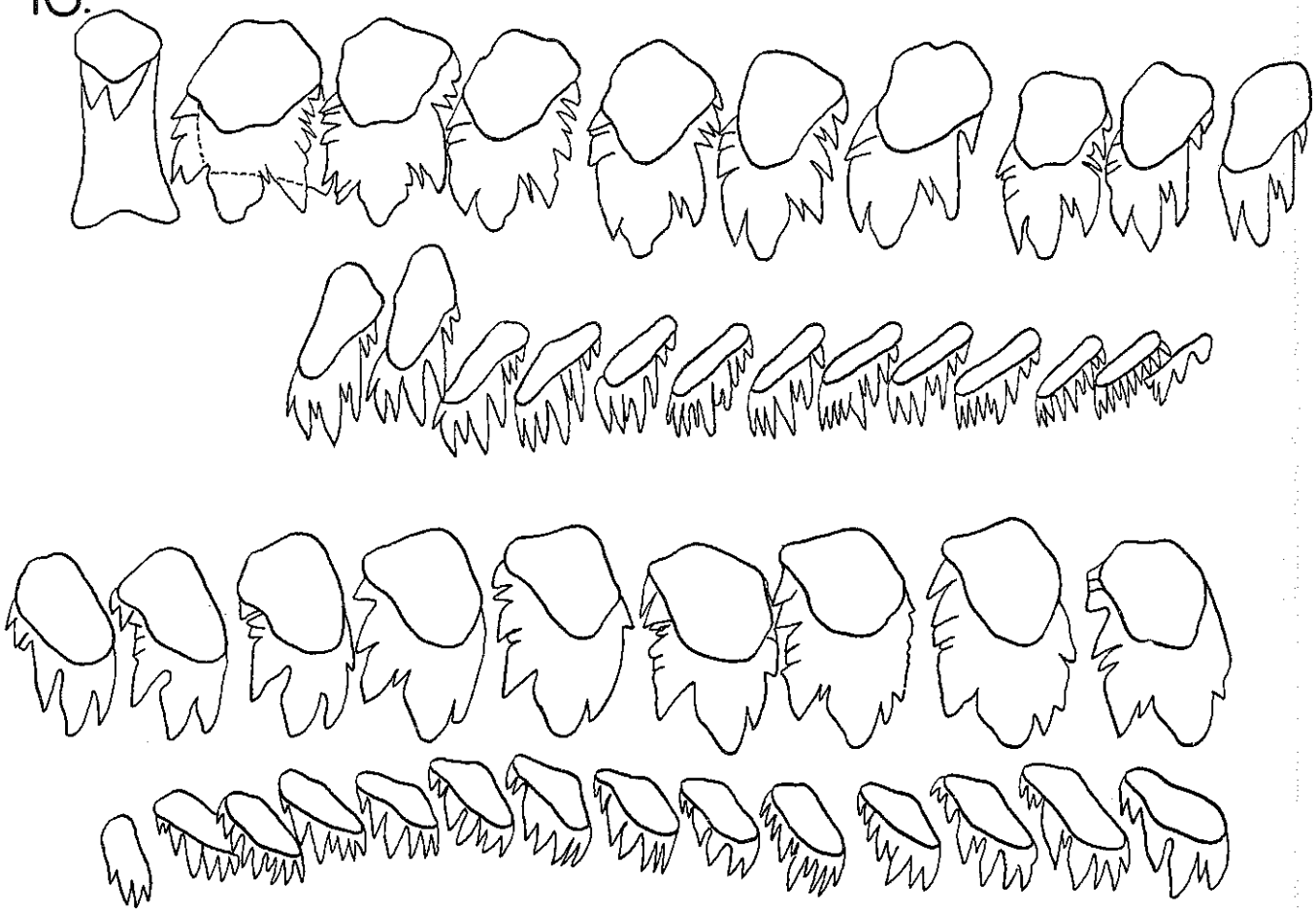


0.05 MM.

15.

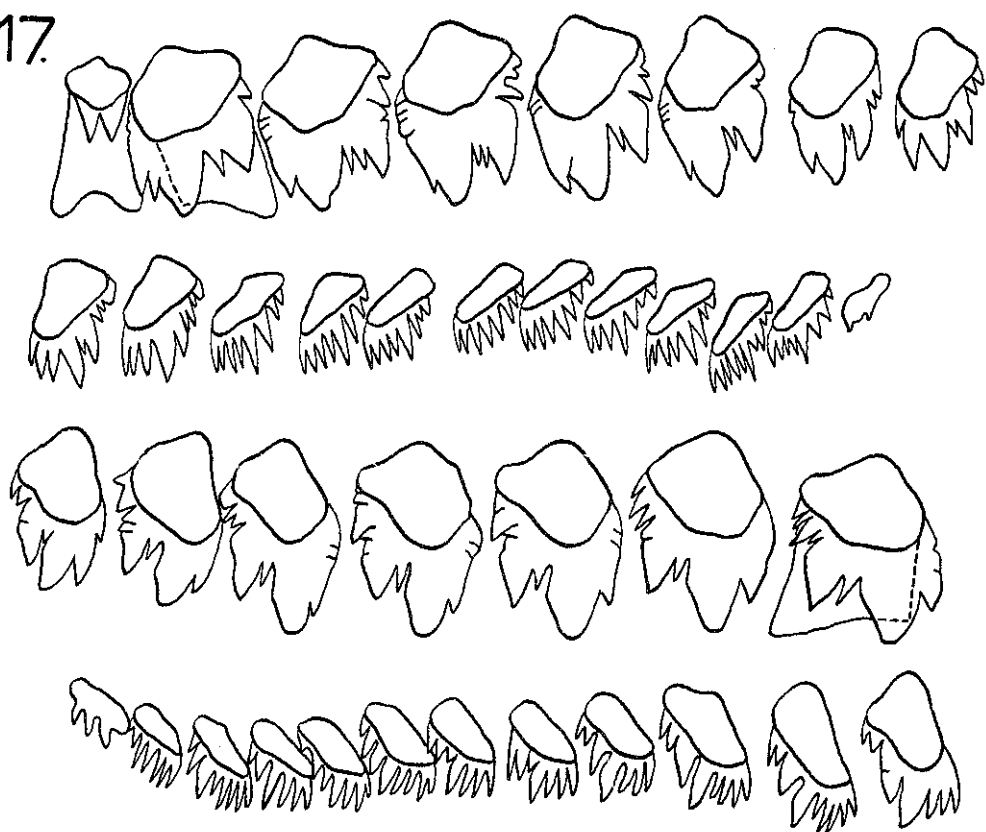


16.

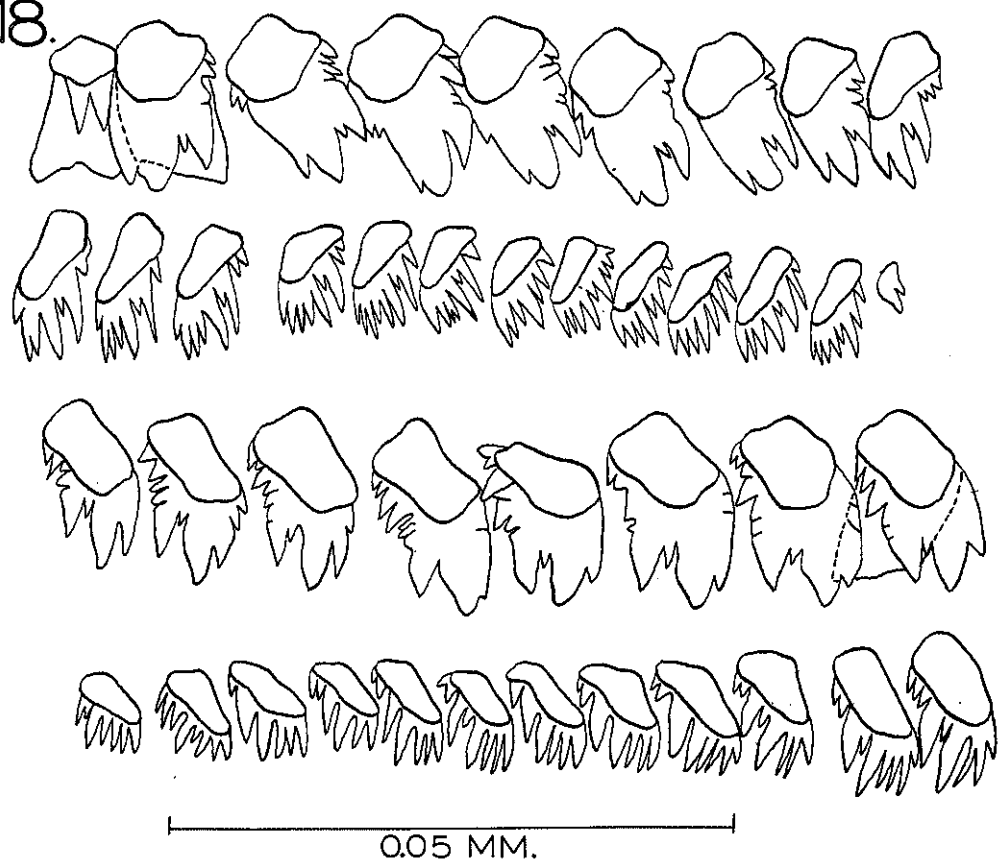


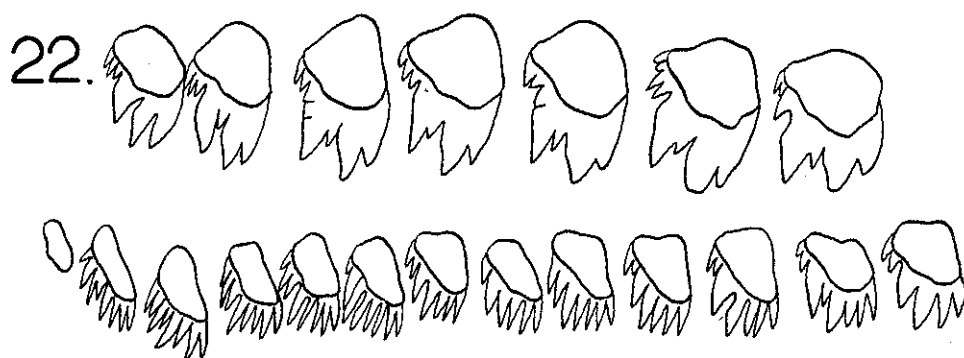
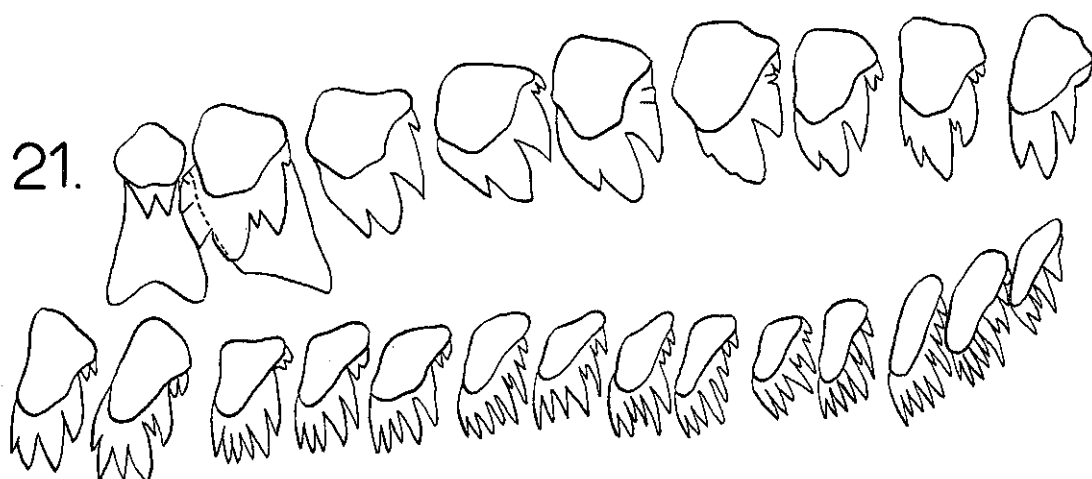
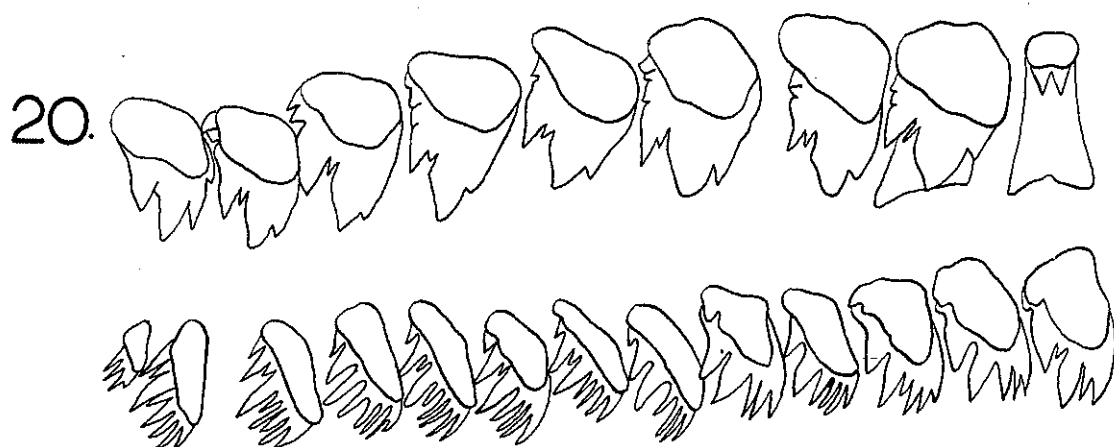
0.05 MM.

17.



18.





0.05 MM.

FIG.19. RIGHT HALF OF RADULA TEETH DEPICTED IN FIG. 29.
 FIG.21. RIGHT HALF OF RADULA TEETH DEPICTED IN FIG. 30.
 FIG.22. LEFT HALF OF RADULA TEETH DEPICTED IN FIG. 28.