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دراسات تشريحية ووظيفية على الجهاز الهضمى للقوقع "بيللاميا يونيكلر"

٤- الغدد اللعابية والهضمية

عبد الونيس بدينى ، منى حماده

يعتبر هذا البحث الجزء الرابع والأخير من دراسة متكاملة على الجهاز الهضمى لأحد قواقع المياه العذبة فى بيئتنا المصرية وهو القوقع المعروف بأسم "بيللاميا يونيكلر" الذى لم يلق اهتماما سابقا. ويتعلق هذا الجزء بدراسة التركيب البين والنسيجى للغدد اللعابية وقناتيهما اللتان تفتحان فى التجويف الفمى ولفصى الغدة الهاضمة وقنواتها التى تفتح بفتحتين فى الجزء الفؤادى للمعدة ومدى ملاءمة هذا التركيب لوظيفة هذه الغدد وللتغذية فى هذا القوقع. وقد نوقشت هذه النتائج مع ماهو منشور عن هذه الغدد فى قواقع أمامية الخياشيم منتمية الى فصائل أخرى. ومما يجد ذكره فى هذا الصدد هو أن خلايا الغدة الهاضمة فى هذا القوقع متنوعة فى الخصائص والوظيفة وقد تمر بمراحل مختلفة من حيث الوظيفة فمنها الغدى ومنها ما يقوم بالهضم داخل الخلية ومنها ما يقوم بالأخراج.

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ANATOMICAL AND FUNCTIONAL STUDIES ON THE DIGESTIVE SYSTEM OF BELLAMYA UNICOLOR (OLIVIER, 1801) IV- THE SALIVARY AND DIGESTIVE GLANDS

(WITH 8 FIGURES & 2 PLS.)

BY

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SUMMARY

The macro and micro anatomy of the salivary and digestive glands of Bellamya unicolor has been carried out in this paper. The structure of these glands and their ducts has been correlated to their functions. It has been found that the two salivary gland ducts pour their mucoid secretion into the buccal cavity. The two lobes of the digestive gland consist of a number of tubules formed of secretory, digestive and excretory cells. The two common digestive gland ducts open into the distal limb of the cardiac stomach.

INTRODUCTION

This is the fourth and last paper of a series of publications on the functional morphology of the digestive system of the Egyptian viviparid snail Bellamya unicolor. It is concerned with the structure and function of its salivary and digestive glands. A review of the literature shows that, as far as can be ascertained, there is no complete work on these glands in the viviparid snails. But similar studies on other mesogastropods as Marisa cornuarietis (LUTFY and DEMIAN,1967) and Littorina saxatilis (BOGHEN and FARLEY, 1974) are available. Therefore, the present study seems to be necessary for the elucidation of the characters of these glands in one of the members of the family Viviparidae which has not yet taken sufficient consideration. Also, it may reveal the relation between the role of these glands in nutrition and the partially ciliary feeding habit of the species under investigation. Furthermore, it may help in the comparative study between the different families of mesogastropods and prosobranchs in this respect.

MATERIAL AND METHODS

The specimens of B.unicolor used in the present work were collected, sorted out, reared and dissected as mentioned in two previous papers (BEDDINY and HAMADA, 1982 a&c). To follow the fine ducts of the digestive gland, 1% aqueous solution of light green was injected into the mouth opening of the snail during dissection.

For histological studies, and for the differentiation of mucus, the methods mentioned in a previous paper (BEDDINY and HAMADA, 1981) were adopted.

RESULTS

a- The salivary glands:

In B.unicolor, there are two lobulated salivary glands which are almost superimposed at their posterior ends lying over the dorsum of the pro-oesophagus, just behind the oesophageal pouches. They extend anteriorly from this point, become separated from each other and pass below the transverse cerebral connective to lie on the dorsolateral sides of the posterior half of the buccal mass. Each gland is yellow in colour, roughly triangular in shape from the dorsal aspect, with a posterior base and an anterior apex. Its lobules decrease in number towards its anterior end. It measures about 1.8 mm in length and 0.5 mm in greastest breadth. The upper surface of these glands is convex and their lobules are bounded to the oesophageal pouches, the pro-oesophagus, and the surrounding linings of the body cavity by connective tissue and muscular strands. A smooth fine duct about 0.5 mm long emerges from the anterior end of each gland, at a point nearly close to the end of the second third of the buccal mass. The salivary gland duct passes forwards along the dorsolateral part of the buccal mass to become embedded in its dorsal wall and to open into the buccal cavity at the anterior end of the corresponding dorsal buccal ridge.

In sections, (PL.I Figs. 1&2) each salivary gland appears consisting of a large number of branched tubules bounded together by connective tissue and their lumina are connected. The tubules are oval or rounded in cross section. Each tubule has a central lumen surrounded by a single layer of columnar secretory cells, followed externally by a very thin coat (about 4 u thick) of connective tissue with scattered circular muscle fibres. The secretory cells are 30 u in height on the average, and show great variations in form in the same tubule, apparently corresponding to the different phases in the process of elaboration of the salivary secretion. Of these forms, one can easily differentiate the elongated thin cells which are nearly full of small acidophilic granules acquiring dark blue colour with Mallory's triple stain, their nuclei are oval and basal. The second form has a pyramidal shape, large size and its core is occupied by two or three large masses of secretory spherules, taking a faint blue colour with Mallory's triple stain. The cytoplasm of this form is found at the periphery of the cell and acquires a violet colour with the previously mentioned stain. The third phase of the secretory cells is that distinguished by its swollen shape due to the increase in the amount of secretion which takes the form of vacuolated liquid secretion. The scanty cytoplasm becomes in the form of a thin peripheral film. The nuclei of the two latter forms of cells are oval, small and shifted to one side. Some of the cells of the third phase become ruptured at their apices to pour their secretion into the lumen of the tubule. The secretion at its different stages of formation assumes a voilet colour with toluidine blue, indicating its mucoid nature. It is apparently reasonable to consider the first form of cells as an early stage in the sequence of the elaboration of the salivary secretion, followed by the second and thrid forms. This is however in accordance with the belief of most of recent workers that there is only one type of gland cell in the gastropod salivary glands, whose aspect varies with different functional phases of the cells (CARRIKER and BILSTAD, 1946).

Examination of serial sections through the two salivary glands shows that no distinct duct can be distinguished between the secretory tubules. The salivary secretion of each gland passes from one tubule to the other to reach the lumen of an anterior tubule from which emerges the free salivary gland duct.

In sections, (PL. I, Fig. 3) this duct has an oval outline, a relatively wide regular lumen and thin wall near its origin. Its lumen narrows gradually as it passes forward to reach its minimum diameter at its anterior end opening into the buccal cavity. The wall of the duct consists of an inner simple epithelial lining of tall columnar cells about 20 u in height, covered externally by a thin coat, about 7 u thick, of connective tissue and circular muscle fibres. Most of the cells of the lining epithelium are ciliated and narrow with oval large nearly central nuclei containing clear nucleoli. The cytoplasm of these cells is acidophilic with few small vacuoles. Together with these cells, there are few scattered pear shaped cells with highly vacuolated and granulated cytoplasm and with broad bases and narrow apices. Their nuclei are oval, relatively small in size and shifted to one side. Also very rare mucus secreting goblet cells may be encountered in the epithelial lining of the duct. This indicates that the salviary gland ducts of B.unicolor, as it is the case in most prosobranchs, (FRETTER and GRAHAM, 1962) are not purely conducting, but also secretory.

b- The digestive gland:

It is a distinctly large bilobed brown gland, occupying most of the space of the spire especially that of the three apical whorls of the visceral mass. It is covered by the thin common integumentary covering of the visceral mass which is rich in black pigments dorsally. After the removal of the pigmented integument, the outer surface of the digestive gland shows yellow mottling, dividing it into a large number of polygonal areas. The two lobes of the gland are unequal in size and connected together ventrally by connective tissue. The small lobe is roughly ovoid in outline, about 2.3 mm in the long axis, and lies on the right side of the visceral mass below the two portions of the stomach, just anterior to the large lobe. The latter is much larger in size than the first and extends from the ventral side of the cardiac portion of the stomach backwards till the distal apex of the visceral mass, occupying most of the volume of the three apical whorls. This posterior lobe is therefore, in the form of a spirally coiled cone which measures about 10 mm long, when uncoiled. It is noticeable that the dorsal aspect of the stomach is the only part which is not covered by the tubules of the digestive gland.

The integument, covering the digestive gland and the other constituents of the visceral mass (PL. I, Fig. 4), can be microscopically differentiated into an outer thin epithelium, followed internally by a compact layer of circular muscle fibres, about 4 u in thickness, and a wide area of vacuolated connective tissue provided with blood vessels. The epithelial layer is mainly formed of flattened cells with central nuclei, interspersed with columnar and cuboidal cells which may be vacuolated and glandular or containing black granules and have lateral oval nuclei. By toluidine blue stain,it is proved that the secretion of the glandular cells has a mucoid nature. The black pigmented cells are present in large number on the dorsal part of the epithelium. The epithelial cells rest on a distinct basement membrane.

In sections, (PL. II, Figs. 5, 6&7) each lobe of the digestive gland appears consisting of a tremendous number of branched blind tubules, packed together by a connective tissue which is contin ous with that of the integument covering the visceral mass and rich in blood spaces. It is remarkable, however, that some of the connective cells are in direct contact with the digestive gland tubules, either by lying close to their outer surfaces or by sending cytoplamic processes to adhere them.

The tubules of each lobe open into fine conduits which lead into a common duct. The two common ducts of both lobes of the digestive gland open close to each other, into a small depression in the bottom of the distal limb of the cardiac stomach, close to the partition between its limbs (PL. II, Fig. 5). This small depression may correspond to the hepatic vestibule of <u>Marisa cornuarietis</u> (DEMIAN, 1964 and LUTFY & DEMIAN, 1967). It seems worthy of mention that the connections between the tubules of the digestive gland can not be distinguished in the dissected specimens, under the binocular microscope, unless a coloured solution as light green solution is injected into the alimentary tract through the mouth. In the latter case, numerous fine ductules can be seen interspersed between the tubules. As the openings of the two common digestive gland ducts into the cardiac stomach can not be traced in the injected specimen, this is probably due to the close contact between the tubules of the digestive gland and the ventral surface of the stomach.

Each tubule of the digestive gland or each hepatic tubule (PL. II, Fig. 6), has an epithelial lining of one layer of tall columnar cells arranged around an irregular lumen, and covered externally by a very thin layer of circular muscle fibres, about 2.4 u thick. Its lumen varies in size being wide or narrow, according to the state of activity of the cells, the size of the tubule and the plane of the section. According to the morphology and activity of the epithelial lining cells of the hepatic tubule,they can be differentiated into digestive and secretory cells. In some hepatic tubules, other cells which are tall, narrow and show no differentiation can be discerned. Such cells (PL. II, Fig. 6), may be regarded as precursor cells which can give rise to any of the two types of cells mentioned before. A review of the literature has shown that, there is frequent confusion, regarding the identity and designation of the corresponding hepatic tubule elements of the different gastropods, and the functions attributed to them.

The digestive cells (PL. II Fig. 6) correspond to the gland cells of PRASHAD (1925), the absorbing cells of GRAHAM (1932), the digestive cells of CARRIKER and BILSTAD (1946), CLELAND (1954), PAN (1958), FRETTER and GRAHAM (1962), and BOGHEN and FARELY (1974), the hepatic cells of MICHELSON (1955), the digestive and excretory cells of LUTFY and DEMIAN (1967) and the principal cells of MARTOJA and THIRIOT - QUIEVREUX (1975) in a number of gastropods. The digestive cells of the species under investigation, are by far, the most abundant and largest elements in the epithelial lining of the hepatic tubule. They are tall and broad columnar or cone-shaped with domed distal apices and flat bases,resting on a thin and distinct basement membrane. They vary in length within one and the same tubule according to the state of activity, ranging from 37.2 to 42 u in length. They usually have acidophilic cytoplasm and basal oval or spheroidal nuclei with distinct nucleoli. In some cases,especially when the digestive cell is highly charged with the products of digestion, the nucleus become irregular in shape due to the depressions and identations of its membrane. The cytoplasm shows different degrees of vacuolation and its contents take different forms, sizes and colours according to the activity phases. For this reason, the activity of the digestive cells can be categorized into three phases: absorption, digestion and excretion. Similar phases of the digestive cells have been described in other gastropods by MORTON (1955), MERDSOY and FARLEY (1973) and BOGHEN and FARLEY (1974). It is noticeable that there are intermediate stages between the three phases.

In the case of the phase of absorption, the digestive cells appear tall columnar with their apical two thirds occupied by vacuoles. The contents of the latter acquire a light blue colour with Mallory's triple stain and a red colour with haematoxylin-eosin stain, indicating their weak acidophilic nature. The basal regions of the cells, on the other hand, contain minute granules which do not take the colour of any of the stains used.

The digestive cells, in the phase of digestion, become cone-shaped and distended because they are packed with vacuoles. The contents of these vacuoles show less intense colour with the previously mentioned stains than those of the first phase. It is remarkable that the size of the vacuoles increases towards the bases of the cells. This is apparently due to the fusion of small vacuoles.

In the third phase (PL. II, Fig. 7), the digestive cells appear short, pyramidal or cone shaped. They are rarely seen in sections and characterized by the reduction in the number of vacuoles which become concentrated at their apical halves and rarely at their bases. The distinct large vacuole of each cell contains a characteristic big yellowish body which is probably formed by the accumulation of small spherules. The excretory bodies usually retain their natural colour and exist inside colourless vacuoles. They are apparently released into the lumina of the hepatic tubules after the rupture of the apical membranes of the cells containing them.

The secretory cells (PL. II, Fig. 7) , in the present species correspond to the gland cells of PRASHAD (1925), the secretory cells of ANDREWS (1965), the ferment cells of GABE (1966) and the secretory cells of BOGHEN and FARLEY (1974). In B.unicolor, the secretory cells are less numerous than the digestive cells. They are tall and broad columnar cells about 44.4 u long and 8.4 u broad. They may be present in the form of a number of adjacent cells within the hepatic tubules. They are characterized by the presence of a great amount of large secretory granules filling most of their central spaces. The relatively few cytoplasm is weakly acidophilic and found at the periphery of the cell, between the granules and around the basal ovoid nucleus. The latter presents two or three clear central nucleoli. Some of the secretory cells have their apices ruptured and their contents protruding into the lumen of the hepatic tubule.

The precursor cells (PL. II, Fig. 6) are distinctly narrow, being about 3.6 u broad; with clear homogeneous acidophilic cytoplasm and central elliptical nucleus. Their bases contain few small granules. They are singly scattered between the other cells of the epithelial lining of the hepatic tubule. It is likely, however, to postulate that such cells can be transformed into any of the other two main types of cells of the tubule.

The histological structure of the basic unit of the digestive gland of B.unicolor, shows that in the present prosobranch snail, as in many other gastropods, there is extracellular and intracellular digestion. The extracellular digestion takes place by the enzymes secreted by the secretory cells in the lumen of the hepatic tubules and reaching the lumen of the cardiac stomach. The intracellular digestion occurs within the digestive cells. Moreover, absorption takes place by the latter cells and it is reasonable to assume, that the distribution of the absorbed digested fluid may be performed by the aid of the connective tissue cells lying close to the outer surface of the tubules. In addition,the waste products of the metabolic process are accumulated in the digestive cells at the excretory phase, to be ejected into the lumen of the tubules. It is probable, however, that some of the excretory material reaches the latter cells through their bases which may come in contact with certain connective tissue cells or with blood spaces in the surrounding connective tissue. Similar postulations were advanced by ANDREWS (1965) in Pomacea canaliculata and by LUTFY and DEMIAN (1967) in Marisa cornuarietis.

The wall of the two common digestive gland ducts, (PL. II, Fig. 8), and their tributaries can be easily distinguished from that of the hepatic tubules by its histological structure. The first consists of an outer muscular coat surrounding a highly folded epithelial lining of almost ciliated columnar cells. The muscular coat is made up of smooth muscle fibres, arranged in two layers; an inner circular layer, about 5 u thick and an outer longitudinal one, about 2.4 u thick. The columnar cells of the epithelial lining have nearly an equal height of about 25 u, and rest on an undulating basement membrane to form the folds. Most of these cells have granulated acidophilic cytoplasm and oval central nuclei. Dispersed between these cells, there are swollen cells with large colourless vacuoles and laterobasal spindle shaped nuclei. It is noticeable that some of the latter cells open into the lumen of the duct. The apical part of most cells contains compact acidophilic cytoplasm and mostly carries short cilia.

The lumen of the common digestive gland duct and its branches is usually, in normal snails, occupied by coarse and fine granules acquiring red colour with Haematoxylin-eosin and blue colour with Mallory's triple stain. Also they give positive results with PAS, Bromophenol blue and Sudan black preparations, indicating that they are formed of carbohydrates, proteins and lipids.

It is noted that the hepatic tubules open directly into the ductules without the intervention of clear non-secretory necks. Also some of the hepatic tubules open directly, in the same manner, into the two common digestive gland ducts. Such system of ductules and ducts emphasises the commonly known fact that it carries the enzymatic secretion and excretory products from the lumina of the hepatic tubules to the cardiac stomach and the partially digested food particles in the reverse direction.

DISCUSSION

In B.unicolor, the salivary glands are well developed and appear to participate in the secretion of mucus necessary for the lubrication of the radula and for connecting the collected particles together. Also they probably secrete certain digestive substances attacking carbohydrates as it is the case in other herbivorous prosobranchs (YONGE, 1932) and pulmonates (KRIJGSMAN, 1925 & 1928).

The digestive gland and B.unicolor, as in some of the mesogastropods as in Marisa cornuarietis (LUTFY and DEMIAN, 1967) and Littorina saxatilis (BOGHEN and FARLEY, 1974) secretes enzymes for extracellular digestion in the stomach, performs intracellular digestion, and participates in absorption and excretion.

As a result of this study it becomes clear that in spite of the adaptation of this snail for ciliary feeding via the mantle cavity with its food groove, filamentous gills and mucus-secreting cells, yet it retains the main characters of the digestive system of herbivorous mesogastropods. Such characters are the presence of well developed salivary glands, digestive gland, and small oesophageal pouches, and the absence of the crystalline style. Thus, the habit of ciliary feeeding in the Egyptian viviparid species, as in Viviparus viviparus (COOK, 1949) would seem to be a relatively recent acquisition.

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EXPLANATION OF PLATES

Fig. 1: Photomicrograph of T.S. through the salivary glands.
Fig. 2: Photomicrograph of an enlarged section of a follicle of the salivary gland.
Fig. 3: Photomicrograph of a part of T.S. through the salivary gland duct.
Fig. 4: Photomicrograph of T.S. of the visceral mass showing the integument of the digestive gland and the visceral mass.

PL. II

Fig. 5: Photomicrograph of T.S. of the visceral mass passing through the two openings of the two common digestive gland ducts into the distal limb of the cardiac stomach.
Fig. 6: Photomicrograph of a section through the digestive gland tubule, showing the precursor and digestive cells.
Fig. 7: Photomicrograph of a section through the digestive gland tubule, showing the secretory and excretory cells.
Fig. 8: Photomicrograph of a part of T.S. through the digestive gland duct showing its structure.

KEY TO LETTERING OF FIGURES

ci.co.ep. = ciliated columnar epithelium; c.m.l. = circular muscle layer; co.c. = columnar cell; c.t. = connective tissue; c.t.c. = connective tissue cell; c.t. & m.f. = connective tissue and muscle fibres; di.g.c. = digestive gland cell; 2 di g.d. = two common digestive gland ducts; ex.c. = excretory cell; f.c. = flattened cell; l.m.l. = longitudinal muscle layer; lu. = lumen; pr.c. = pear shaped cell; pe.c. = precursor cell; pl. c.st. = proximal limb of cardiac stomach; p.c. = pyramidal cell; sec.c. = secretory cell; t.c. = thin cell of salivary gland; tb.s.g. = tubules of salivary gland.

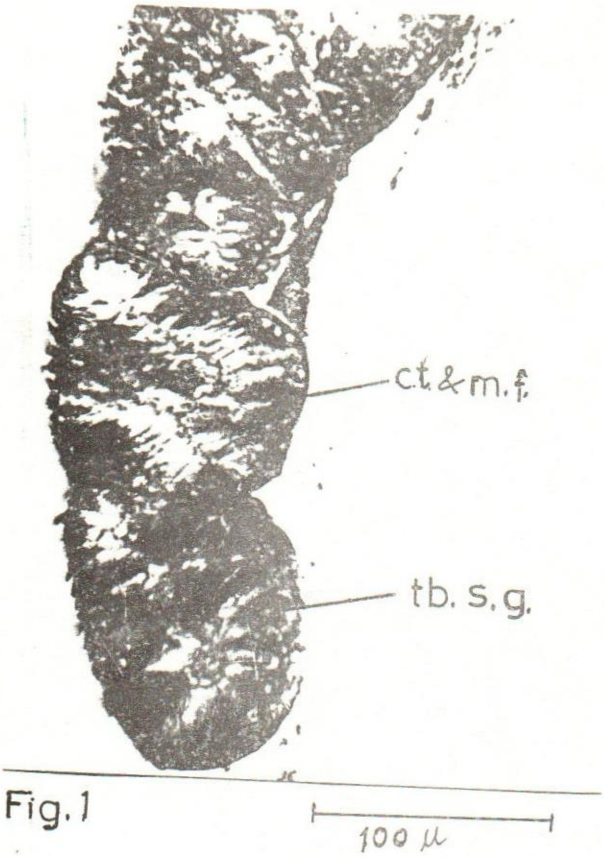

Fig. 1

Fig. 2

Fig. 3

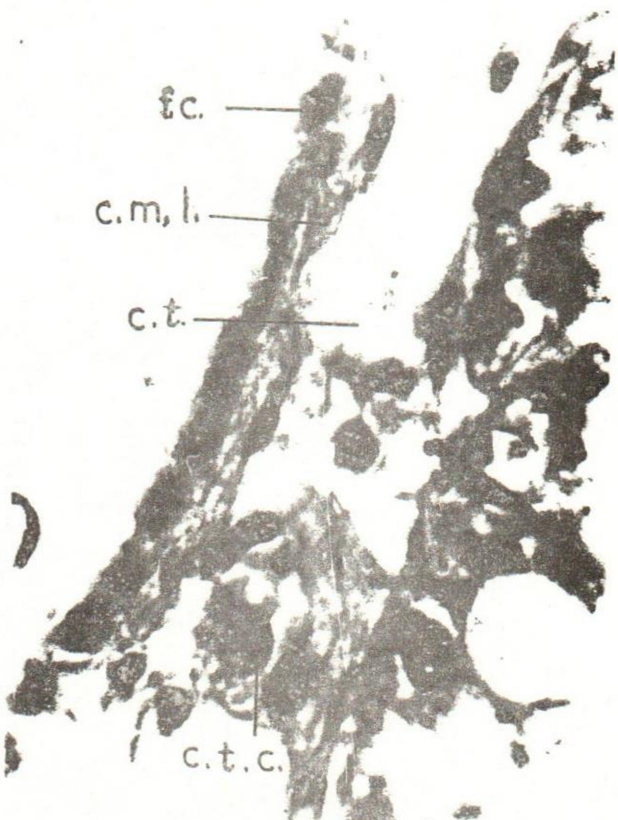

Fig. 4

Fig. 5 220 μ

Fig. 6 55 μ

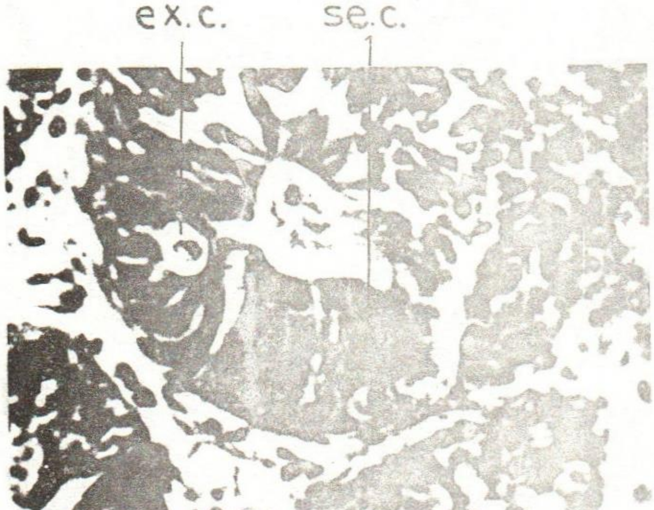

Fig. 7 40 μ

Fig. 8 30 μ