

AN ABSTRACT OF THE THESIS OF

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Title: AN ULTRASTRUCTURAL STUDY OF TENTACLE
DEVELOPMENT IN CORDYLOPHORA LACUSTRIS

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Morphological changes which occur during tentacle formation have been described in the colonial athecate hydroid Cordylophora lacustris. These changes involve an outpocketing of mesoglea into a finger-like extension of the hydranth. Gastrodermal cells line the inside of this extension of mesoglea while ectodermal cells cover the outside. Electron micrographs reveal the presence of several distinct cell types. Their function and possible role in tentacle differentiation is discussed.

An Ultrastructural Study of Tentacle
Development in Cordylophora lacustris

by

Michael Gene O'Rand

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AN ULTRASTRUCTURAL STUDY OF TENTACLE DEVELOPMENT IN CORDYLOPHORA LACUSTRIS

I. INTRODUCTION

Developmental processes concerning the hydrozoan coelenterates, have been the object of numerous investigations, yet only within the last several years have ultrastructural studies been conducted to lay the morphological groundwork necessary for an understanding of the processes and changes that occur during development. Questions such as those being asked by Clarkson (1969), as to whether or not regeneration in hydra is based upon the existence of long term messenger ribonucleic acid, must be based on an understanding of the morphological events occurring during this time. Similarly, developmental processes in colonial hydroids must also be based on a knowledge of the animal's normal morphology. Thus, if the events responsible for the development of growth patterns and numerous specialized structures (i. e. tentacles, gonophores, dactylozooids, etc.) found in colonial forms are to be explained, then a firm morphological baseline must exist from which to work.

In studying a particular differentiation process the ultimate aim is to understand the events occurring from the time the genetic message is sent out until the adult structure is complete. Before events on the molecular level can be characterized however, those tissues

involved in the process must be characterized and their role understood. The formation of a tentacle by the hydranth of a colonial hydroid is perhaps one such differentiation process which might lend itself to analysis first on the morphological level and secondarily on a biochemical level. The present study is designed to describe the changes in morphology which occur during normal tentacle development in Cordylophora lacustris Allman.

Cordylophora lacustris, first described by Allman (1853), is a brackish-water colonial athecate hydroid which has been the subject of many developmental studies, including those of Beadle and Booth (1938), Diehl and Bouillon (1966), Fulton (1963), Kirschner (1934), Kuhn (1914), Moore (1952, 1952), Morgenstern (1901), Pauly (1902), Penzlin (1957), Schulze (1871), Tessenow (1959), and Zwilling (1963). Ultrastructural studies have been undertaken by Jha and Mackie (1967) and Overton (1963). These were concerned with nerve elements and intercellular connections respectively.

II. MATERIALS AND METHODS

The colonies used in the present study, collected at Woods Hole, Massachusetts, were provided by Dr. R. L. Miller. These colonies are grown in a controlled environment following the optimum growth conditions outlined by Fulton (1960). The colonies have been growing in the laboratory for approximately three years and have been sub-cultured repeatedly. They are grown on 1" x 3" glass microscope slides in 250 cc pyrex beakers in a constant temperature bath at 22°C. The pH of Fulton's culture solution was adjusted to 7.3 but light and oxygen tension were not controlled. Light was the normal daily cycle for Oregon. Each colony except those being examined after 48 hours starvation was fed Artemia nauplii every morning. Fresh batches of Artemia were hatched in sea water every other day and washed in distilled water before being given to the colonies. The entire colony was fed in such a way to insure that each individual got at least one Artemia; most received five or six. This was determined by visual observation. After feeding, the culture solution was changed and then changed again six hours later. The procedure was repeated at each feeding.

In his studies on mitosis in hydra Campbell (1967b) showed that there was a definite increase in the number of dividing cells of all cell types after feeding. Since feeding is also likely to affect mitosis

and subsequent development processes in Cordylophora, the examination of all animals in this study was relative to the feeding time (time zero). Individual animals in different stages of tentacle development were examined at four or five hours and 48 hours after feeding. Tentacle development has been arbitrarily divided into three stages: stage I - the tentacle bud, stage II - the immature tentacle, stage III - the adult tentacle. For each time period four to eight animals at each stage were cut from seven different colonies growing under controlled conditions.

The animals were allowed to relax in a small dish and then fixed in cold 3% glutaraldehyde in 0.2 M phosphate buffer at pH 7.3 for two hours. They were then washed in buffer several times and stored in cold buffer overnight. Following post fixation in 1% osmium tetroxide for one hour, they were then dehydrated in a graded series of ethanol: 50% for one hour, 70% for one-half hour, two changes of 95% for one hour, and three changes of 100% for a total of one hour. Specimens were given 30 minutes in propylene oxide with one change and then a 1:1 mixture of propylene oxide and Araldite. The Araldite embedding procedure was according to Luft (1961). The animals were left overnight in the 1:1 mixture and then flat embedded in aluminum pans at 60°C for 24 hours. In each step during the preparation procedure an adult hydranth fixed with tentacles fully extended was carried along to insure that the tissues were not damaged. Rough

handling or careless pipeting resulted in tentacles becoming detached from the hydranth.

The specimens were cut on a Porter-Blum microtome and thin sections mounted on Formvar covered copper grids (75 mesh). Grids were stained with uranyl acetate and Millonig's lead hydroxide (1961) and examined in an RCA EMU 3H microscope. Thick sections were cut approximately one-half microns and stained with a modified method of Schantz and Schechter (1965). Solutions of ferric ammonium sulfate, hematoxylin, and safranin O were placed in separate Coplin jars and kept in the oven at 65° C. Slides with thick sections were immersed for 30 minutes in each solution. They were rinsed for ten seconds in distilled water and dried in the oven between each solution. The results clearly differentiate nucleus, nucleolus, cell membranes, mesoglea, lipid droplets from other inclusions and vesicles, and nematocysts. Electron micrographs were printed on Kodak F-5 paper and light micrographs, taken through a Zeiss phase contrast scope with Panatomic-X film, were printed on Kodak Polycontrast paper.

III. OBSERVATIONS

Examination of animals at different times after feeding revealed no significant differences in tentacle development stages. The only obvious difference was in the amount of ingested material present in the digestive cells. Therefore the following observations apply to all time periods.

The Tentacle Bud

The tentacle bud stage can be most readily described as an immature hydranth with a low ridge of cells below the hypostome. The distal tentacles, which are the first to differentiate, appear as small projections on this ridge (Fig. 1, 23). In this condition the coelenteron of the stem or stolon is confluent with that of the immature hydranth and extends for approximately two-thirds of its length (Fig. 2, 3). In medial longitudinal sections the ridge can be seen as a bulge slightly distal to the coelenteron cavity (Fig. 3, 4). The tentacle will differentiate from this bulge. Medial sections of this hydranth show the cell types present to be morphologically similar to those seen in the adult hydranth.

Hydranth Ectoderm

1. Epitheliomuscular cells. Epitheliomuscular cells (Fig. 5)

are characterized by a large nucleus which may have a nucleolus and often a protein body as described by Mackie et al. (1964). Usually numerous vacuoles are present, with the nucleus occupying the central portion of the cell. The nucleus is usually surrounded by a series of small peripheral vacuoles. The outer nuclear membrane appears studded with ribosomes while mitochondria, golgi, and dilated rough endoplasmic reticulum are found throughout the cytoplasm. Numerous inclusions are often present in the proximal portions of the cell, as well as lipid droplets and heterogeneous granules similar to those seen in the gastroderm. The basal portions of the cells are characterized by myofibrils adjacent to the mesoglea. At some points they appear to insert into the mesoglea. The myofibrils are usually seen running parallel to the long axis of the animal.

Intercellular attachments between epitheliomuscular cells (Fig. 5, 6) similar to those described by Overton (1963) in the epidermis of the stolon, are present. They appear as thickenings of the adjacent cell membranes. In accordance with Overton's findings these desmosomes have not been seen in areas where the cell surface would be expected to be metabolically active (i. e. the tentacle bud).

The external surface of the epitheliomuscular cell is characterized by small finger-like projections of cytoplasm which are directly beneath the outer acellular layer. The acellular layer surrounds the

entire hydranth and is continuous with the perisarc of the stem.

2. Interstitial cells. Interstitial cells (I-cells) are cells of a non-epitheliomuscular nature found in the ectoderm. Cells of similar description are occasionally found in the gastroderm (Fig. 6, 7, 8, 9). Interstitial cells can be characterized by their abundant mitochondria, sparse dilated endoplasmic reticulum, and free ribosomes. The free ribosomes usually give the cytoplasm of the I-cell a darker appearance than that of the adjacent epitheliomuscular cells. Figures 6 and 7 show the manner in which I-cells are surrounded by the processes of epitheliomuscular cells. Interstitial cell nuclei are small, centrally located, and according to Mackie et al. (1964) lack a protein body. Generally the cytoplasm of I-cells is not vacuolated and few granules or inclusions are ever seen. Contrary to the observations of Jha and Mackie (1967), Cordylophora hydranths do have interstitial cells.

Some I-cells may be nerve cells as described by Jha and Mackie (1967), but this cannot be determined without careful serial sectioning to locate a sensory projection or neurite and comparison with silver stained material. Although not numerous, these small compact cells (approximately five microns in diameter) occur adjacent to the mesoglea and may occur in clusters or nests (Fig. 10). They are most often seen near tentacle-hydranth junctions in the mature hydranth.

3. Nematocysts. Developing and mature nematocysts have

been observed scattered throughout the hydranth ectoderm and gastroderm (Fig. 4, 7, 8, 10, 12). Developing nematocysts (cnidoblasts) are most often seen in the interstitial cell clusters near tentacle-hydranth junctions (Fig. 10). The cnidoblast appears essentially the same as the interstitial cell, having mitochondria, rough endoplasmic reticulum and few granules or inclusions. The nucleus is usually distorted somewhat due to the developing nematocyst.

Hydranth Gastroderm

The hydranth gastroderm of the tentacle bud stage showed cell types similar to those found in the adult hydranth, as mentioned previously. However, the mouth does not completely differentiate until after tentacle development so that distally, gastrodermal cells appear in close apposition to one another. Some of the cells appear as digestive cells while others appear secretory (Fig. 11).

1. Digestive cells. A digestive cell (Fig. 12, 13, 14) is characterized by its large nucleus which is usually surrounded by small peripheral vacuoles. The outer nuclear membrane is studded with ribosomes. In medial sections numerous microvilli and flagella are also characteristic of digestive cells (fig. 13, 14). The cytoplasm is often seen as thin strands surrounding large vacuoles which may be filled with various ingested material depending upon the nutritive state at fixation. Figure 9 shows the basal portions of digestive cells

where each large vacuole is separated from the adjacent vacuole by the cytoplasm of two different cells. The cytoplasm contains rough endoplasmic reticulum, mitochondria, and golgi. Granules of varying density may be seen in the basal regions of digestive cells in the proximal regions of the hydranth where it appears that large and small granules are connected or are coalescing (Fig. 9). In the apical regions of the cell (Fig. 13, 14) and the more distal regions of the hydranth (Fig. 11), digestive cell nuclei appear surrounded by granules of varying density. Intercellular connections are often seen between gastrodermal cells in the more stable regions of the hydranth (Fig. 12, 13).

2. Secretory cells. In the adult hydranth numerous types of secretory cells may be present as noted in other hydroids by Bouillion (1966), Rose and Burnett (1968), and Brock, Strehler, and Brandes (1968). However, in the hydranths investigated during tentacle development, the most obvious secretory cells were those characterized by a small nucleus, compact cytoplasm filled with dilated rough endoplasmic reticulum often seen in stacks (Fig. 15), and zymogen-like granules. This cell type was never observed to have microvilli or flagella. In the tentacle bud hydranth many secretory cells appear as in Figure 11. Here they are situated at the apex of the hydranth gastroderm and appear smaller than those in the adult hydranth (Fig. 15). There are also some small compact cells seen

in the gastroderm which are not easily identified. They may be termed interstitial as in Figure 6 or secretory as in Figures 7 and 8. They are surrounded by cytoplasmic processes of digestive cells much as interstitial cells in the ectoderm are surrounded by epitheliomuscular cell processes. Their exact role is not known. Figure 12 shows another small cell which is occasionally seen in the gastrodermis. Its role is also unknown.

Mesoglea

The mesoglea present in the tentacle bud hydranth courses its way between the gastroderm and ectoderm as in the adult. It can be characterized by its fibrillar nature, low electron opacity, and thin projections into both gastroderm and ectoderm (Fig. 5, 6, 7, 8, 9). Small particles can be seen scattered throughout the fibrils which appear to run parallel to the long axis of the hydranth.

Tentacle Bud

In the electron microscope the tentacle bud (Fig. 4, 16) is seen as an outpocketing of the mesoglea filled with gastroderm cells on the inner side and ectoderm cells on the outer side. The ectoderm of this bud region is morphologically similar to hydranth ectoderm. The epitheliomuscular cells in the bud region appear vacuolated but are often filled with numerous inclusions.

The gastroderm cells seem to be morphologically the most similar to hydranth digestive cells although few microvilli or flagella are ever seen. Large numbers of ribosomes are seen in the cytoplasm, but most characteristic is the presence of granules of variable density. The variation in density within these granules (Fig. 16) appears like that of the granules seen in hydranth digestive cells (Fig. 12, 13, 14) and may represent in part, the result of compression during sectioning. They have a halo-like periphery which appears in later stages of tentacle development to be bounded by a membrane. The interior of these granules is less dense than the surrounding dense band directly inside the halo-like periphery. Their heterogeneity can be compared to the more homogeneous looking zymogen-like granules of the secretory cell seen in Figure 15. Some of the cells described under hydranth secretory cells might also be in the bud region but they are not immediately obvious. Secretory cells have not been seen in the later tentacle gastroderm.

The Immature Tentacle

In the hydranth of the immature tentacle the ridge of cells below the hypostome has enlarged considerably and four small tentacles protrude just below the hypostome (Fig. 17, 23). The hydranth cell types are as described in the tentacle bud hydranth. The immature tentacles are characterized by a further outpocketing of mesoglea

away from the hydranth. The rounded apex of the previous stage is now quite pointed (Fig. 18). In a median section the hydranth gastroderm is confluent with the tentacle gastroderm (Fig. 19a), but in sagittal sections above and below the median the mesoglea separates the hydranth and tentacle gastroderm (Fig. 19b).

Tentacular Ectoderm

1. Epitheliomuscular cells. Epitheliomuscular cells present in the tentacular ectoderm are morphologically similar to those of the hydranth (Fig. 18). The nucleus is generally centrally located among numerous vacuoles of various size. It may possess a protein body as in Figure 18. Dilated rough endoplasmic reticulum is present and mitochondria are scattered about the cytoplasm.

The basal myofibrils present in the hydranth cells do not appear prominent in the immature tentacle epitheliomuscular cells. The outer surface of the ectodermal cells is covered with an acellular material which is continuous with that of the hydranth.

2. Interstitial cells. Numerous non-epitheliomuscular cells are scattered along the mesoglea of the immature tentacle. Figure 18 shows several at the tip of the immature tentacle. Some may differentiate into nematocysts as reported by Kirchner (1934) or into some other cell type while some may be nerve cells. The sensory hair seen in Figure 18 appears to be of the type described by Jha and

Mackie (1967) as being characteristic of nerve cells. Furthermore, tubules can be seen running through the cell body. Basal bodies can be seen in adjacent cells suggesting other possible sensory hairs in the immature tentacle tip.

3. Nematocysts. Developing and mature nematocysts appear in the immature tentacle in much the same manner as interstitial cells. They do not seem to be clustered or oriented toward the surface at this stage.

Tentacular Gastroderm

The tentacular gastroderm cells of the immature tentacle appear similar to those in Figure 4 or those hydranth gastroderm cells in Figure 11. The nucleus is relatively large and generally close to the median plane of the tentacle. It is surrounded by small peripheral vacuoles and the outer nuclear membrane may be studded with ribosomes. The cytoplasm has the characteristic vesicles of variable density which have been previously described. Some of the granules may be seen surrounded by a membrane and free inside the vacuoles (Fig. 19a, 19b). The cytoplasm also has numerous free ribosomes as well as rough endoplasmic reticulum and mitochondria (Fig. 19a, 19b). At this stage there is considerably more gastroderm present due to the larger mesogleal outpocketing. It appears quite compacted within the outpocketing as the vacuoles are generally small.

Mesoglea

The mesoglea is continuous with hydranth mesoglea and similar in its fibrillar structures and low electron opacity. As was previously mentioned the mesoglea does not cut off the tentacle gastroderm from the hydranth completely since a median section shows the hydranth gastroderm to be confluent with that of the tentacle. Figure 18 shows the distal end of the mesoglea in the tentacle tip.

The Adult Tentacle

The adult tentacle is shown in Figures 20 and 23. The four most distal tentacles directly below the hypostome were those investigated in this study.

Tentacular Ectoderm

The ectoderm of the adult tentacle contains the cell types as described for the immature tentacle. Figure 21 shows a medial longitudinal section of a tentacle in an advanced state of maturation. The adult tentacle is identical to this but of considerably greater length. The distal end is blunt and knob-like while the ectoderm's exterior surface is scalloped. Each scallop is filled with epithelio-muscular cells and nematocysts. They can be seen as black spots along the tentacle in Figure 20. Figure 21 also shows nematocysts

and interstitial cells scattered along the length of the tentacle. Characteristic of the adult tentacle's epitheliomuscular cells are the well developed myofibrils adjacent to the mesoglea (Fig. 22).

Tentacular Gastroderm

The tentacular gastroderm is as described previously for the immature tentacle. The gastroderm seen in Figure 21 differs from that in the immature tentacle only in its ladder-like appearance. The gastroderm vacuoles become larger and the cells appear less closely packed as they stretch out along the tentacle. The vacuoles are surrounded by a thin band of gastrodermal cytoplasm (Fig. 22). Each rung in the ladder usually consists of one or two large nuclei and their associated cytoplasm.

Mesoglea

The mesoglea seen in the adult tentacle (Fig. 21) is as described previously. The myofibrils of the epitheliomuscular cells can be seen adjacent to the mesoglea (Fig. 22). The mesoglea of the tentacle is continuous with the hydranth mesoglea except in medial sections where it is proximally discontinuous. Medial sections of the distal part of the tentacle indicate that the mesoglea is continuous in this region.

IV. DISCUSSION

The stages in the formation of a tentacle have been described in terms of morphological changes that occur during the differentiation process. The process can be thought of as an outpocketing of hydranth mesoglea into a finger-like extension from the hydranth.

The hydranth gastrodermal cells seen in the earliest mesogleal outpocketing certainly have the general morphological characteristics of the hydranth digestive cells. The fact that these cells are in the outpocketing surrounded by other cells and do not have a free surface facing the coelenteron could account for the reduced appearance of microvilli and flagella. This would also account for their lack of food inclusions. Rather their inclusions tend to be lipid or membrane-bounded granules of a heterogeneous nature. It is possible that these granules are in fact manufactured by these cells at an earlier stage prior to their arrival at the tentacle site. The dilated rough endoplasmic reticulum of these cells would certainly indicate that active synthesis is occurring.

As the outpocketing lengthens it would seem that more gastrodermal cells would be added to the tentacle base. Although there is no evidence for this in Cordylophora, evidence from other hydroids makes this plausible. The migration of epitheliomuscular cells along the mesoglea has been shown in Hydra by Shostak and Globus (1966).

The migration of gastrodermal cells from the hydranth into the tentacle during development and later in its adult state has been shown in Hydra by Shostak (1968). Working with Tubularia croeca, Campbell (1967a) reported that "at the base of the distal tentacle whorl the gastrodermal core of the tentacles runs along the hydranth mesolamella." This investigation has established that the tentacular gastroderm is continuous with the hydranth gastroderm during all stages of tentacle development in Cordylophora. Furthermore, mitotic studies by Campbell in Hydra (1967b) and Tubularia and Hydractinia (1967a) indicate that there is little or no mitotic activity in the tentacle itself but rather at its base.

Perhaps the most interesting question which can now be asked is: What is responsible for the initial outpocketing of mesoglea? If one assumes the constancy of the gastrodermal cell population as Shostak (1968) reports for Hydra, then the initial outpocketing may be due to a specific biochemical event occurring in certain cell types. Alternatively, the physical pressure of cells packing into the hydranth's apex by continual distal migration could be responsible for such an outpocketing. Localized mitotic activity has been tentatively ruled out because no gastrodermal mitotic activity in the bud was ever observed. In any event, it seems most likely that the gastrodermal and ectodermal cells in the bud region influence the mesoglea in some manner. Indeed, the synthesis of mesogleal protein has been

suggested by Shostak, Patel, and Burnett (1965) as possibly responsible for the determination of form in Hydra.

The heterogeneous granules appearing in the tentacle gastroderm cells in the bud, which are similar to those seen in hydranth digestive cells, seem to warrant further investigation. Since they are seen free in cellular vacuoles in later stages of tentacle development, their function may be of importance in the process of differentiation.

The cluster of small compact cells in the tentacle tip in Figure 18 would also seem to warrant further investigation. This cluster may influence the development of the differentiating cells of the immature tentacle in some manner.

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APPENDIX

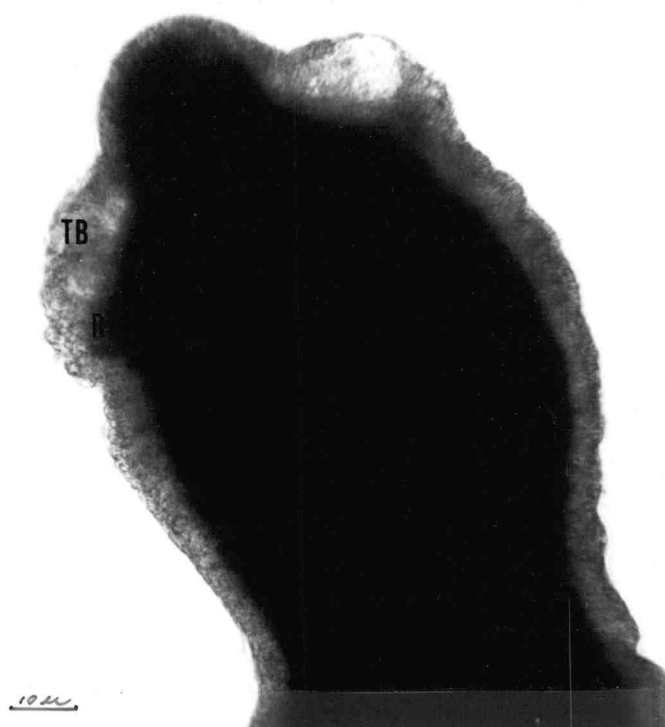
Figure 1. Stage one hydranth showing the low ridge of cells (R) below the hypostome and the tentacle buds (TB). 875 X

Figure 2. Light micrograph of stem-hydranth junction showing the coelenteron (C) cavity lined with microvilli of the digestive cells. 7900 X

LIST OF ABBREVIATIONS

BB	Basal body
C	Coelenteron
D	Digestive cell
E	Ectoderm
Ep	Epitheliomuscular cell
Fl	Flagellum
G	Gastroderm
GI	Gastrodermal inclusion
G	Golgi
HG	Heterogeneous granules
Ia	Intercellular attachments
I	Interstitial cell
R	Low ridge of cells below hypostome
M	Mesoglea
Mv	Microvilli
Mi	Mitochondria
My	Myofibrils
Ne	Nematocysts
No	Nucleolus
N	Nucleus
A	Outer acellular layer
PB	Protein body
RER	Rough endoplasmic reticulum
S	Secretory cell
TB	Tentacle bud
X	Undetermined cell type
V	Vacuole
Z	Zymogen-like granule

1



2

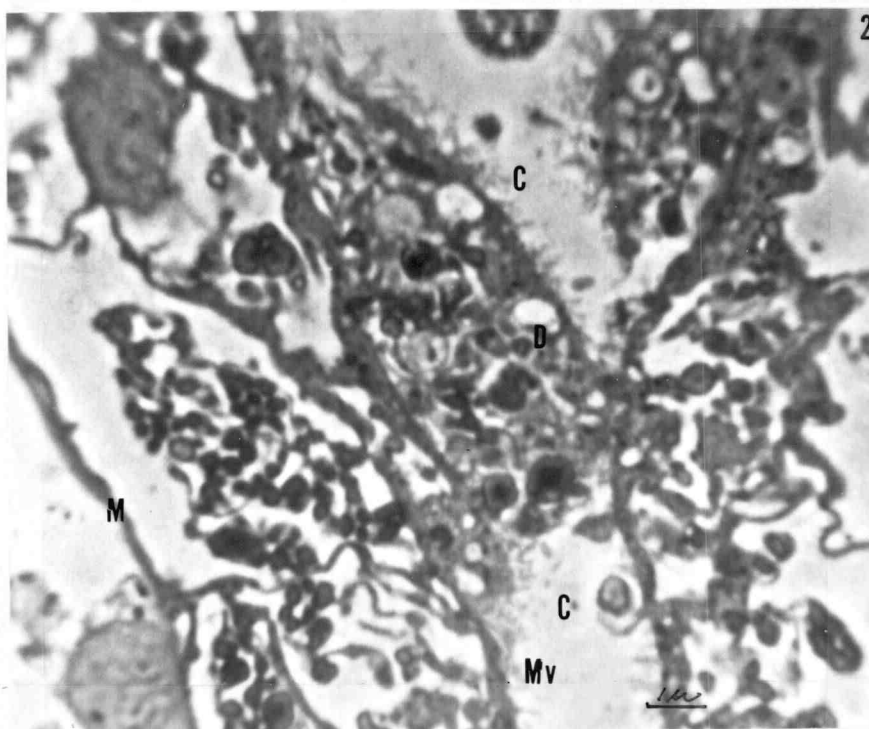


Figure 3. Light micrograph of a medial longitudinal section of the tentacle bud hydranth. The tentacle bud (TB) is distal to the coelenteron and cells appear to be packed into both the tentacle bud and the hydranth's apex. 3400 X

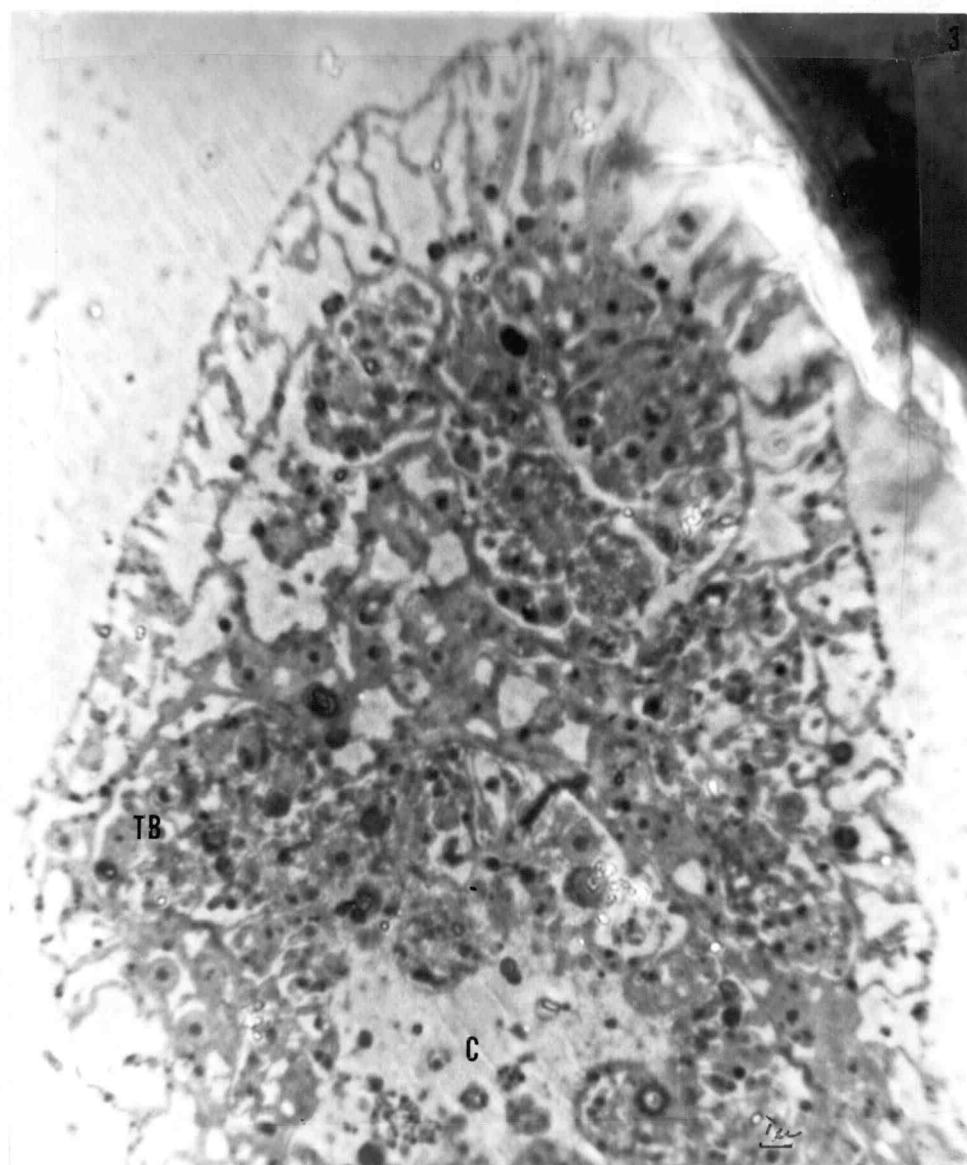


Figure 4. Electron micrograph of a medial longitudinal section of the tentacle bud. Heterogeneous granules (HG) can be seen in the gastroderm adjacent to the mesoglea.
4900 X

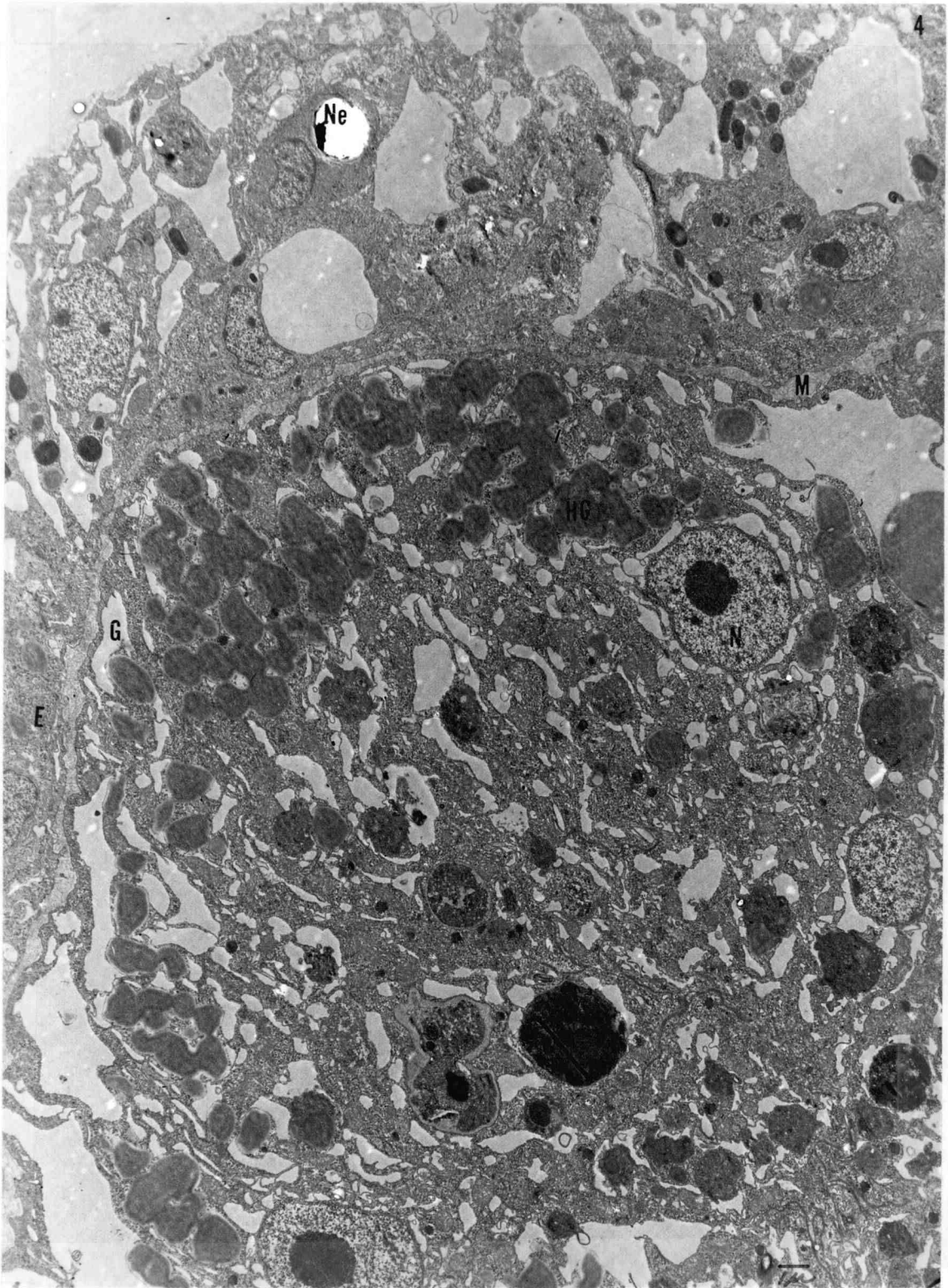


Figure 5. Epitheliomuscular cells of the hydranth ectoderm.
Myofibrils may insert into the mesoglea (arrow).
14,300 X



Figure 6. Interstitial cells of the hydranth ectoderm and gastroderm which are adjacent to the mesoglea and surrounded by the processes of adjacent cells. 9600 X

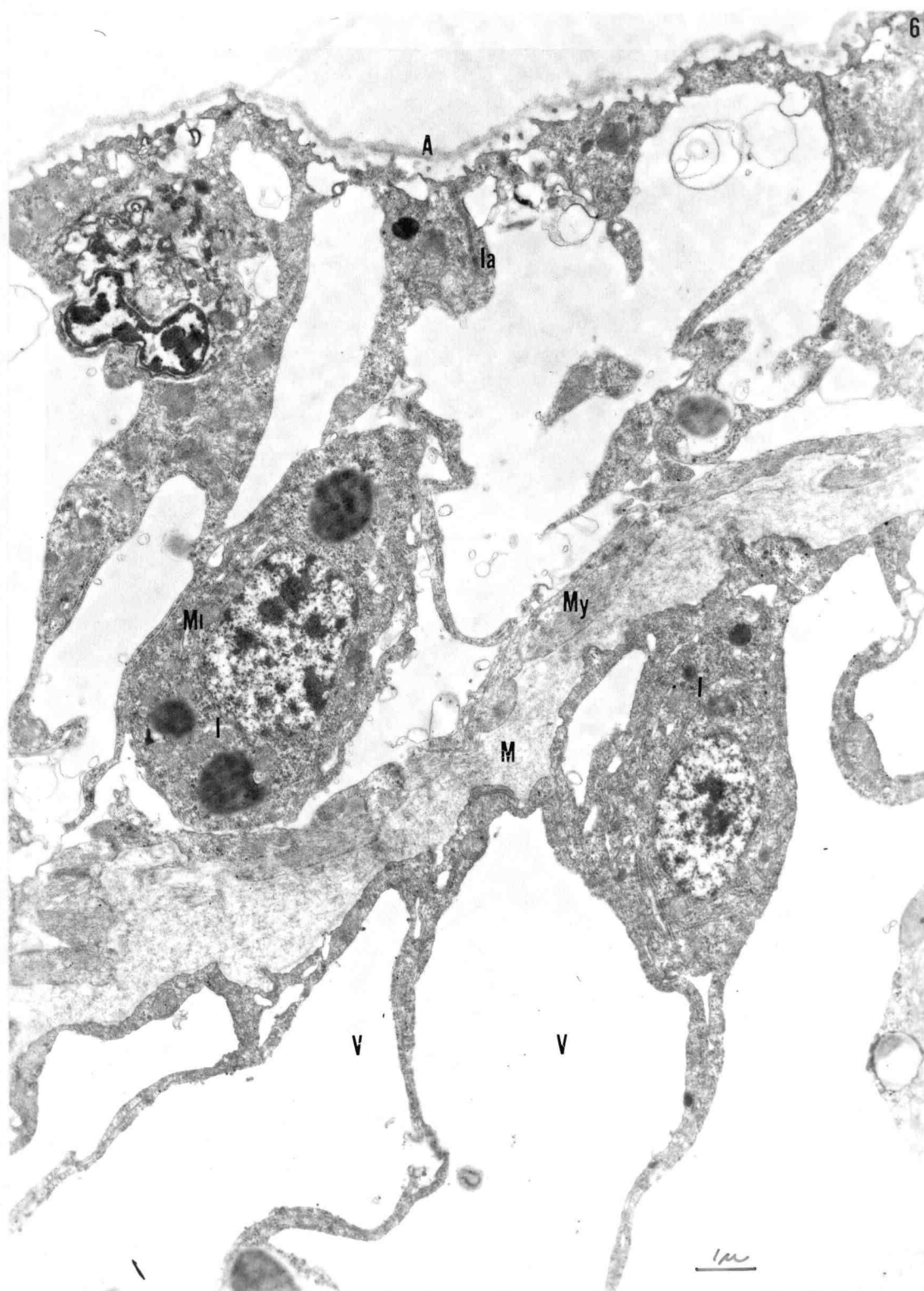


Figure 7. Three interstitial cells in the ectoderm and two secretory cells in the gastroderm. Free ribosomes can be seen in the interstitial cell cytoplasm. 9600 X

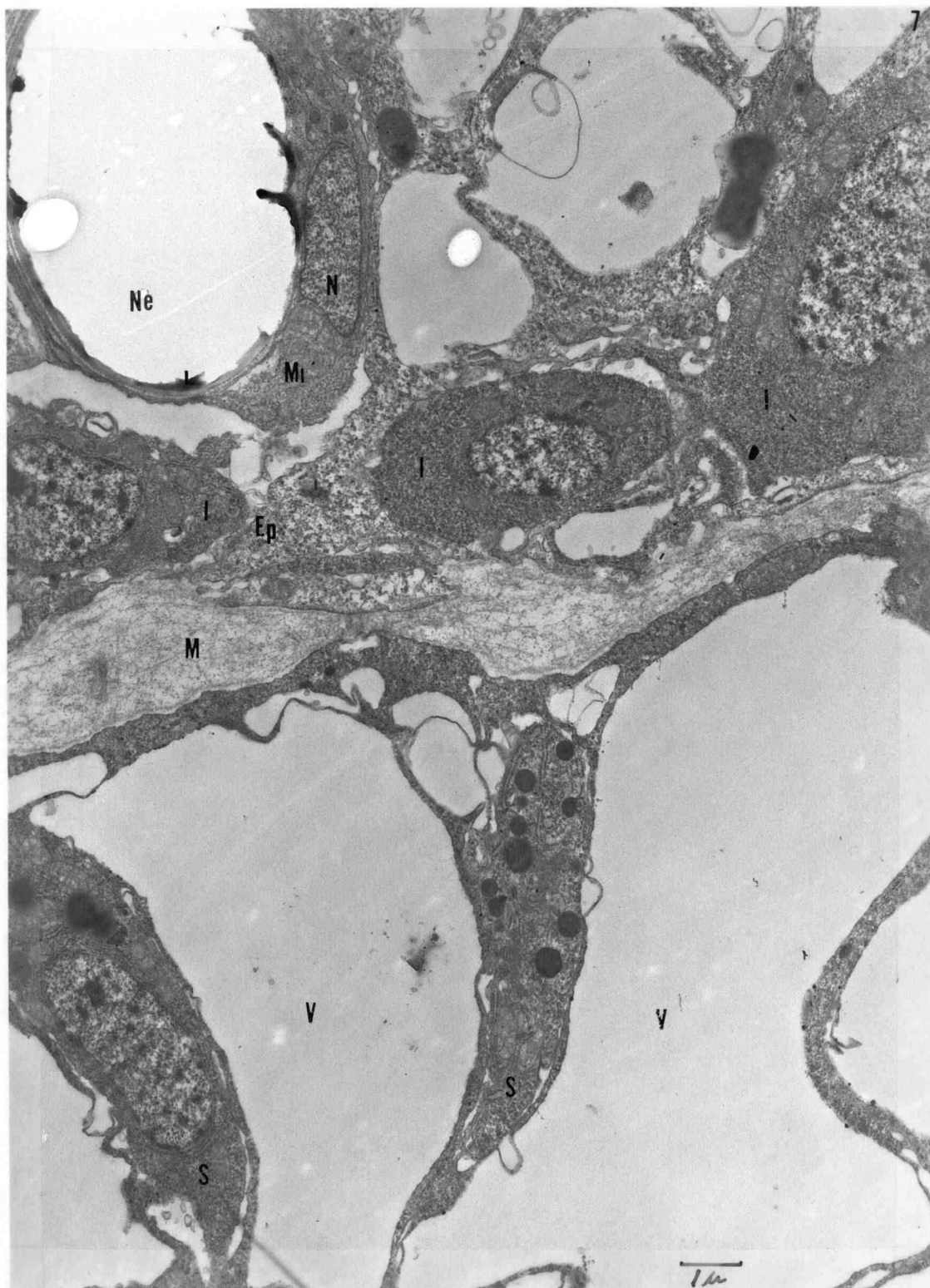


Figure 8. Higher magnification of Figure 7. 14,300 X

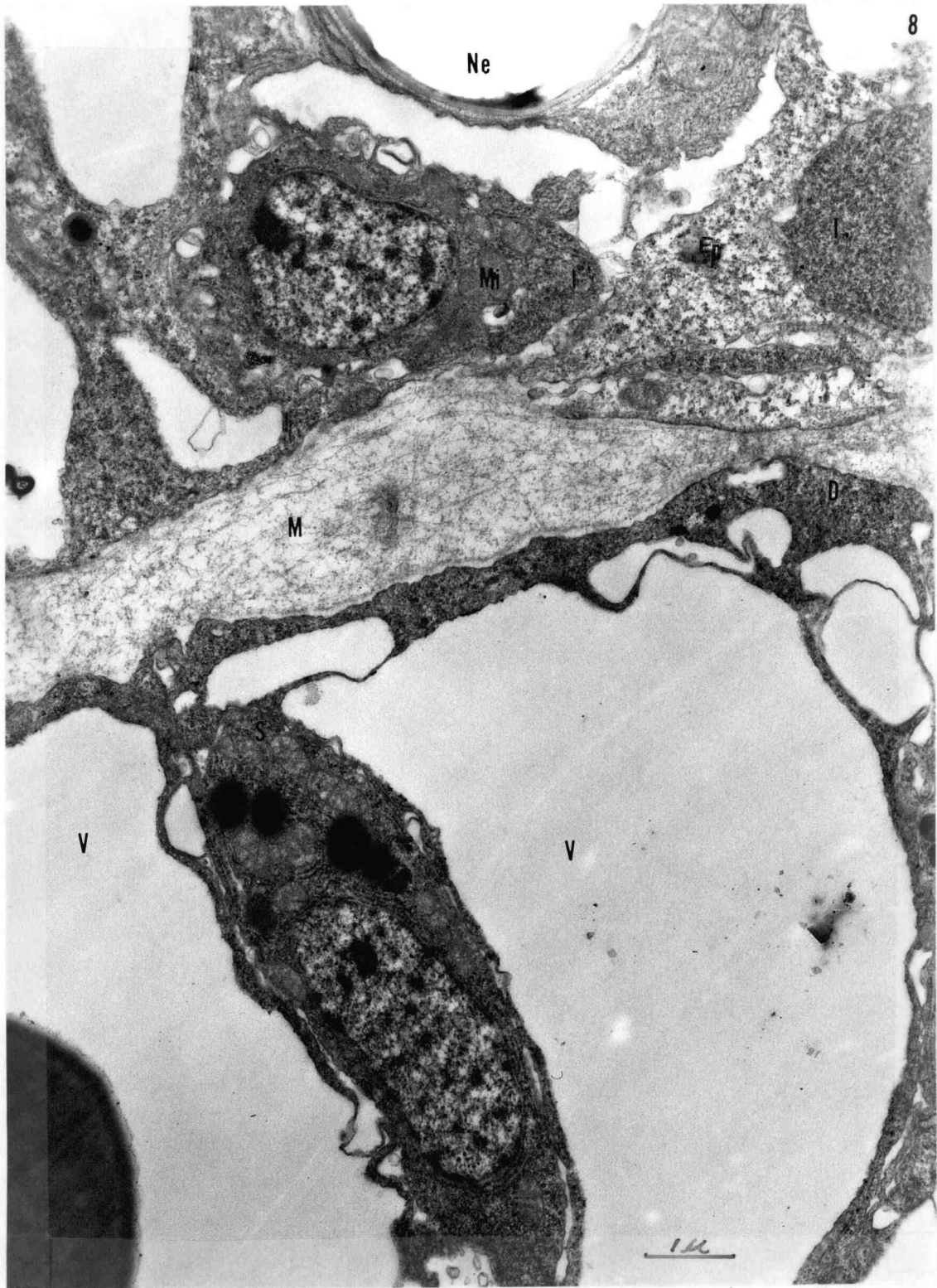


Figure 9. Interstitial cell adjacent to the mesoglea. Gastrodermal cell vacuoles contain granules (HG) which appear to be connected or coalescing (arrow). 9600 X

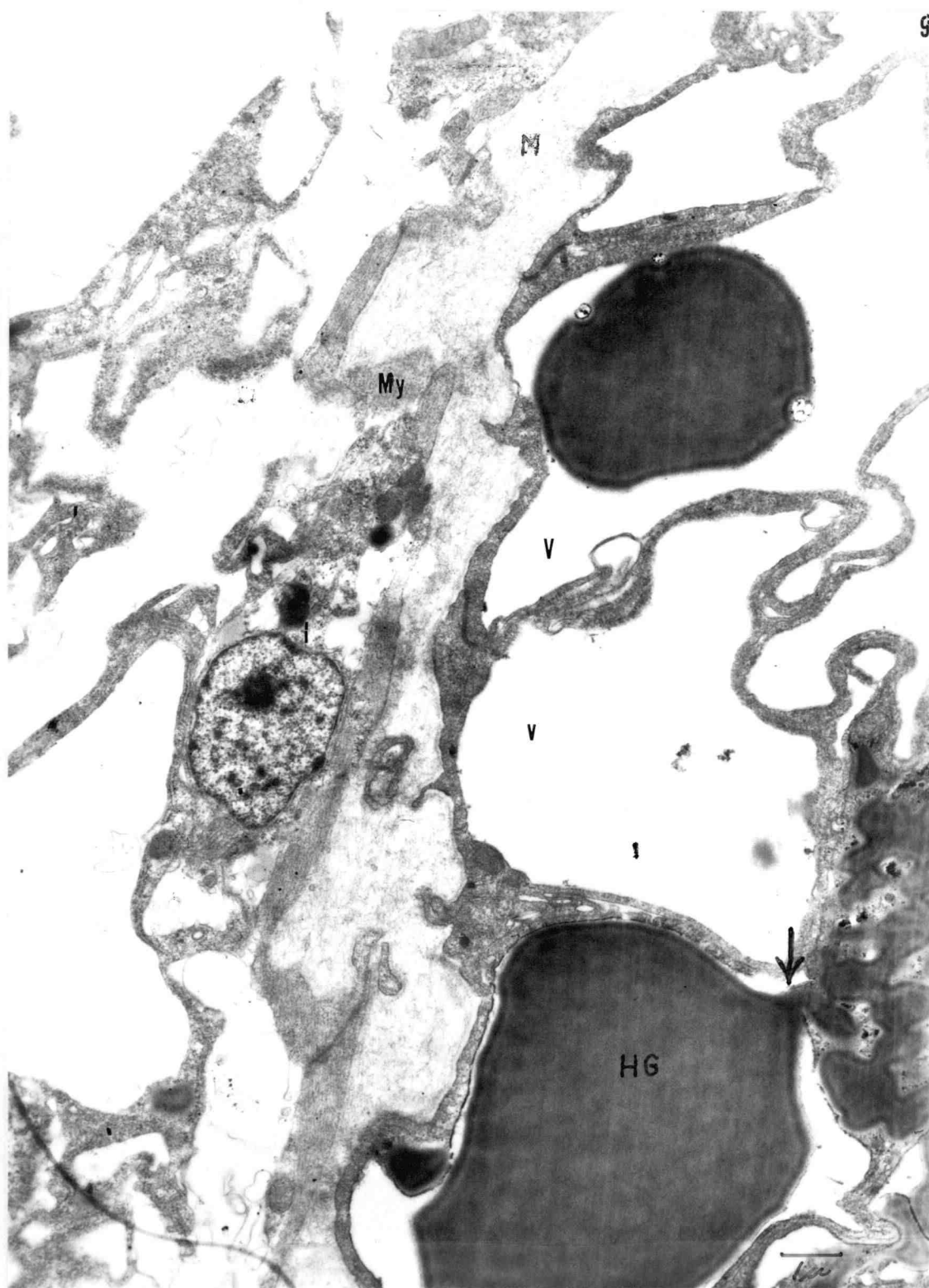


Figure 10. Light micrographs of cross sections of an adult hydranth close to a tentacle-hydranth junction showing interstitial cell clusters (arrows). Nematocysts appear as black spots in the clusters. Both micrographs 8700 X

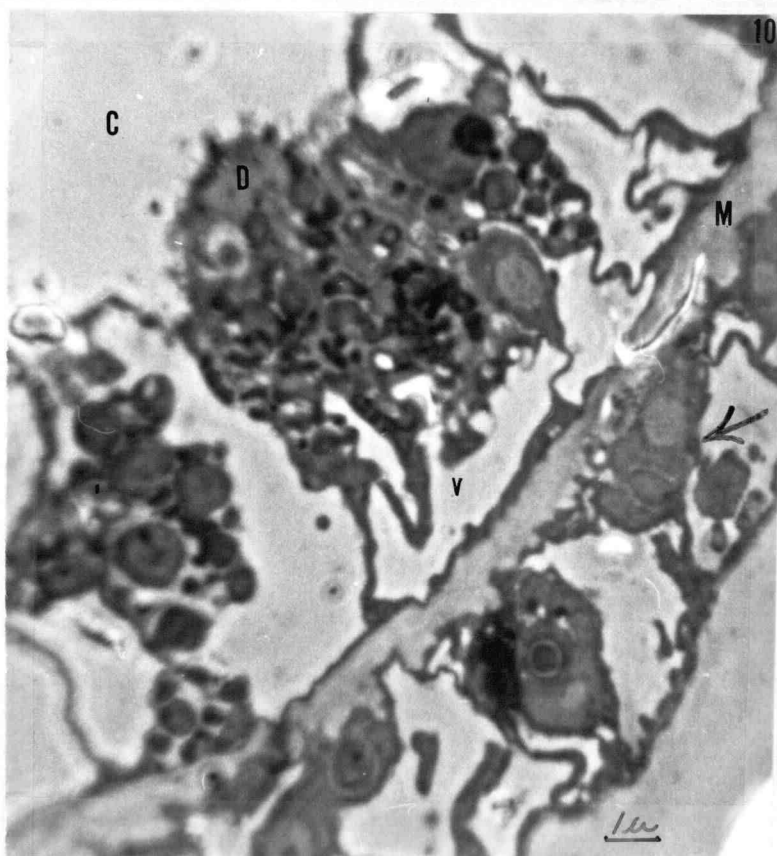
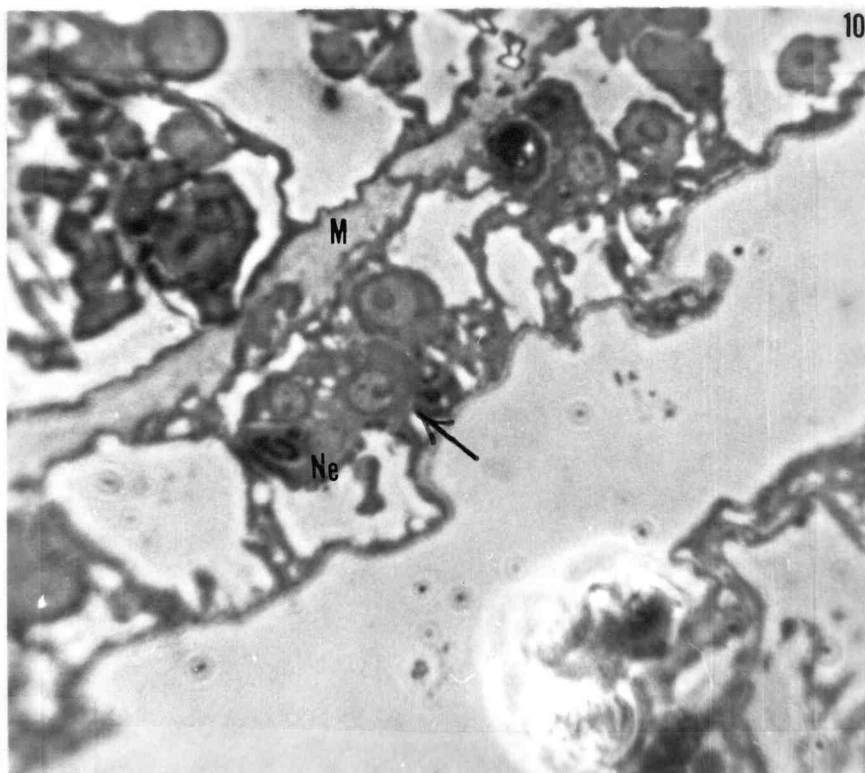


Figure 11. Longitudinal section of the tentacle bud hydranth's apex. Cells appear in close apposition to one another. Note zymogen-like granules (Z) and heterogeneous granules (HG). 7280 X

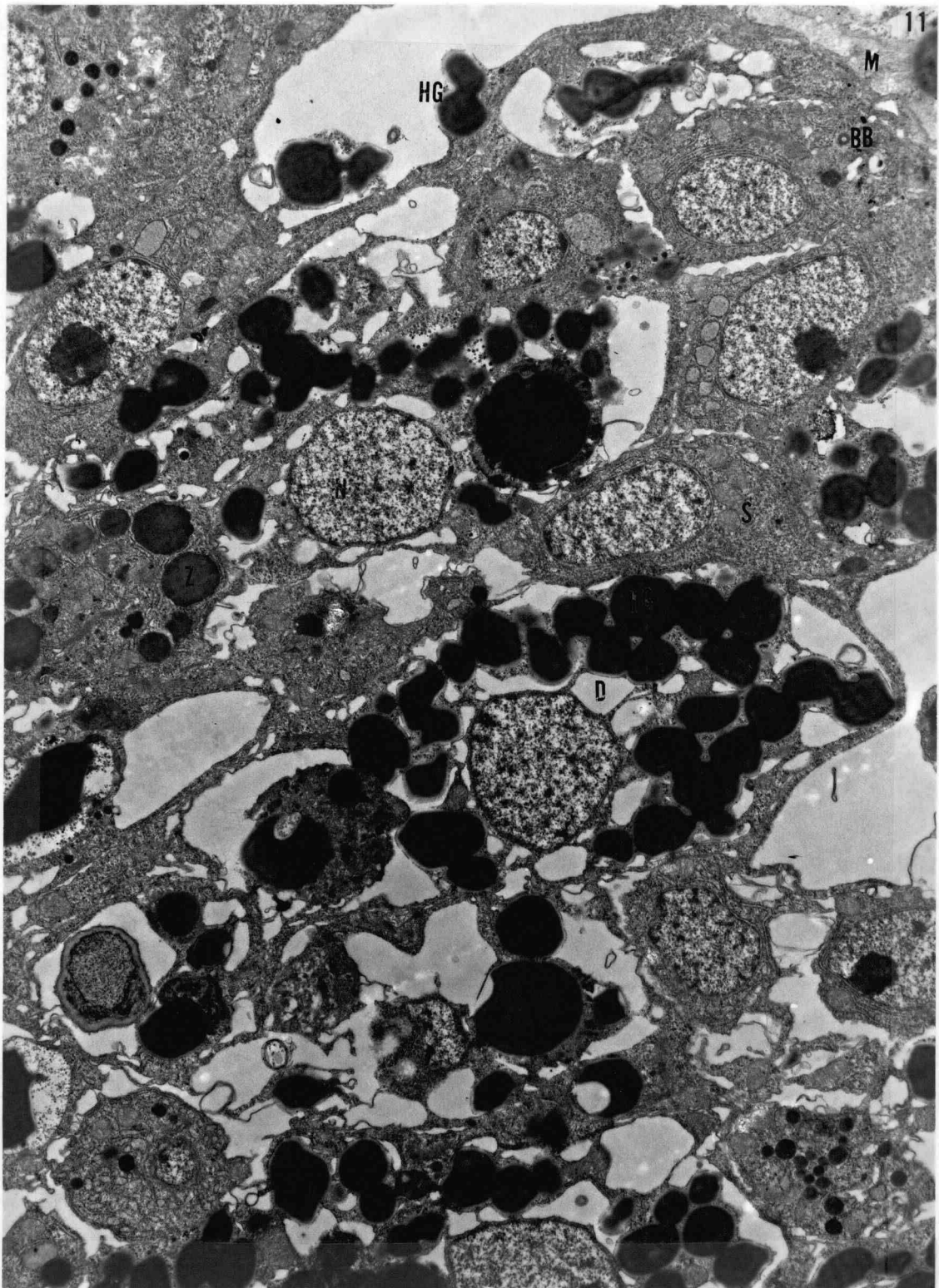


Figure 12. Digestive cells of the hydranth gastroderm. 9600 X

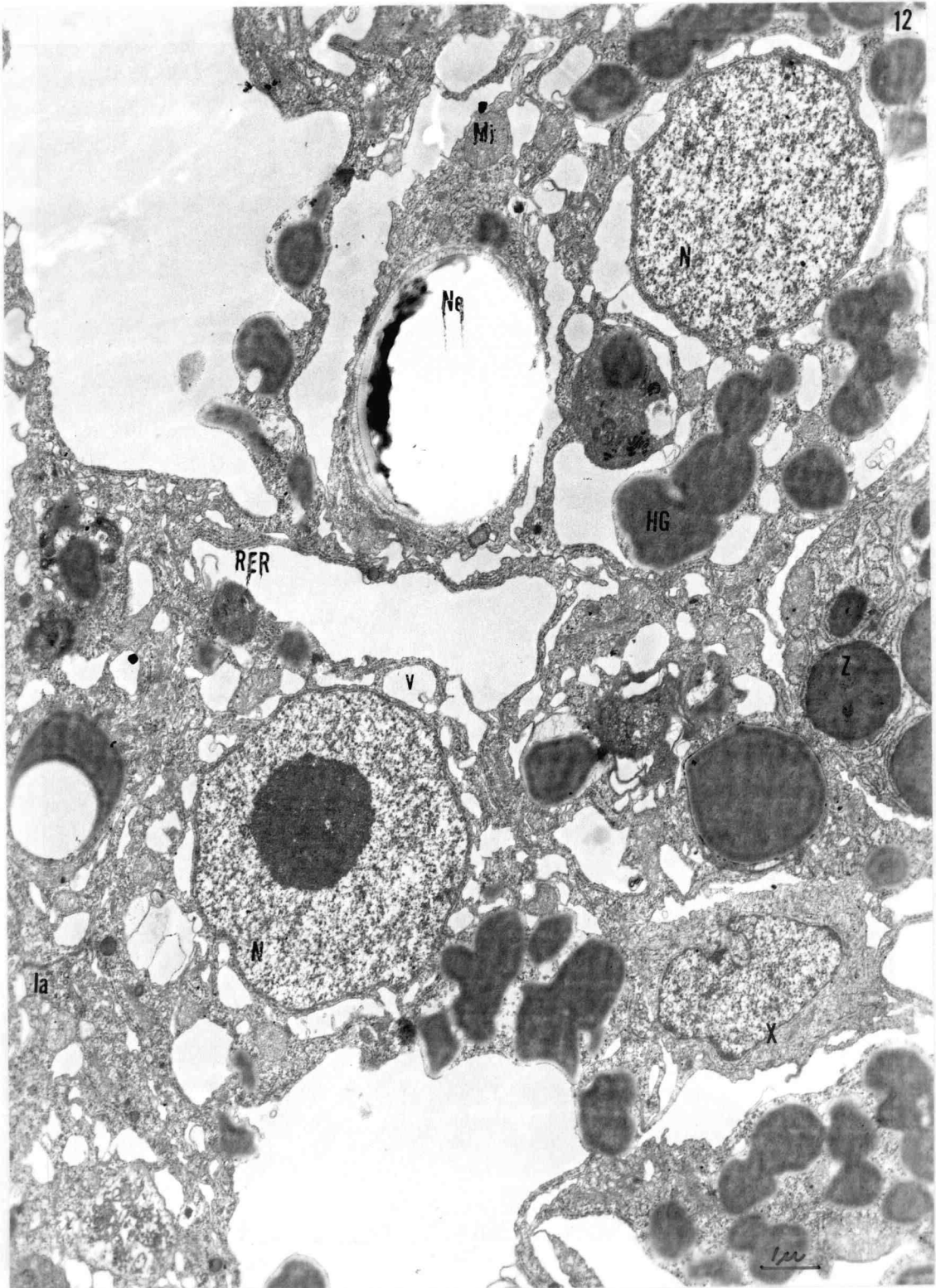


Figure 13. Digestive cells of the hydranth gastroderm. 9600 X

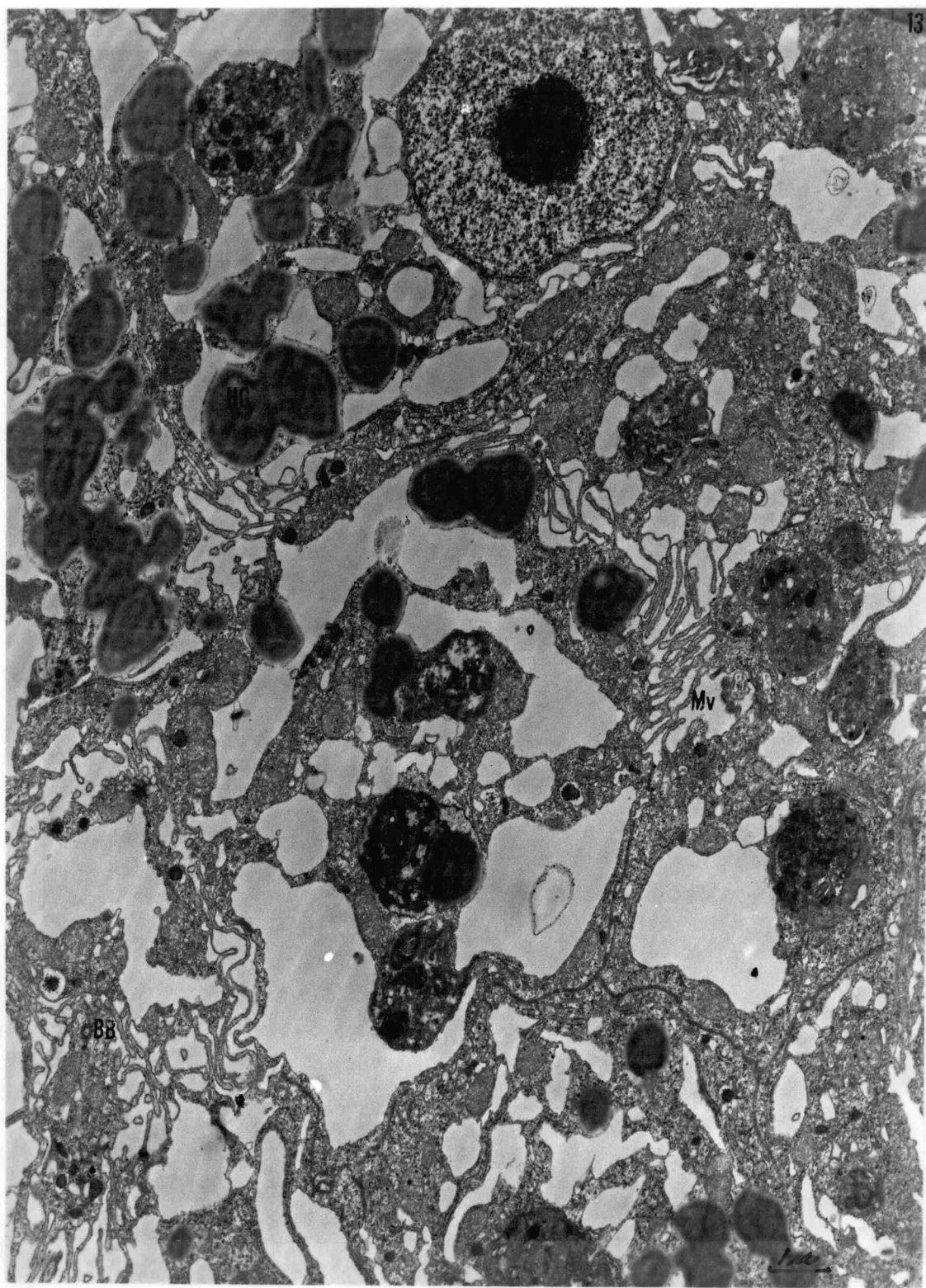


Figure 14. Digestive cell with microvilli (Mv) projecting into the coelenteron. Note cross-sections of flagellum (Fl).
9600 X

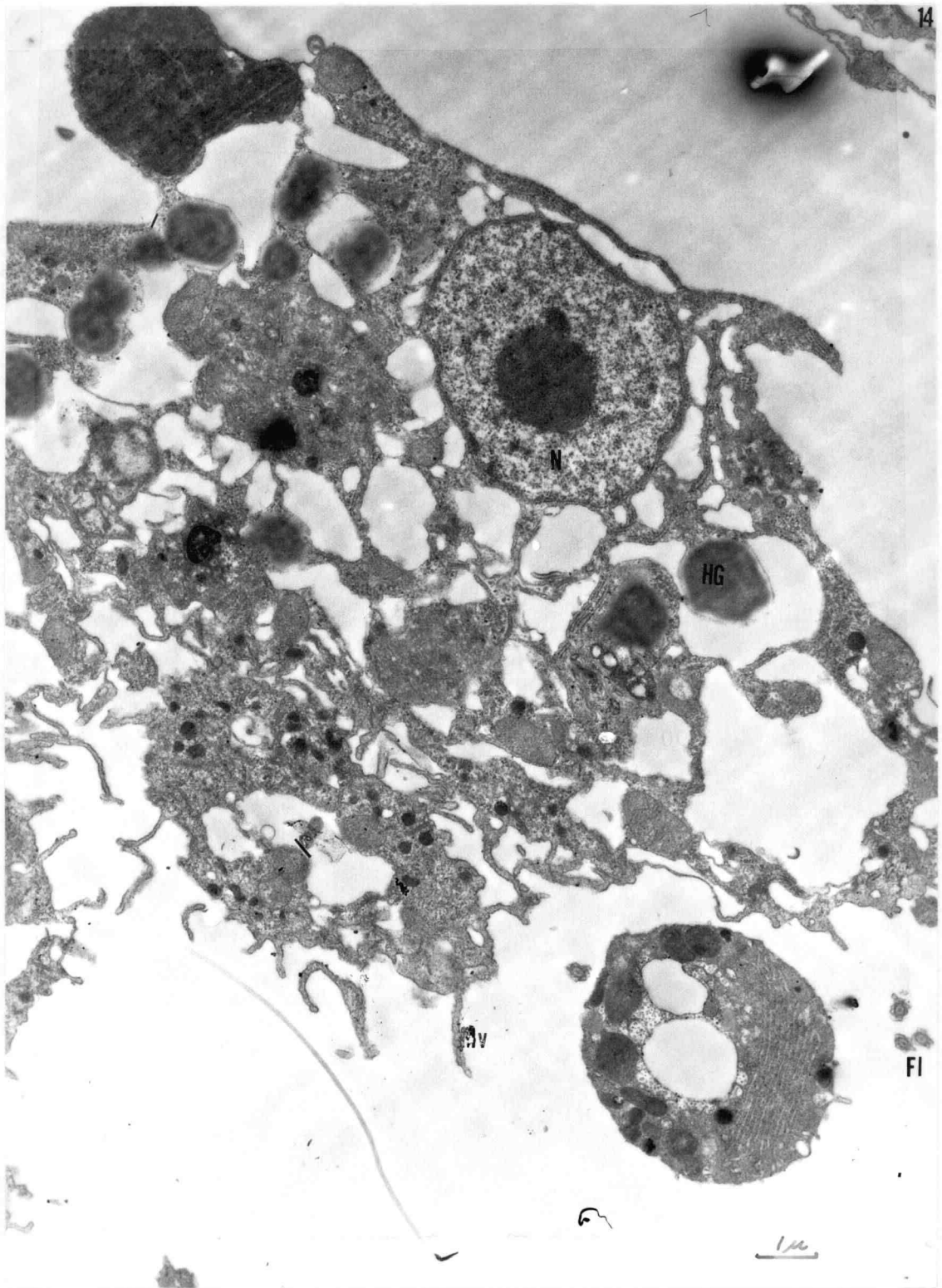


Figure 15. Secretory cell of the hydranth gastroderm with zymogen-like granules (Z) and stacked RER. Heterogeneous granules (HG) can also be seen in the adjacent cell's cytoplasm. The two structures above the secretory cell have not been identified.

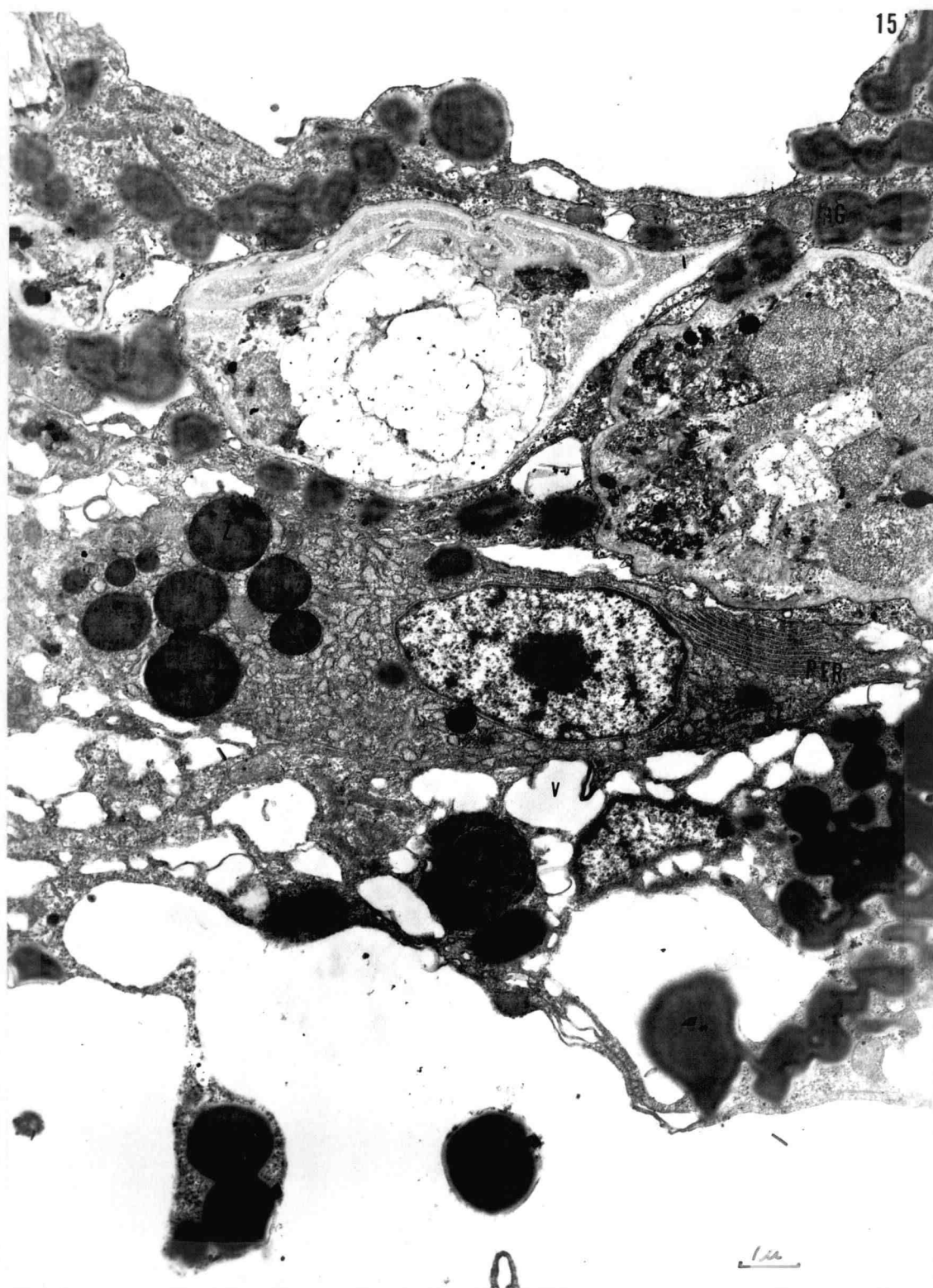


Figure 16. Tentacle bud gastroderm showing the heterogeneous granules (HG) adjacent to the mesoglea. 14,300 X

Figure 17. Stage two hydranth showing the enlarged ridge of cells below the hypostome and the small immature tentacles. 900 X

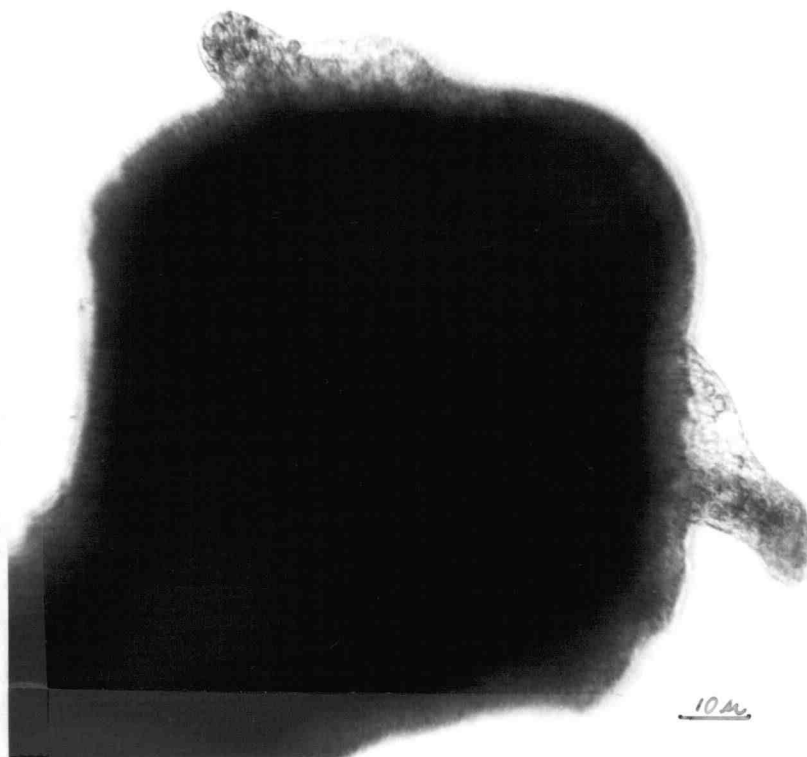
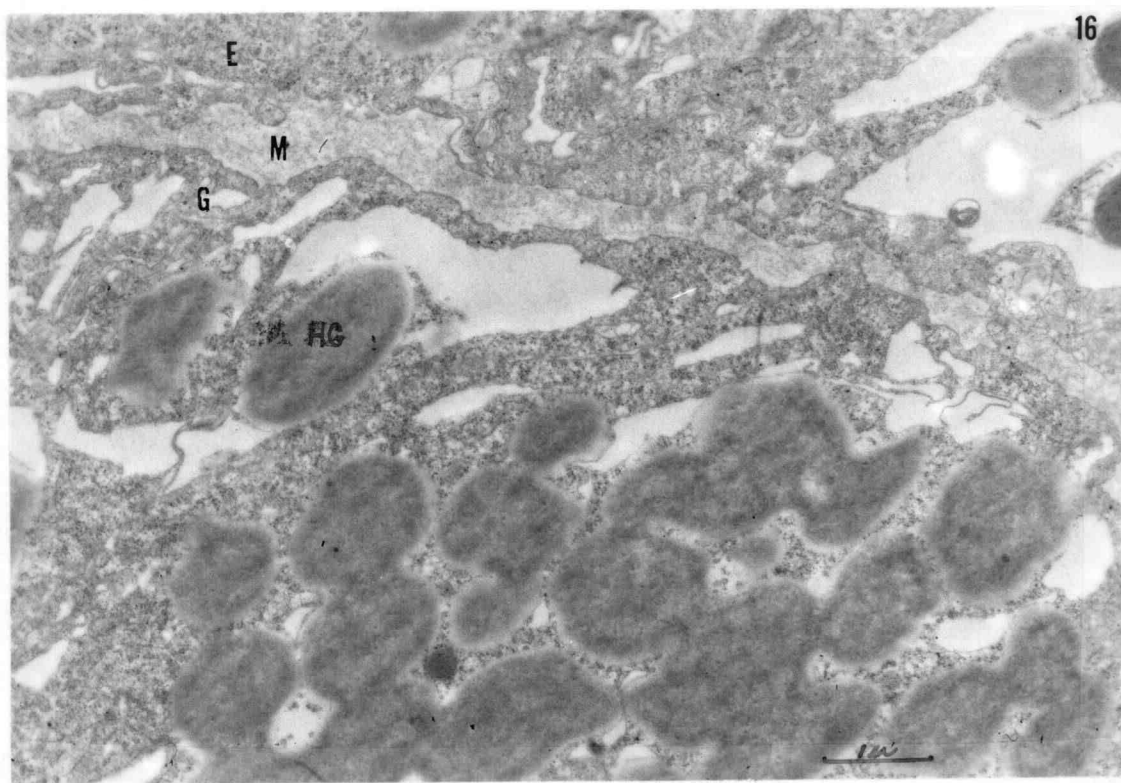


Figure 18. The immature tentacle tip. A sensory hair (arrow) can be seen in one cell with tubules in the cell body. 9600 X

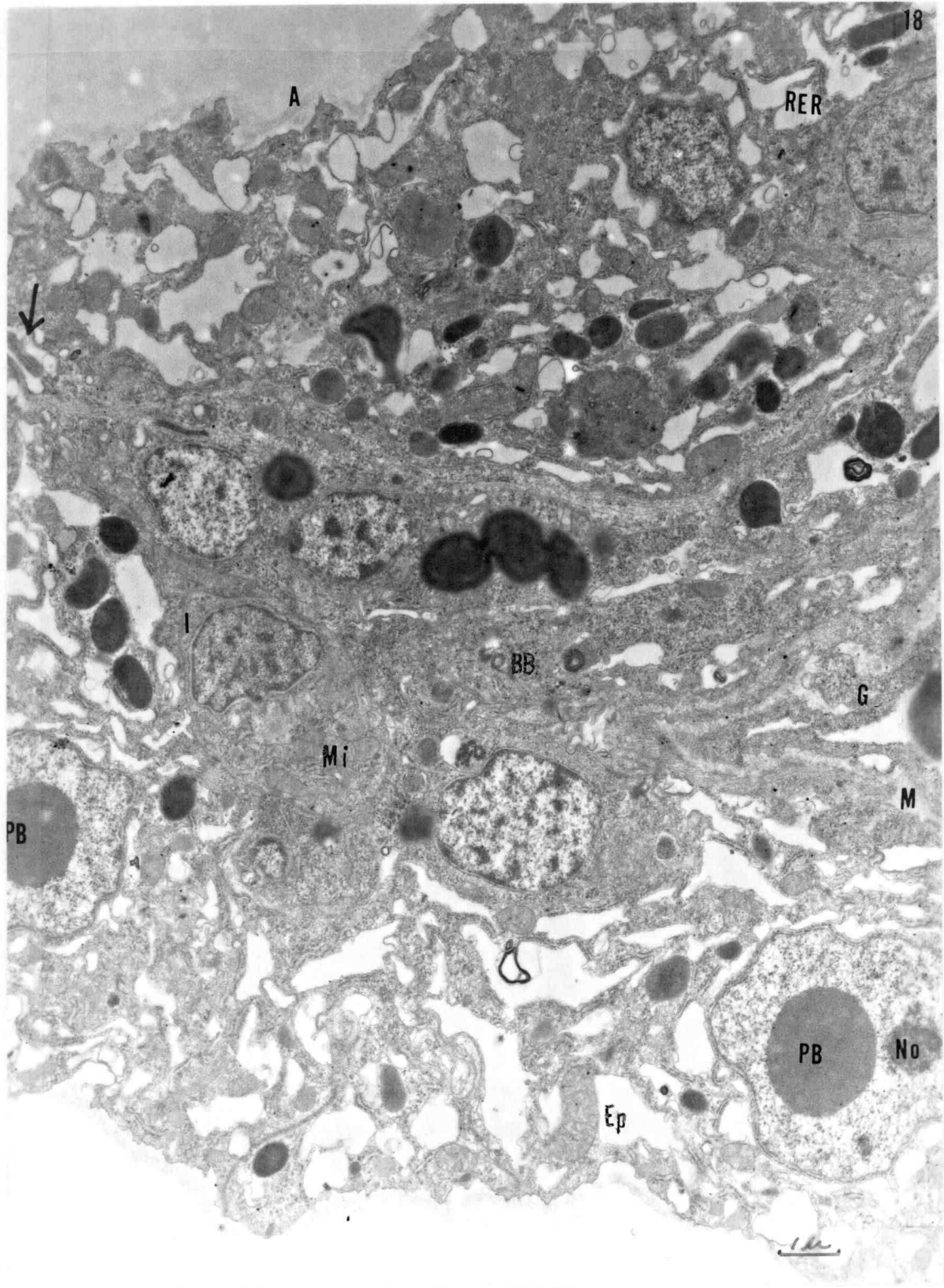
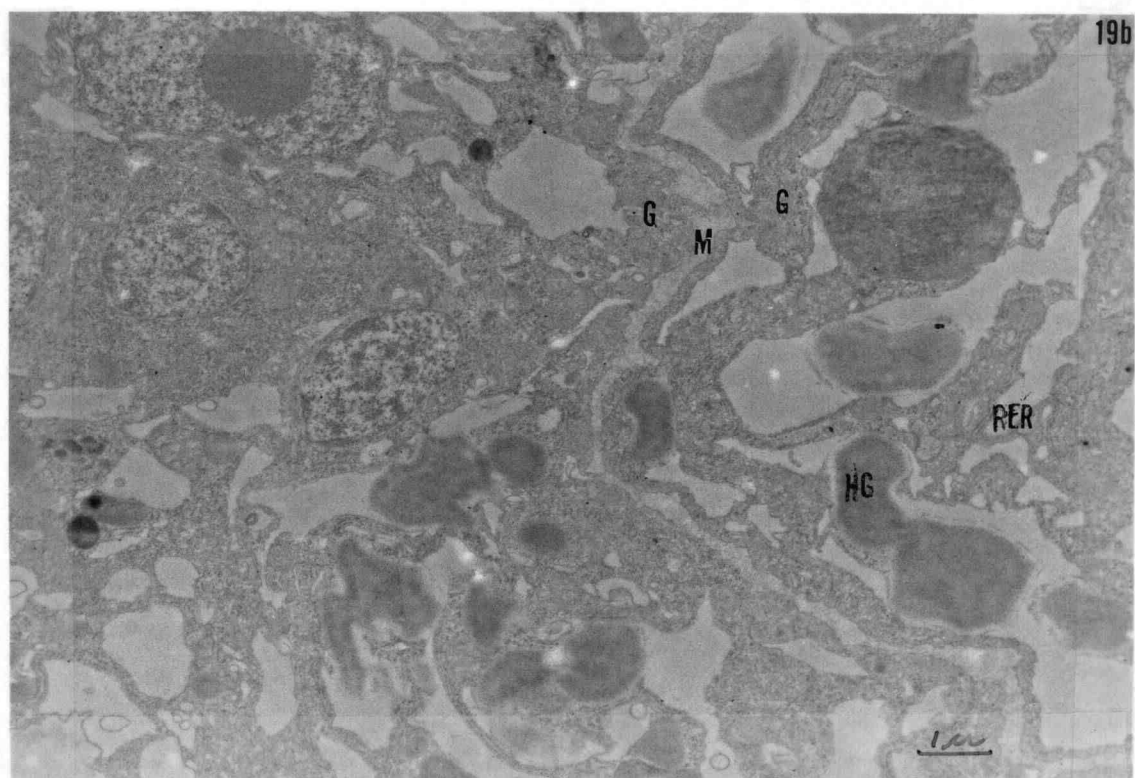
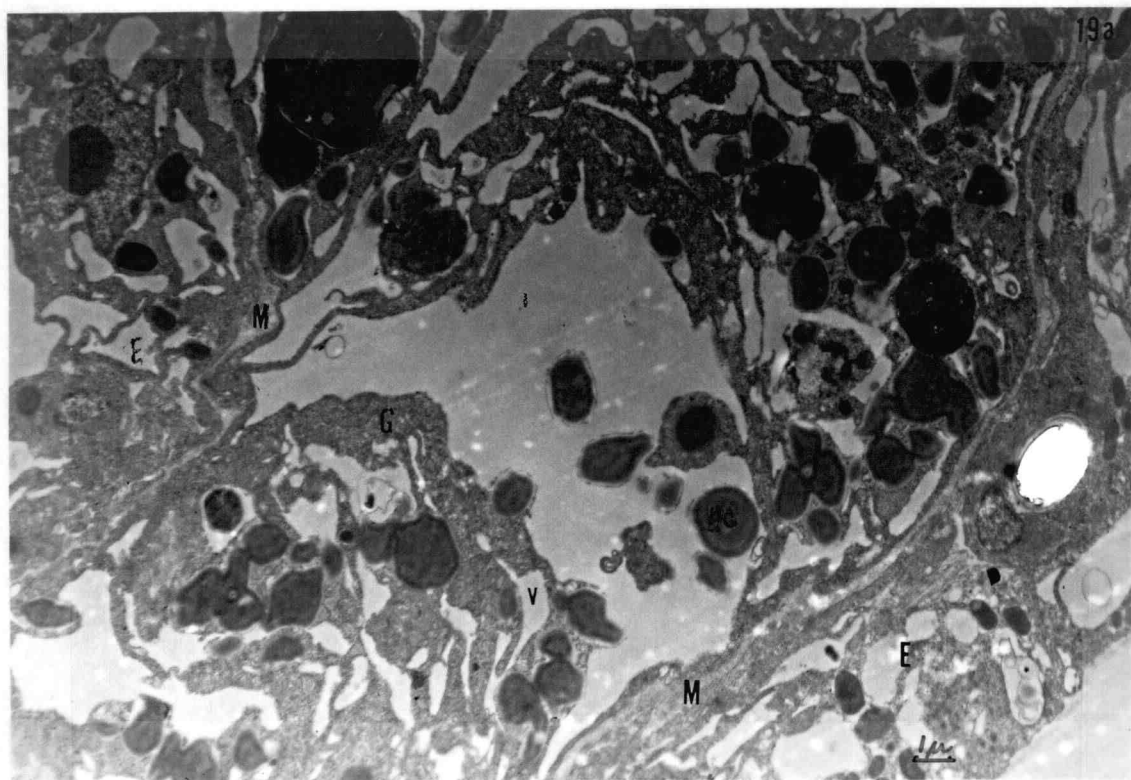


Figure 19a. A median section of the immature tentacle showing the confluent gastroderm between the hydranth and the tentacle. 4900 X

Figure 19b. A sagittal section of the immature tentacle showing the mesoglea separating the hydranth and tentacle gastroderm. 9600 X



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Figure 20. Stage three hydranth showing the adult tentacles below the hypostome. 887 X

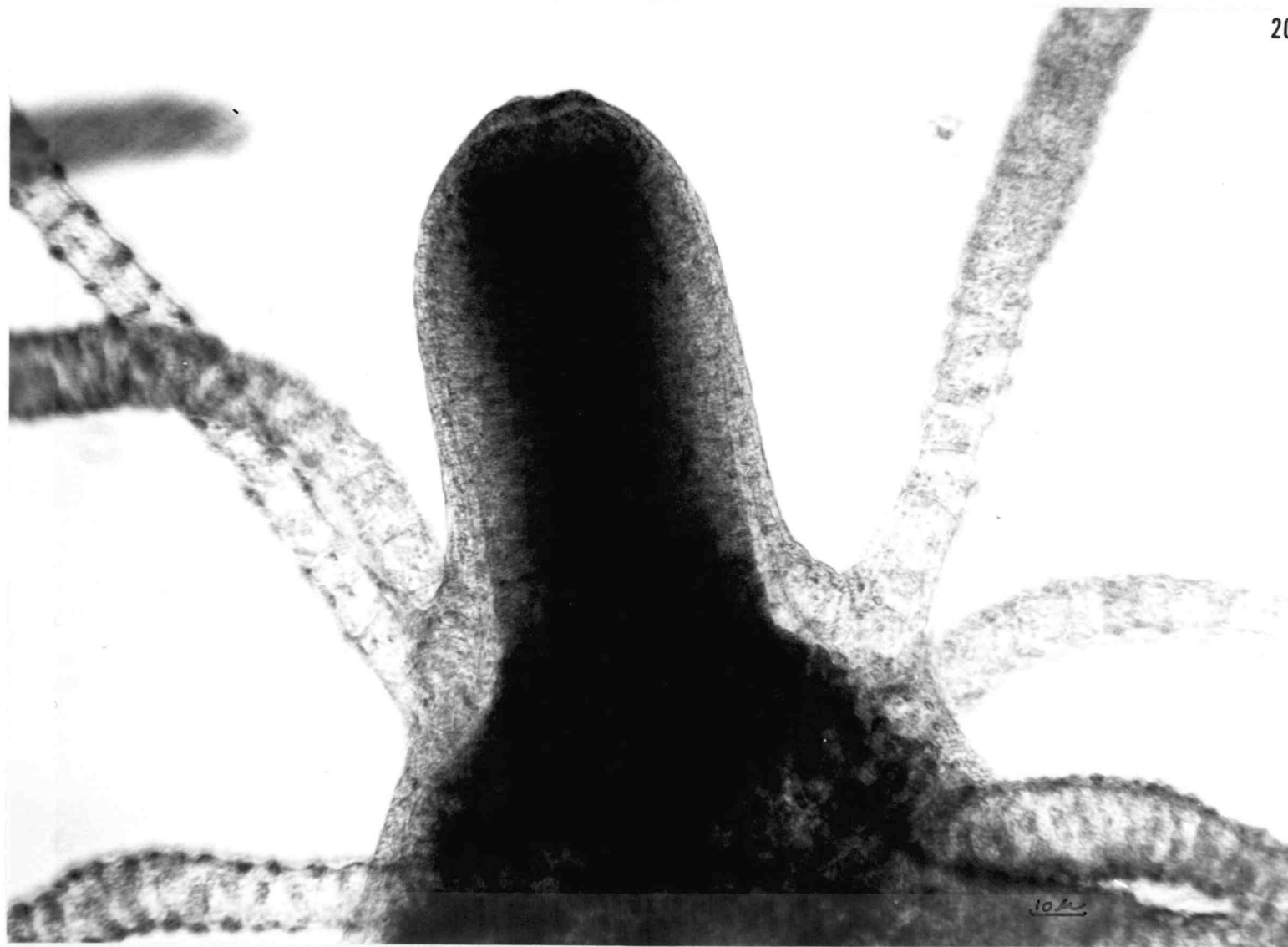


Figure 21. A montage of three electron micrographs of medial longitudinal sections of a tentacle in an advanced state of maturation. The black lines are folds in the sections. 2900 X

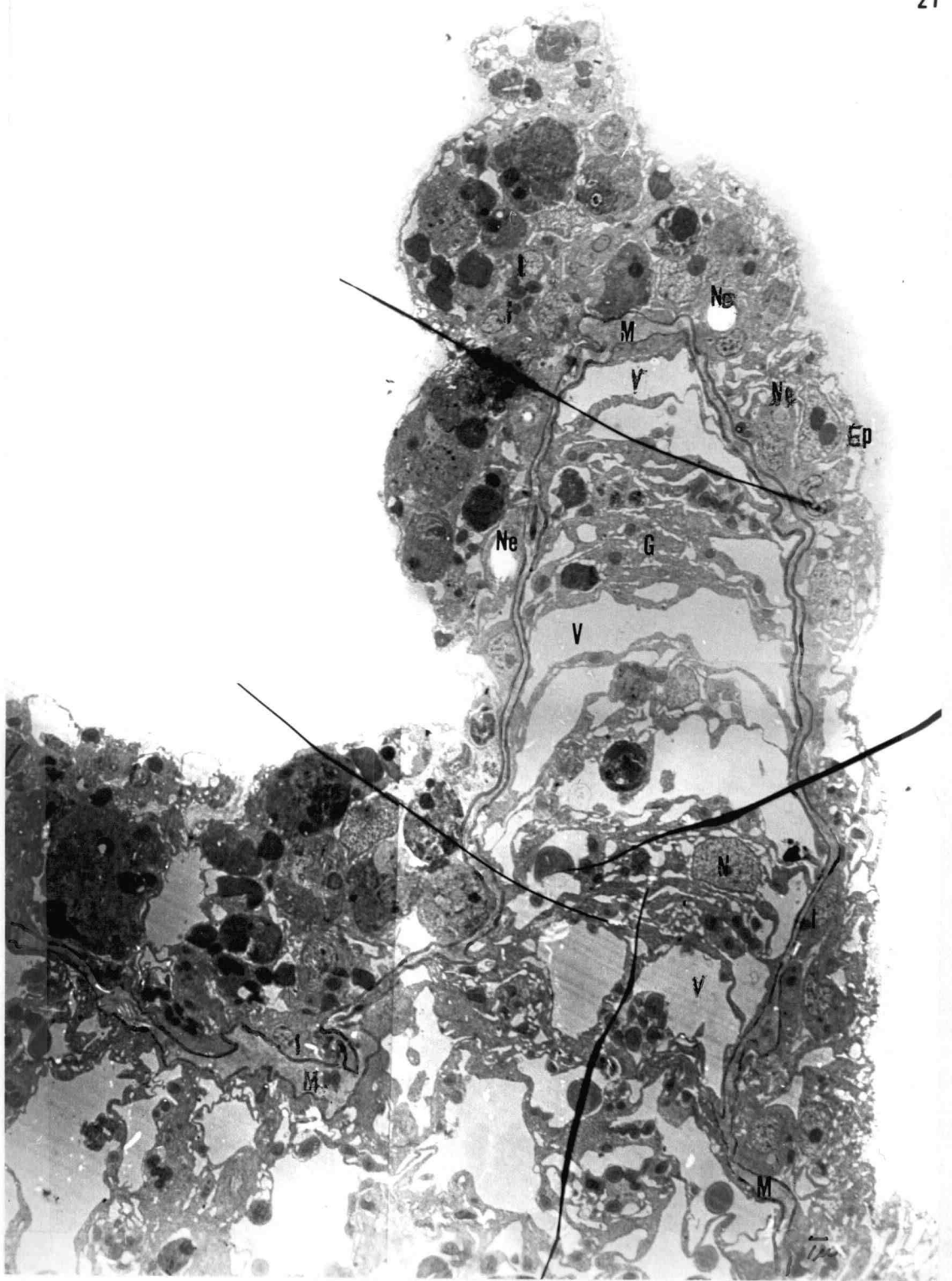
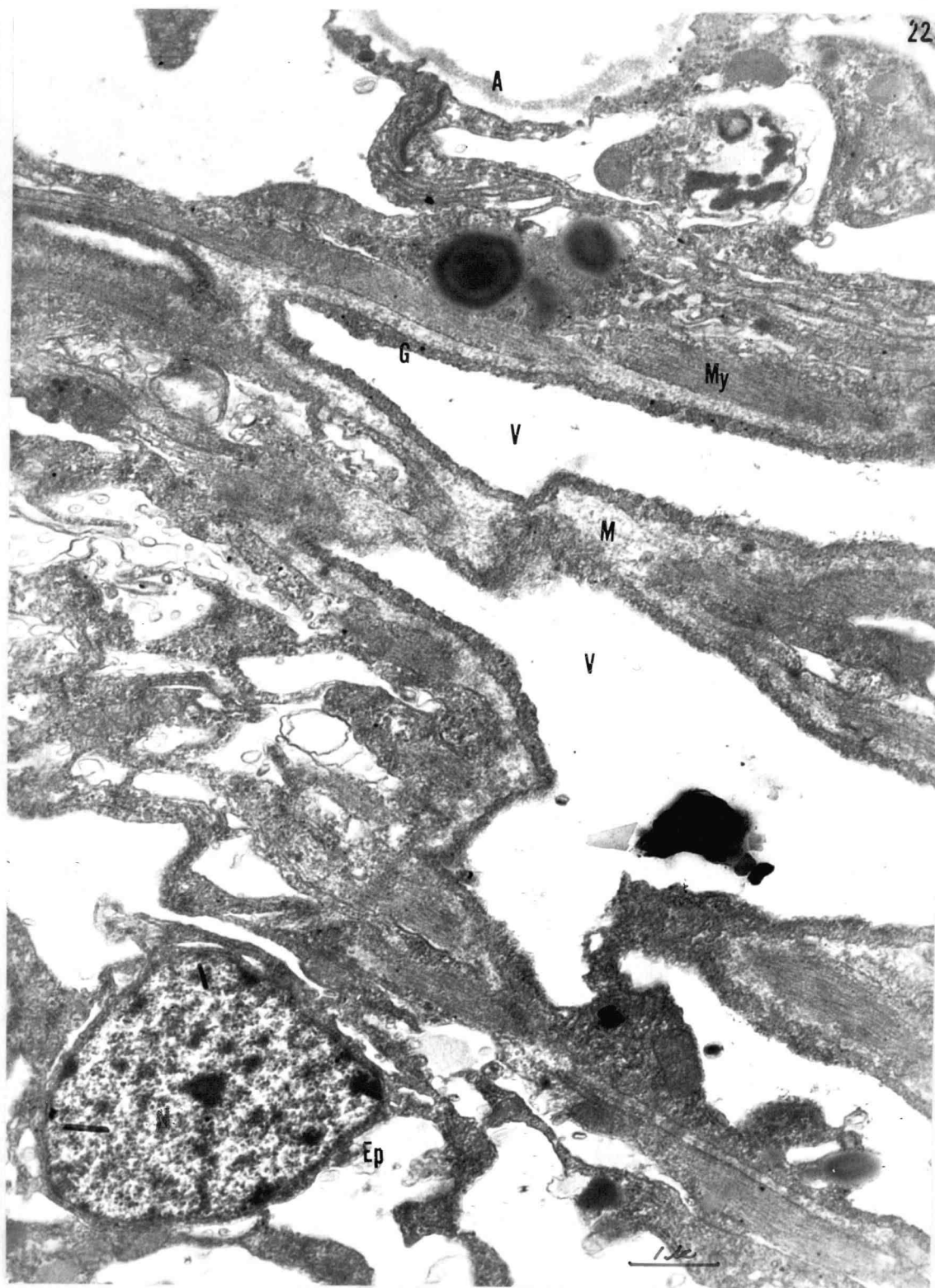


Figure 22. A tangential section of an adult tentacle. 14,300 X

22



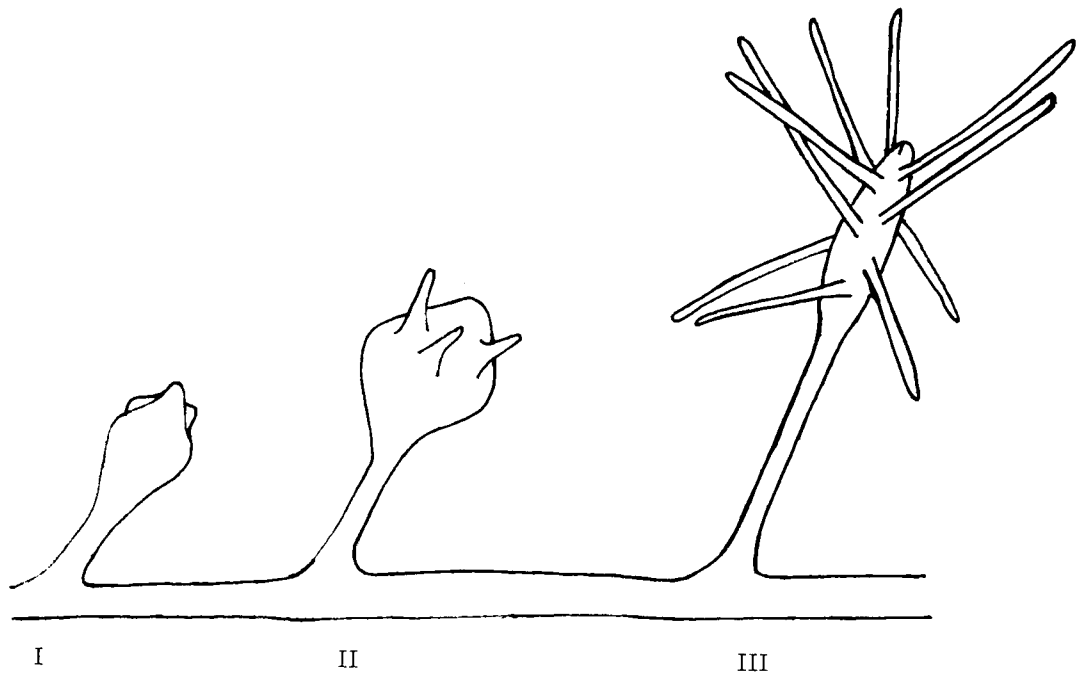


Figure 23. Sketch of the three stages of tentacle development.

- I. The tentacle bud.
- II. The immature tentacle.
- III. The adult tentacle.