

ON THE MORPHOLOGY AND FINE STRUCTURE OF  
THE ALIMENTARY CANAL OF *COROPHIUM*  
*VOLUTATOR* (PALLAS) (CRUSTACEA: AMPHIPODA)

BY J. D. ICELY AND J. A. NOTT†

*N.E.R.C. Unit of Marine Invertebrate Biology, Marine Science Laboratories, Menai Bridge, Anglesey  
LL59 5EH, U.K.*

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† Present address: The Laboratory, Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, Devon, U.K.

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In the mud-dwelling amphipod, *Corophium volutator*, the foregut is lined with cuticle and consists of an oesophagus and a stomach, with the latter divided into cardiac, pyloric and funnel regions. The midgut comprises an intestine that is enlarged considerably by three pairs of diverticula: the small anterior dorsal and posterior caeca and the massive ventral caeca. Anteriorly, the intestine encompasses the funnel region and the ventral caeca open into the floor of the stomach at the posterior end of the pyloric region. The hindgut is essentially a simple tube connecting the intestine with the anus.

Particles of food pass along the oesophagus and enter the stomach through a valve. Rows of setae, or folds of cuticle, divide the stomach longitudinally into food, circulation and filtration channels. Ingested particles with a diameter greater than 2  $\mu\text{m}$  are confined to the food channel and supplied with fluids and enzymes from the circulation channels. The digestive enzymes are produced primarily by the ventral caeca and are supplied to the circulation channels through a valve at the entrance of each ventral caecum. Any fine particles and soluble materials extracted from the food channel in the cardiac region are transported into the filtration channels through the first filter of a two part system. Digestible material continues to be extracted in the pyloric region where the volume of the lumen of the food channel is reduced by the intrusion of the vertex of the ventral pyloric ridge. The basis of this ridge supports the second filter which produces a filtrate with particles less than 0.06  $\mu\text{m}$  in diameter. Material retained on the filter membrane is returned to the food channel by brush-like setae facing the membrane. The final filtrate is transported to the ventral caeca. A valve at the entrance to each ventral caecum prevents contamination of the filtrate by material in the food channel. All indigestible food is passed sequentially along the funnel, intestine and, finally, the hindgut from which it is voided as a faecal pellet.

Most digestion and absorption occur in the ventral caeca where the epithelium is differentiated into the R/F and B cells. The R/F cells have a much thicker and denser microvillous border than the B cells. Each R/F cell also has numerous mitochondria located mainly ventral to the nucleus in the mid-region. Rough and smooth endoplasmic reticula are sited primarily in the apical and basal regions of the cell, respectively. Furthermore, most of the rough endoplasmic reticulum is confined to cells in the distal region of the caecum which probably forms the main site for the production of digestive enzymes. The proximal region of the caecum contains numerous lipid droplets and is probably involved in the absorption, transport and storage of the products of digestion.

Each B cell has a single large, fluid-filled vacuole, distal to which are mitochondria and numerous smaller vacuoles of varying size forming an 'apical complex'. The nucleus is located proximal to the vacuole together with free ribosomes and rough endoplasmic reticulum. Material from the lumen of the caecum is taken by pinocytosis into the 'apical complex'. The large vacuole develops at the expense of the 'apical complex' and the microvillous border. The vacuole is eventually liberated into the lumen of the caecum and the cell disintegrates. These discharges may supply enzymes to other regions of the gut, or they could be waste products derived from intracellular digestion.

The anterior dorsal caeca and most of the intestine contain cells with a normal complement of organelles. These cells probably make a minor contribution to the processes of digestion and absorption. However, the cells of the posterior caeca and those at the posterior end of the intestine have an extensive development of smooth endoplasmic reticulum. In some cells the mitochondria have a dense matrix and there are only a few free ribosomes and cisternae of rough endoplasmic reticulum. The fine structure of the epithelium in the posterior caeca is typical of tissue that transports fluids and ions.

The hindgut has a microvillous border which abuts its cuticular lining. In addition, some cells have numerous mitochondria which are often associated with infolds of the basal cell membrane. The fine structure of this tissue is similar to the 'ion pumps' described in the gut of insects which serve to maintain the normal ionic concentration of the blood. The posterior region of the hindgut has no structural specializations.

## 1. INTRODUCTION

The amphipod, *Corophium volutator* (Pallas) occurs in dense populations within estuarine muds of northern temperate regions (Schellenberg 1928, 1942; Crawford 1937; Segerstråle 1959). These animals inhabit burrows and feed on particles of mud (Hart 1930; Meadows & Reid 1966). Although aspects of the morphology and function of the digestive system in a number of species of the Amphipoda have been described (Thiem 1941; Martin 1964; Kannerworff & Nicolaisen 1969), none of these studies has investigated in detail the morphology of all regions of the gut. In particular, studies on the fine structure of the gut are restricted to the hepatopancreatic caeca in *Orchestia platensis* and *Gammarus locusta* (Moritz *et al.* 1973) and *Gammarus minus* (Schultz 1976) and the posterior caeca of *Orchestia cavimana* (Graf & Michaut 1977, 1980). In this paper the morphology and fine structure of the foregut, midgut and hindgut are described in detail. The general features of the gut of *C. volutator* have been outlined by Agrawal (1963*a*) but some aspects of the description do not concur with the observations made here.

## 2. MATERIALS AND METHODS

### (a) *Specimens*

Animals of both sexes were collected from the mud on the foreshore of the Menai Strait, Anglesey, North Wales. Only adults of body length greater than 5 mm were used for the description of the morphology and most were at intermoult. However, the morphology of the digestive system of juveniles between 3–5 mm length, was examined to ensure that no substantial changes occurred during growth and development.

*(b) Microscopy*

The general morphology and fine structure of the gut was examined by the techniques described in schedules 1–3. In general, only animals with an empty gut were prepared for light and transmission electron microscopy (schedules 1 and 2), because those that had ingested particulate material could not be sectioned readily. The effect of food on the form of the gut was investigated by scanning electron microscopy, using the freeze–fracture technique described in schedule 3.

*(i) Schedule 1*

Animals were fixed in Bouin in seawater overnight at a temperature of 60 °C. The picric acid in this solution was extracted from the fixed tissue by immersion in an aqueous solution containing 10 mg ml<sup>-1</sup> lithium carbonate for 1 h and then rinsing under running tapwater for 5 min. The tissue was dehydrated overnight in two changes of 2-ethoxyethanol (Cellosolve) and then embedded in ester wax. Thick sections were cut and stained with an aqueous solution containing 5 mg ml<sup>-1</sup> azocarmine and Mallory's triple stain.

*(ii) Schedule 2*

The alimentary canal was fixed for 2 h in a solution of 24 mg ml<sup>-1</sup> glutaraldehyde in seawater at 4 °C, which was buffered at pH 7.2–7.4 and adjusted to 1020–1030 mosmol. It was rinsed in buffer and post-fixed for 1 h in 10 mg ml<sup>-1</sup> osmium tetroxide in seawater. After rinsing in seawater for 1 h, it was dehydrated in ethanol and embedded in a low viscosity epoxy resin. Sections for light microscopy were stained in an aqueous solution containing 10 mg ml<sup>-1</sup> toluidene blue and 10 mg ml<sup>-1</sup> borax. Sections for transmission electron microscopy were stained in an aqueous saturated solution of uranyl acetate followed by lead citrate.

*(iii) Schedule 3*

Animals were fixed in a solution of 24 mg ml<sup>-1</sup> glutaraldehyde in seawater at room temperature for 2 h. The pH and the osmolarity were adjusted as in schedule 2. The tissue was rinsed for 1 h in seawater, dehydrated in ethanol and then immersed for 1 h in acetone. Each animal was frozen rapidly in liquid nitrogen and fractured transversely with a razor blade. The fractured specimens were returned to acetone and critical point dried from liquid carbon dioxide. The dried material was mounted on aluminium stubs, coated either with carbon and gold–palladium by evaporation or with gold by d.c. sputtering, and examined by scanning electron microscopy.

### 3. ORGANIZATION OF THE DESCRIPTION

An introduction to the morphology of the gut is presented with figure 1 relating the different regions to the external features of the animal. Subsequently, each major region of the gut is described in detail under separate headings. Figure 2 illustrates both internal and external morphology along the anterior end of the gut, while figures 3 and 4 show transverse sections at intervals along the anterior and posterior regions of the gut, respectively. Also, description of the morphology is supported by electron micrographs.

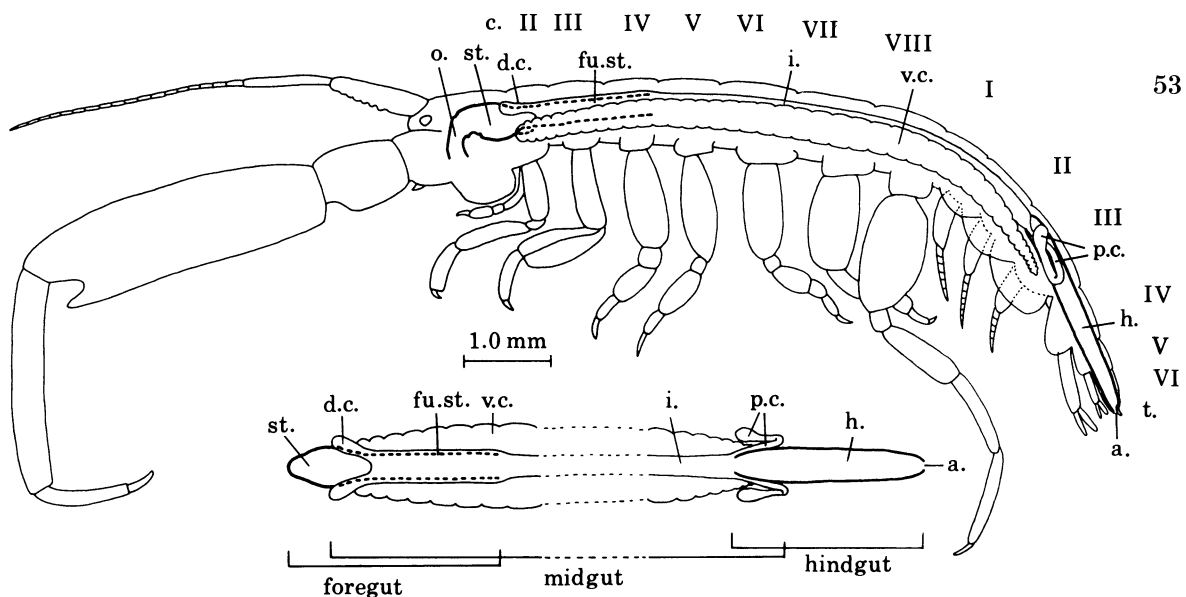


FIGURE 1. Lateral view of the alimentary canal of an adult male. Region of the gut drawn with a thick line represents the cuticularized ectoderm of the foregut and the hindgut; the thin line represents the endoderm of the midgut. Thoracic and abdominal segments are identified by roman numerals. Inset shows a dorsal view of the alimentary canal; the full length of the intestine is not shown. External features of the animal are redrawn from plate 219 in Sars (1895).

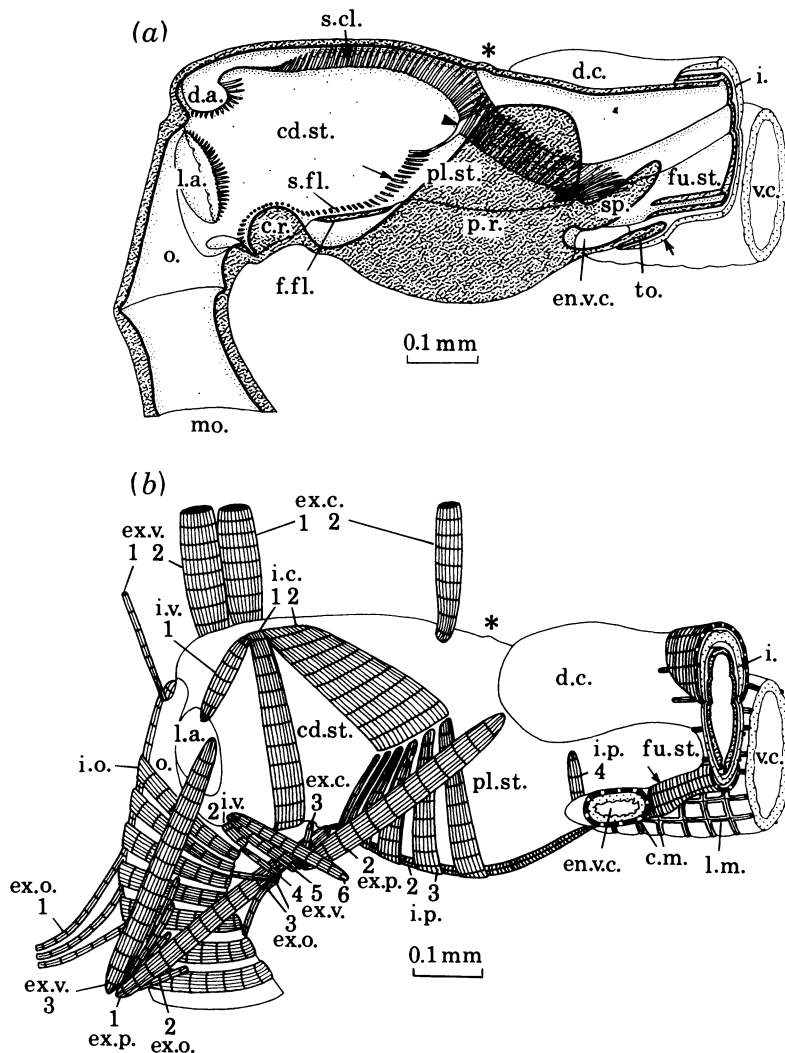


FIGURE 2. (a) Anterior end of the alimentary canal cut along the midline to show the arrangement of the main structures within. Foregut epithelium is indicated by dark shading and midgut epithelium by regular dots. (b) Intrinsic and extrinsic musculature at the anterior end of the alimentary canal. Note that the left hand ventral caecum (en.v.c.) is excised. \* Ridge marking the dorsal boundary between cardiac and pyloric stomach regions. Arrows explained in text.

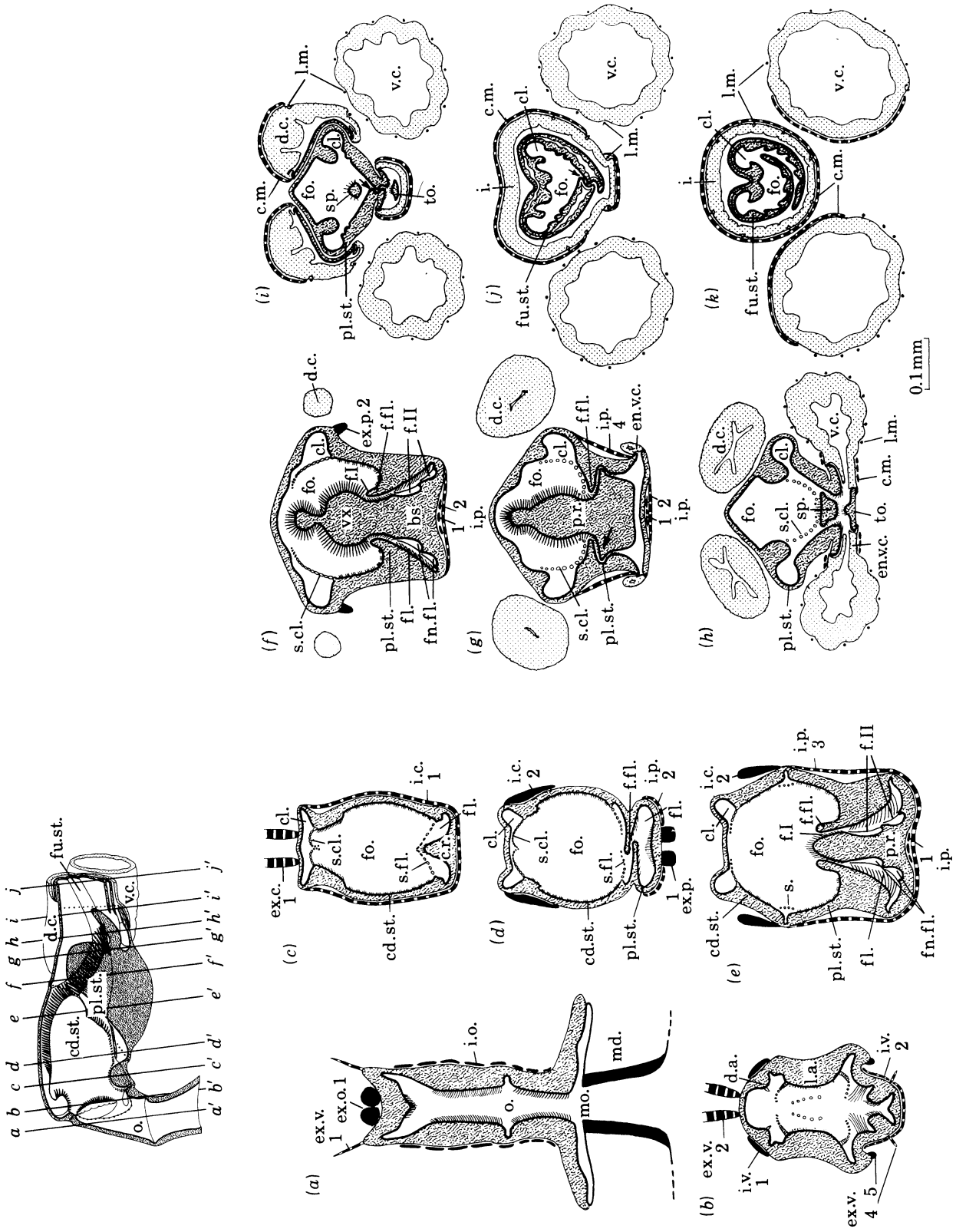


FIGURE 3. Transverse sections *a-j* of anterior end of the gut which correspond to lines *aa'-jj'* on a copy of figure 2*a*; *k* is the posterior end of the foregut shown in figure 2*a*. Difference in shading as in figure 2*a* and *b*. Arrows explained in text.

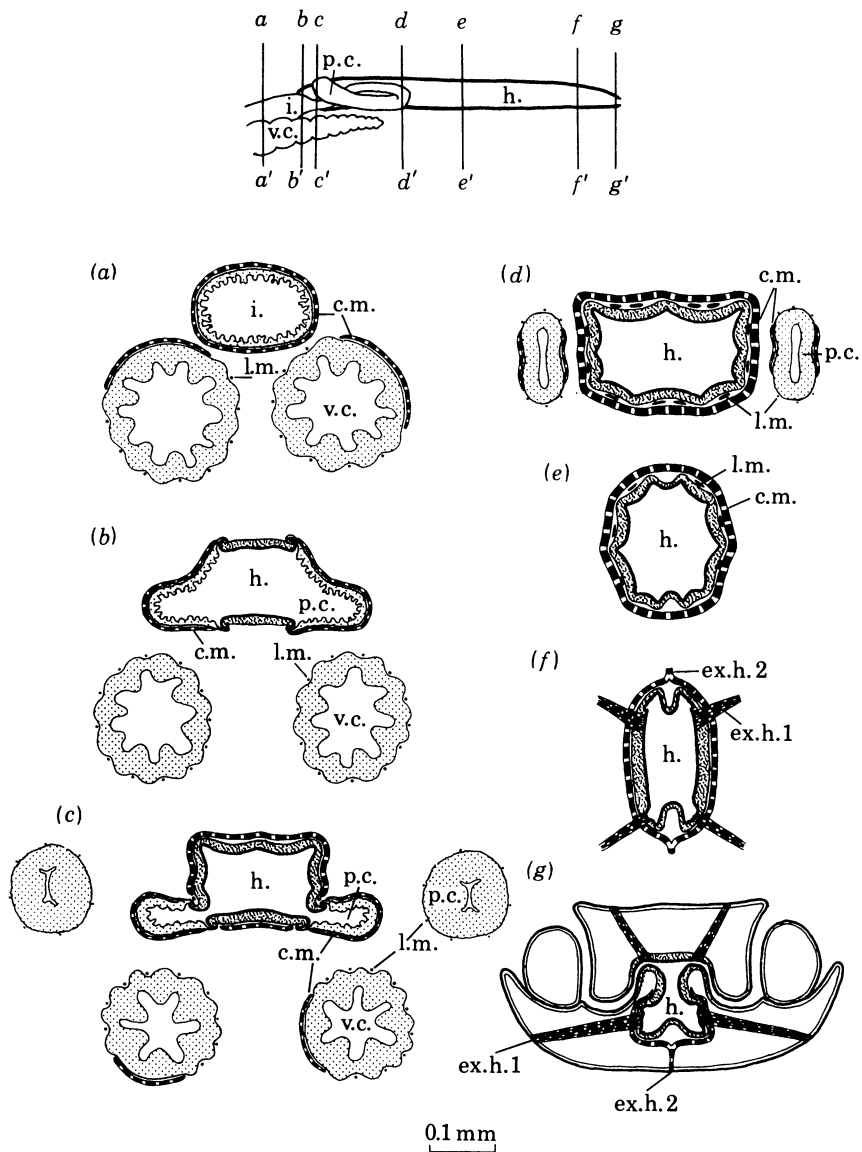


FIGURE 4. Transverse sections *a-g* of the posterior end of the gut, which correspond to lines *aa'-gg'* on drawing of the lateral view. The epithelium of the midgut is shaded by regular dots and that of the hindgut by dark shading.

#### 4. GENERAL FEATURES OF THE ALIMENTARY CANAL

The alimentary canal comprises a foregut, midgut and hindgut. The foregut and hindgut are derived from stomodeal and proctodeal ectoderm, respectively, and are lined throughout with cuticle. The midgut is derived from endoderm and has no cuticle.

The foregut is partly located within the cephalon (*c.* in figure 1) but extends posteriorly as the funnel of the stomach (*fu.st.*) to the junction of the fourth and fifth thoracic segments. The cephalic region is differentiated into the oesophagus (*o.*) and stomach (*st.*).

The midgut occupies the length of the thorax and terminates within the third abdominal segment. The intestine (*i.*) of the midgut links directly with the hindgut and is enlarged

considerably by the development of three pairs of caeca. The paired anterior dorsal caeca (d.c.) are essentially anterior extensions of the intestine that run on either side of the gut and terminate adjacent to the mid-region of the stomach. The paired ventral caeca (v.c.) open into the lumen of the foregut in the mid-region of the stomach (en.v.c. in figure 2). A restricted epithelial lining (short arrow in figure 2), located ventral to the foregut, links the ventral caeca with the intestine (i.). The ventral caeca are very long and extend posteriorly to the anterior region of the hindgut (h.). The paired posterior caeca (p.c.) are posterior extensions of the intestine that run posteriorly for a quarter of the length of the hindgut. They are looped anteriorly midway along their length and terminate lateral to their point of origin, at the junction between the mid and hindgut.

The hindgut (h.) unites with the midgut within the junction of the second and third abdominal segments and continues to the telson (t.) where it opens through the anus (a.).

As an aid to understanding the structure of the gut, the principles underlying its function are described. The digestive cycle is characterized by a short period of primary digestion, and a much longer period of secondary digestion. The primary process occurs in the stomach where ingested particles are confined to a channel within the gut lumen. These particles are supplied with enzymes and fluids from the ventral caeca. Any fine or soluble material released from the

### DESCRIPTION OF PLATES 1, 2 AND 3

FIGURE 5. Transverse fracture of oesophagus (o.) showing I-shaped lumen. Scale bar = 50  $\mu\text{m}$ , s.e.m.

FIGURE 6. Transverse fracture at stomach entrance showing anterior face of ampullar system (d.a. and l.a.). Scale bar = 50  $\mu\text{m}$ , s.e.m.

FIGURE 7. Setation (s.) at entrance to stomach ventral to lateral ampullae (l.a.). Scale bar = 50  $\mu\text{m}$ , s.e.m.

FIGURE 8. Transverse fracture at stomach entrance showing posterior face of lateral ampullae (l.a.). Note three forms of setae on ampullae (s. 1, s. 2, s. 3) and setae (s.) on wall of gut dorsal to the lateral ampullae. Scale bar = 10  $\mu\text{m}$ , s.e.m.

FIGURE 9. Transverse fracture at cardiac stomach entrance (cd.st.) viewed from behind. Food (fd) is confined to food channel by setae (s.fl.) located between food channel and filtration channel (fl.) and setae (s.) on ventral cardiac ridge (c.r.). Scale bar = 10  $\mu\text{m}$ , s.e.m.

FIGURE 10. Transverse fracture of cardiac stomach (cd.st.) viewed from behind. Food (fd) is confined to food channel by setae bounding circulation channel (s.cl.) dorsally and filtration channel (s.fl.) ventrally. Scale bar = 50  $\mu\text{m}$ , s.e.m.

FIGURE 11. Transverse fracture of stomach viewed from behind. Upward curve of setae from floor of food channel (large arrows) marks transition from cardiac region (cd.st.) to pyloric region (pl.st.). Terminations of folds of cuticle and setae (s.cl.) which separate the circulation channels (cl.) from the food channel in the cardiac stomach can be seen, left (arrowhead). Lower setation on vertex of ventral pyloric ridge (p.r.) forms first filter (f. I) of the two tier filtration system. The second filter (f. II) separates two pairs of channels (fn.fl.), which occur in the sides of the pyloric ridge, from the lumen of the first filter (fl.). The ventral pair of filter membranes (\*) of the second filter have been damaged; they curve into the lumen of the first filter. The distal ends of the setae, which form these membranes, should make contact with the base of the dorsal pair of filter membranes of the second filter (small arrows). Scale bar = 50  $\mu\text{m}$ , s.e.m.

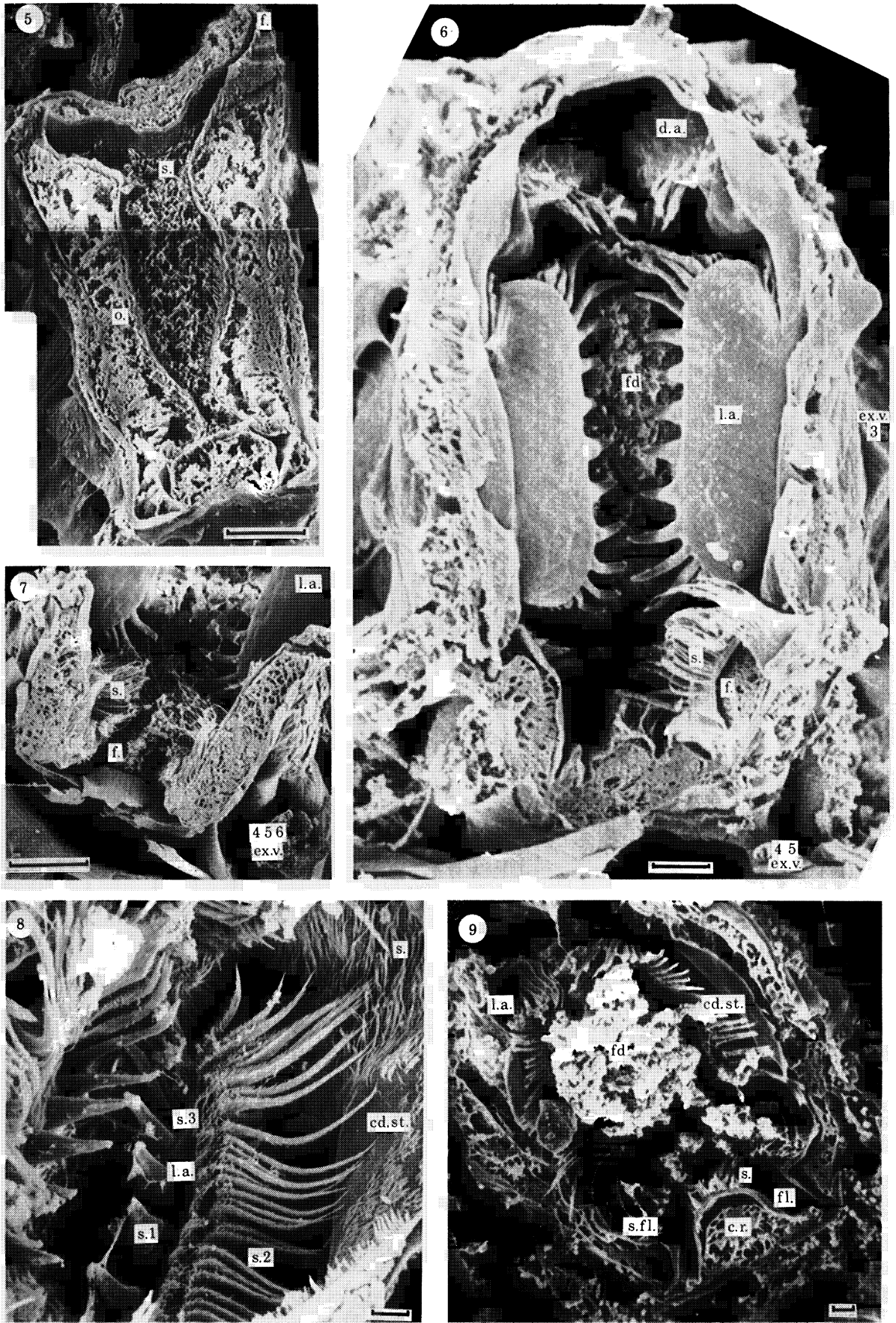
FIGURE 12. Lanceolate setae (arrow) on the vertex of the ventral pyloric ridge and fractured tips of the setae (s.cl.) which separate the food channel from the circulation channels. Scale bar = 1  $\mu\text{m}$ , s.e.m.

FIGURE 13. (a) Meshwork of setae (f. II) which forms the downstream surface (fn.fl.) of the second filter. Scale bar = 1  $\mu\text{m}$ , s.e.m. (b) Arrays of setules (f. II) forming the upstream surface (f. I) of the second filter. Scale bar = 1  $\mu\text{m}$ , s.e.m.

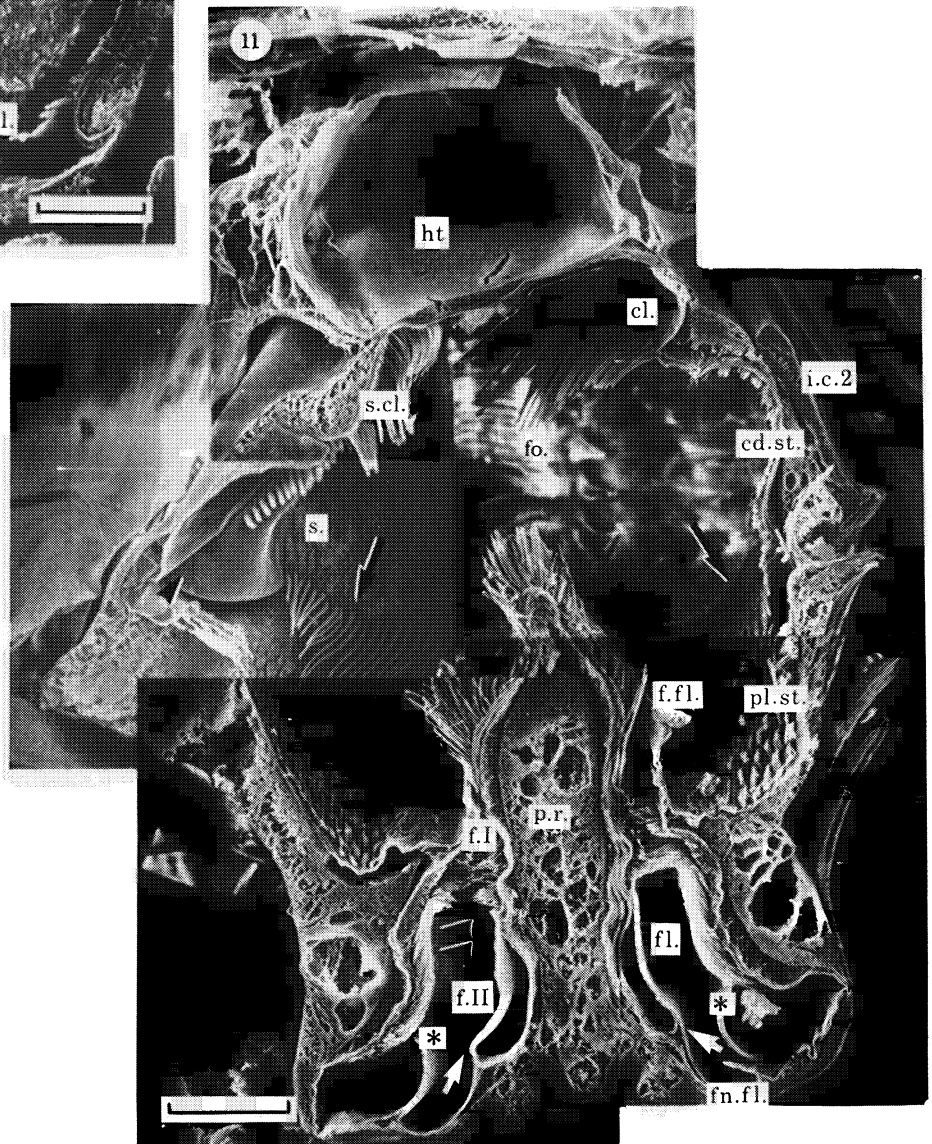
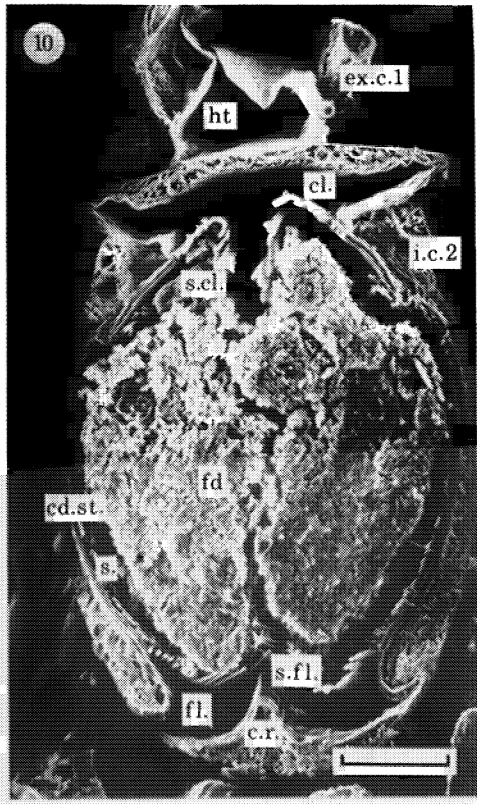
FIGURE 14. (a) Oblique section of the second filter (f. II). Each seta bears two rows of setules which overlap with those from adjacent setae. Scale bar = 1  $\mu\text{m}$ , t.e.m. (b) Transverse section of the setae forming the second filter (f. II). Note the bacteria and other material retained on the filter. Scale bar = 0.5  $\mu\text{m}$ , t.e.m.

FIGURE 15. The setae on the lateral wall of the filtration channel opposing the second filter. Setae in the dorsal row (arrow) are setulated and longer than those in the more ventral rows (arrowheads). Scale bar = 5  $\mu\text{m}$ , s.e.m.

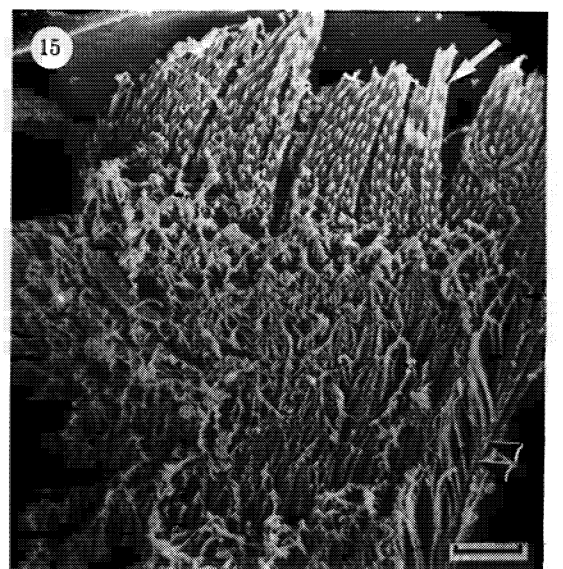
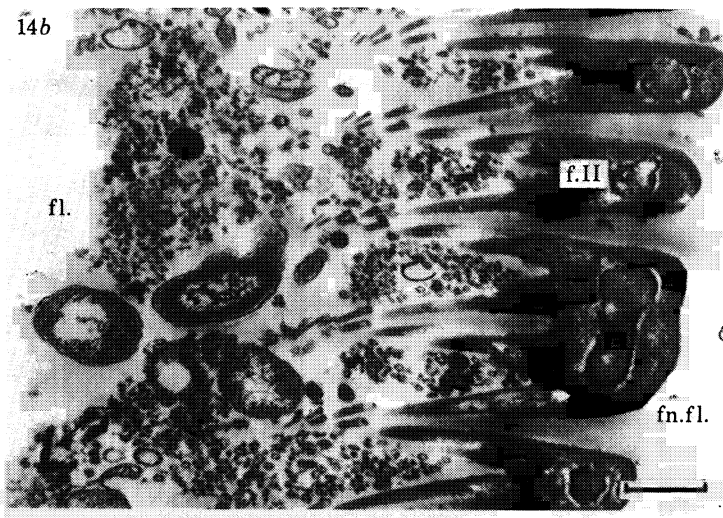
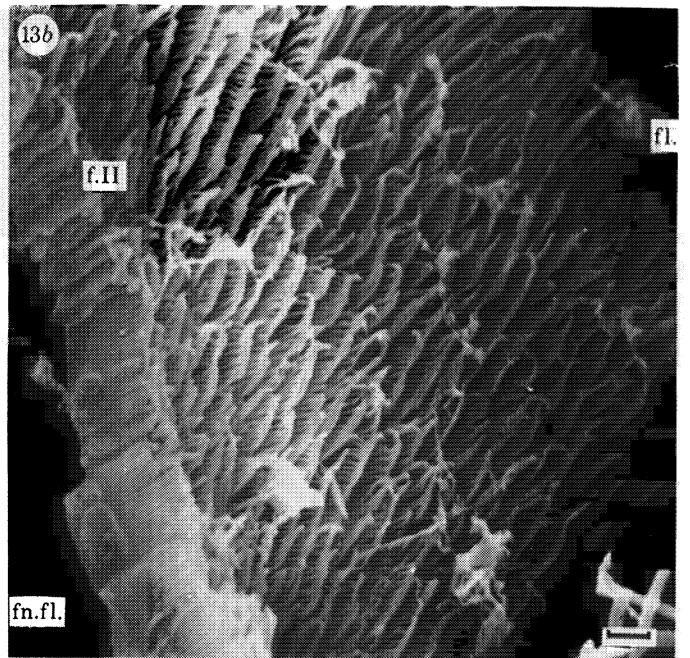
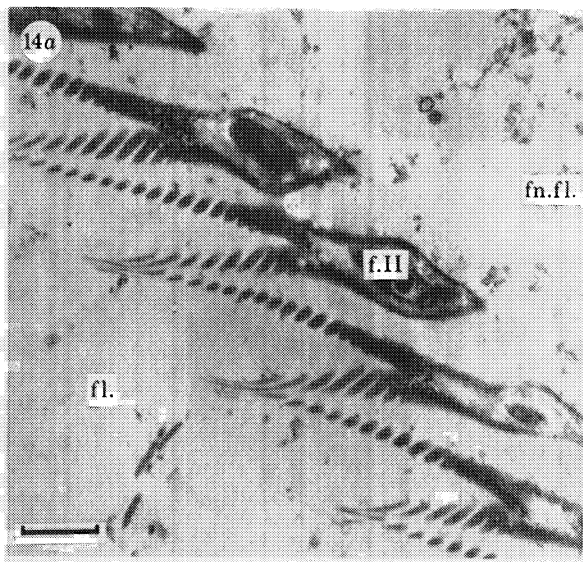
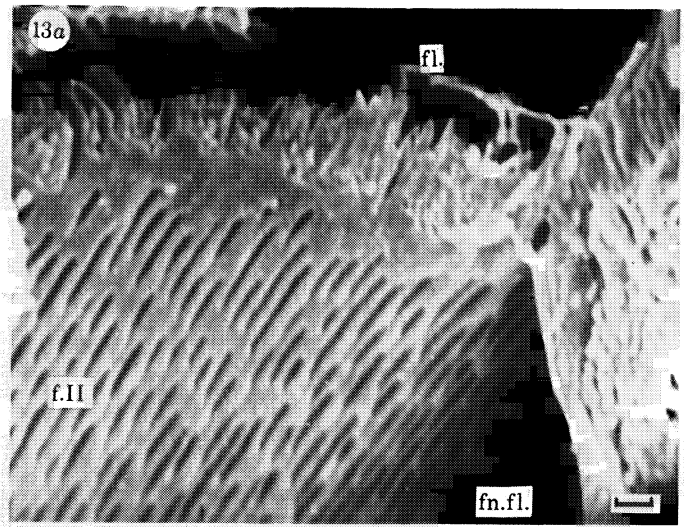
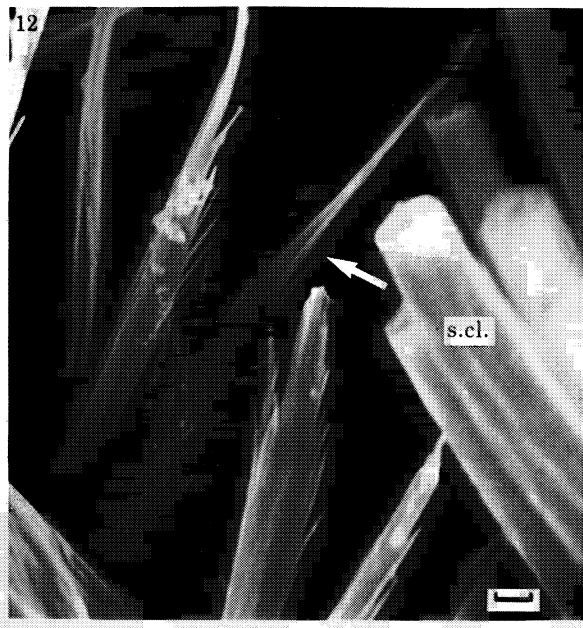




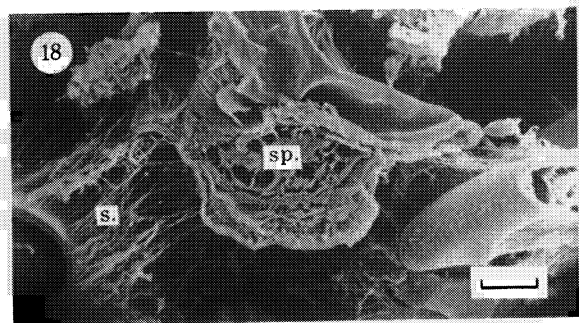
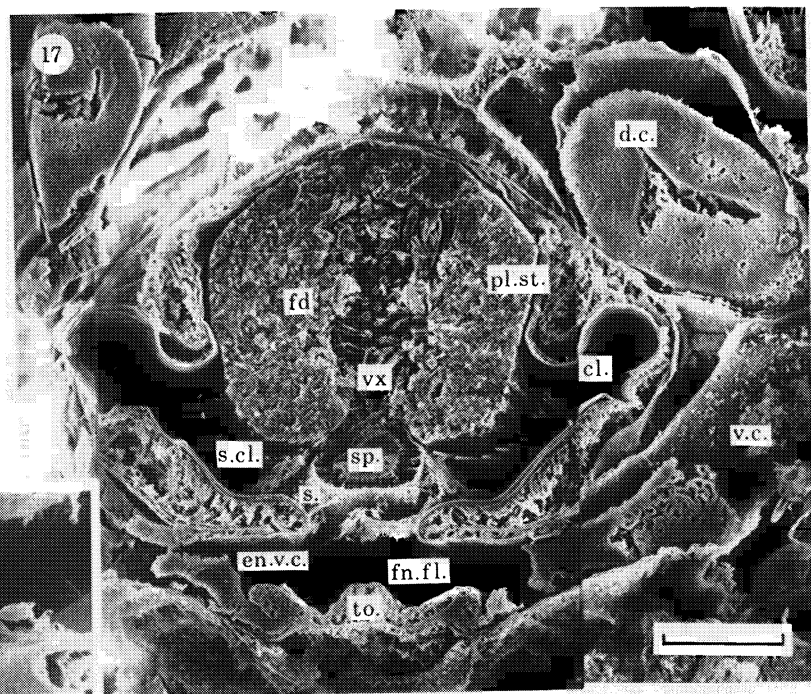
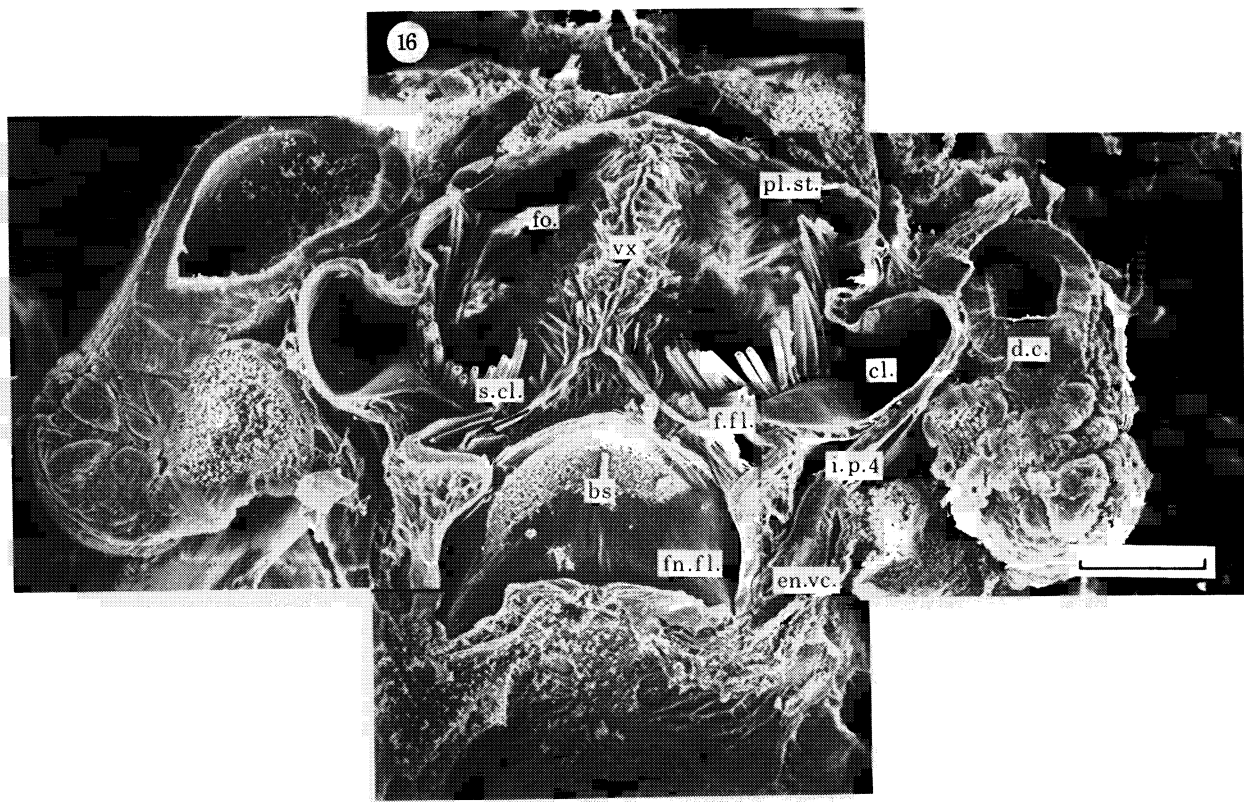
FIGURES 5-9. For description see opposite.



FIGURES 10 AND 11. For description see p. 56.



FIGURES 12-15. For description see p. 56.



FIGURES 16-18. For description see opposite.

## DESCRIPTION OF PLATES 4 AND 5

**FIGURE 16.** Transverse fracture of the pyloric stomach (pl.st.) posterior to the filtration system. Circulation channels (cl.) and ventral caeca (en.v.c.) are approaching the confluence with the filtration channels (fn.fl.). Rows of setae which guard the circulation channels (s.cl.) curve towards the ventral pyloric ridge (bs and vx) such that the setae are directed posteriorly. The vertex (vx) of the ventral pyloric ridge extends almost to the roof of the gut and is covered with setae. Anterior dorsal caeca (d.c.) are adjacent to the walls of the gut. Scale bar = 50  $\mu\text{m}$ , s.e.m.

**FIGURE 17.** Transverse fracture of the pyloric stomach (pl.st.) at the confluence of the circulation (cl.) and filtration (fn.fl.) channels and the openings of the ventral caeca (en.v.c.). Rows of setae guarding the filtration channels (s.cl.) retain solid material (fd) within the food channel. A valve spigot (sp.) is located in the fissure between the circulation channels and the entrance to the ventral caeca. Anterior dorsal caeca (d.c.) are still adjacent to the walls of the gut. Scale bar = 50  $\mu\text{m}$ , s.e.m.

**FIGURE 18.** Valve spigot (sp.), posterior to the setae, which guards the circulation channels. The food channel is separated directly from the entrance to the ventral caeca. Scale bar = 10  $\mu\text{m}$ , s.e.m.

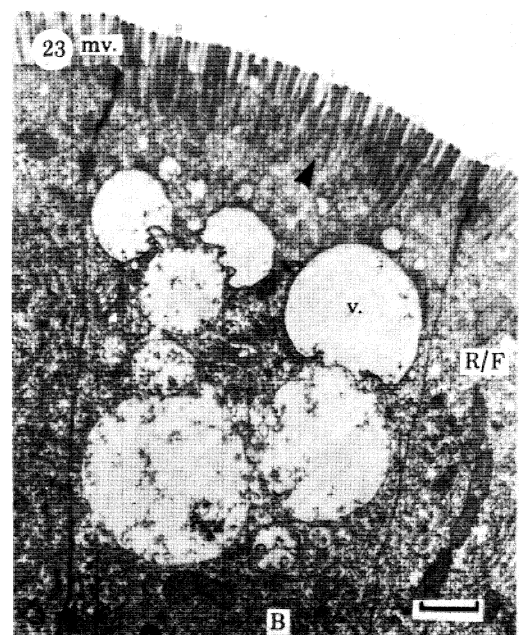
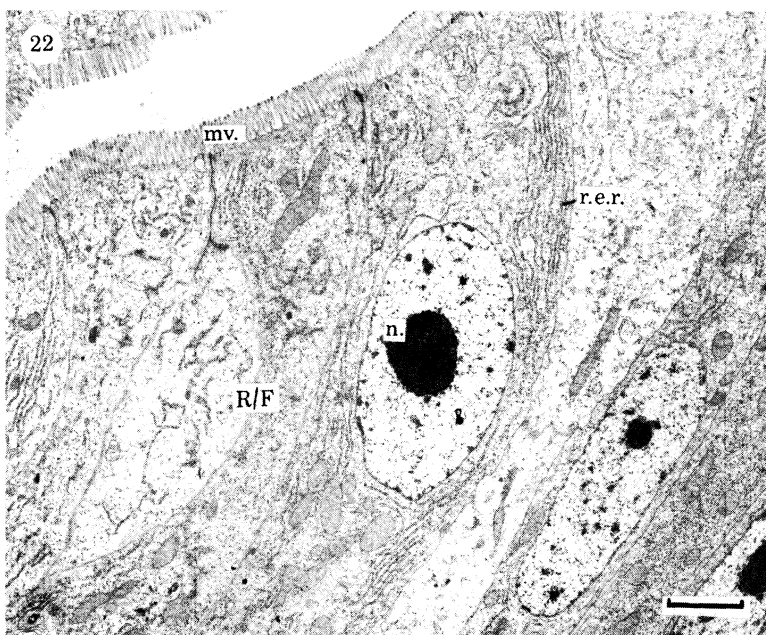
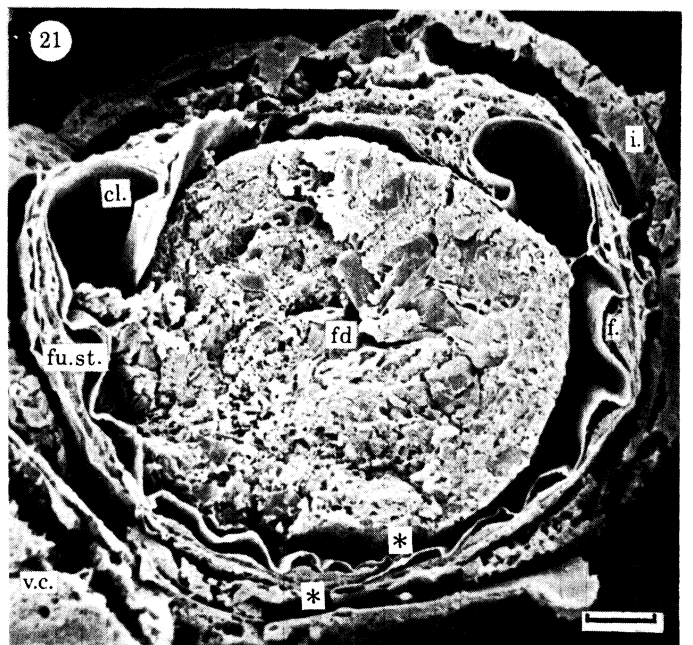
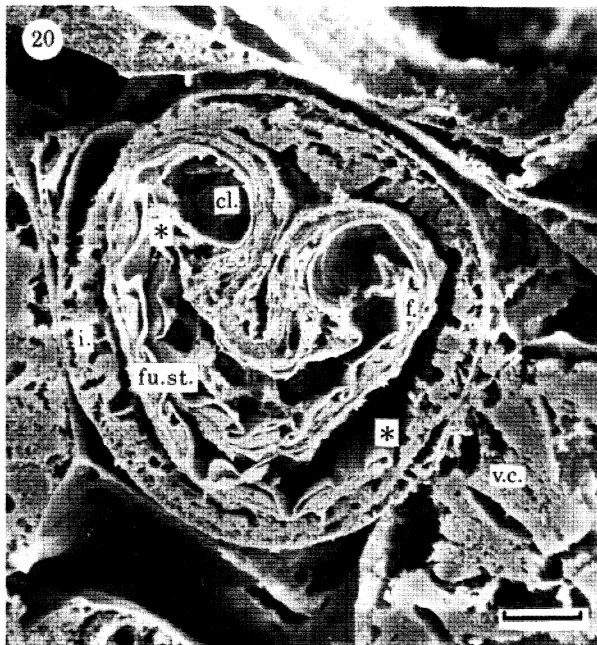
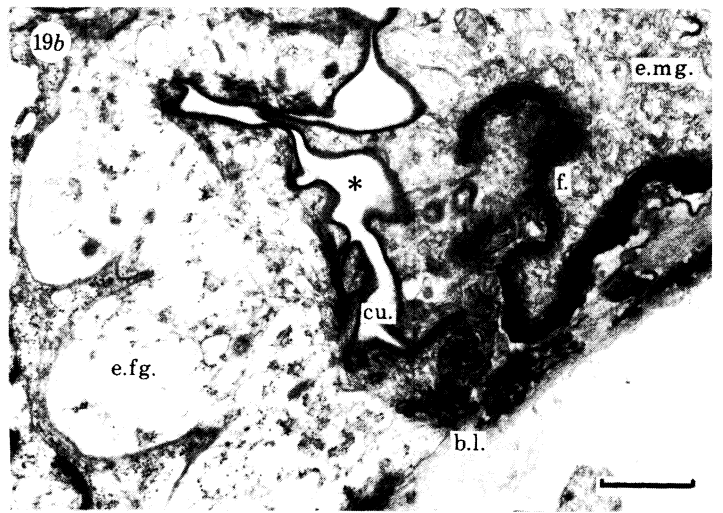
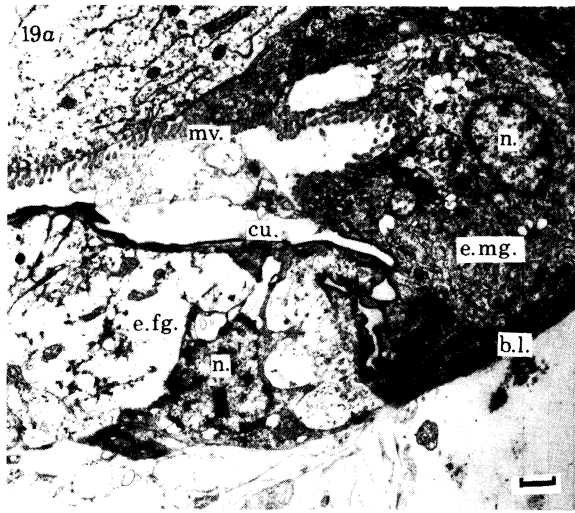
**FIGURE 19.** (a) Junction of the epithelia of the foregut (e.fg.) and the midgut (e.mg.). The ventral caeca are attached to the tongue of cuticularized epithelium which arises anteriorly from the foregut. Scale bar = 1  $\mu\text{m}$ , t.e.m. For purposes of comparison, transmission electron micrographs between figures 19a and 35 are of different regions of the same midgut. (b) Region in figure 19a which shows a cleft (\*) in the cuticular lining (cu.) close to an infold (f.) of the basal lamina (b.l.) Scale bar = 1  $\mu\text{m}$ , t.e.m.

**FIGURE 20.** Transverse fracture of an empty foregut funnel (fu.st.); the walls of the ventral region overlap extensively (\*). Scale bar = 20  $\mu\text{m}$ , s.e.m.

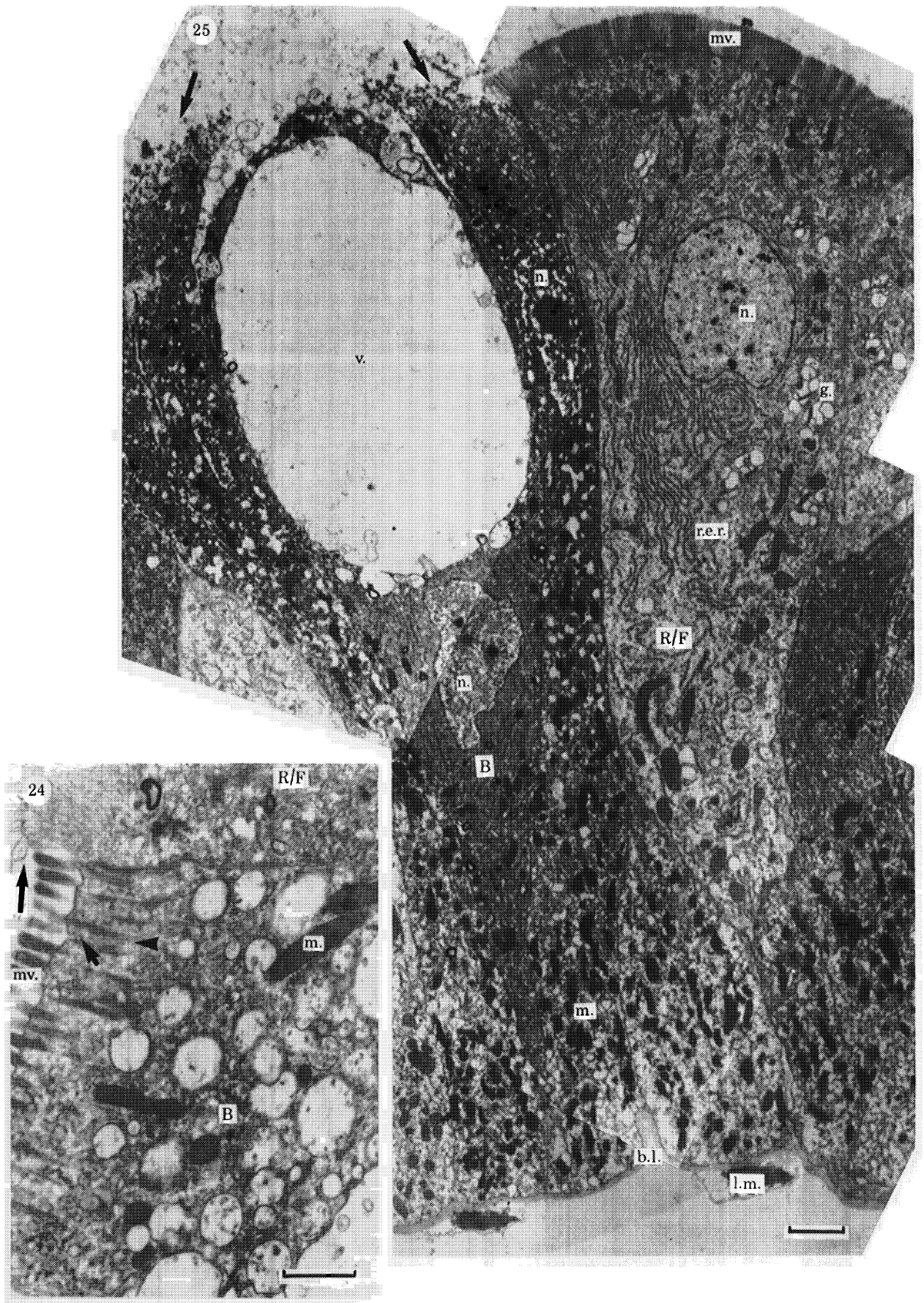
**FIGURE 21.** Transverse fracture of the funnel (fu.st.) which is full of food (fd); the overlap of the walls (\*) is reduced and the dorsal wall configuration changes (cf. figure 20). Scale bar = 20  $\mu\text{m}$ , s.e.m.

**FIGURE 22.** Distal end of the ventral caecum which consists of R/F cells (R/F) only. Scale bar = 2  $\mu\text{m}$ , t.e.m.

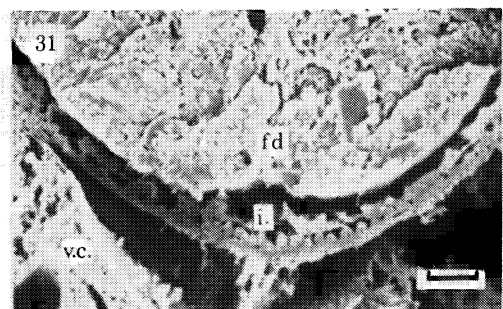
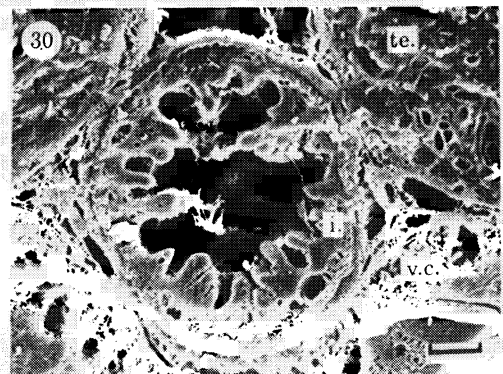
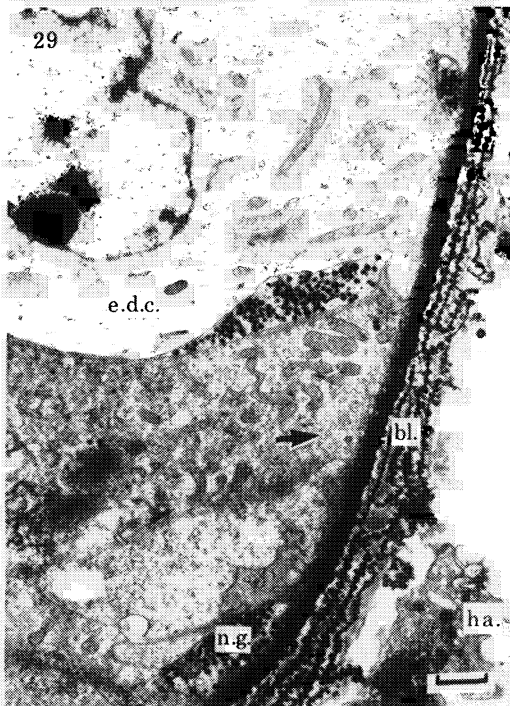
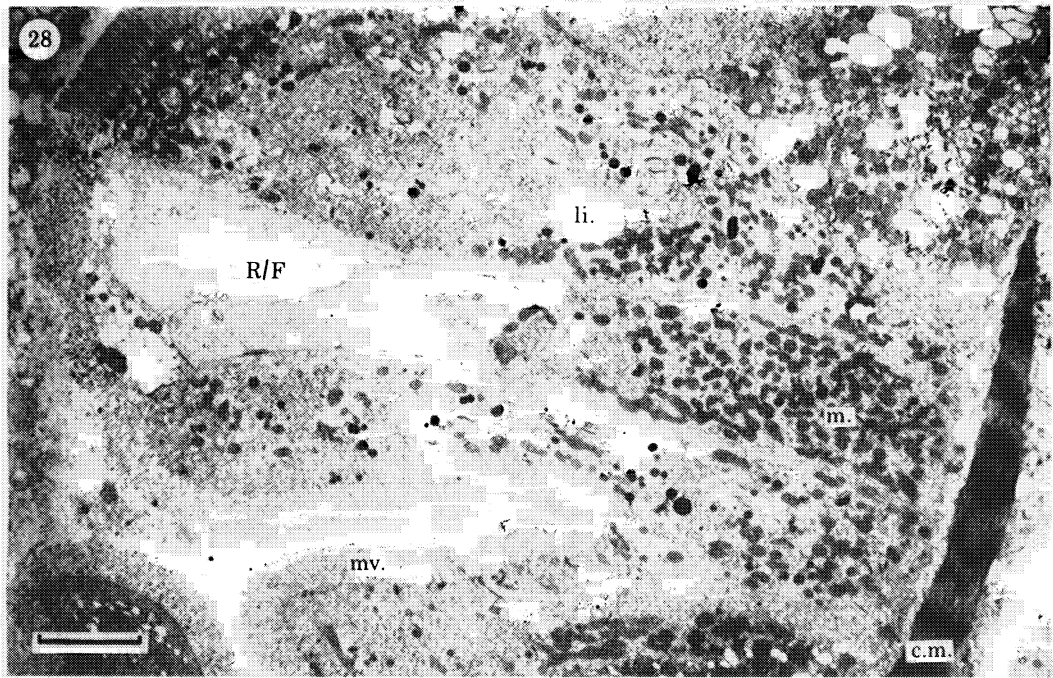
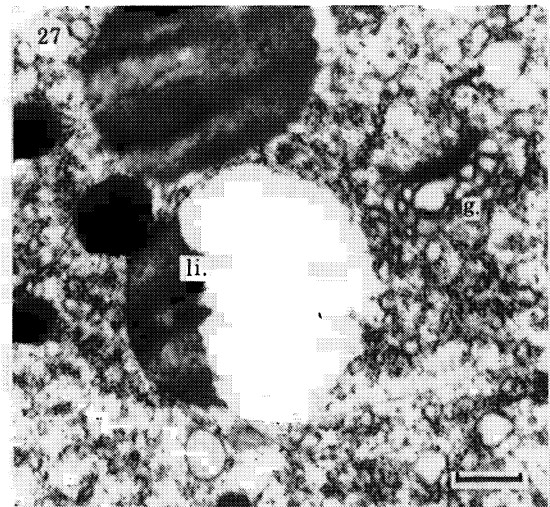
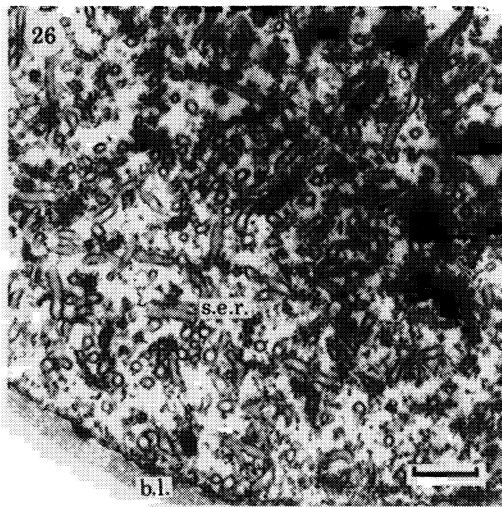
**FIGURE 23.** Ventral caecum proximal to figure 22, where cells on the epithelial ridges contain vacuoles (v.) in the apical regions. Microvilli (mv.) are reduced in height and have fibrous roots (arrowhead) extending into the cytoplasm. These cells are developing into B cells (B). Scale bar = 1  $\mu\text{m}$ , t.e.m.



FIGURES 19-23. For description see previous page.

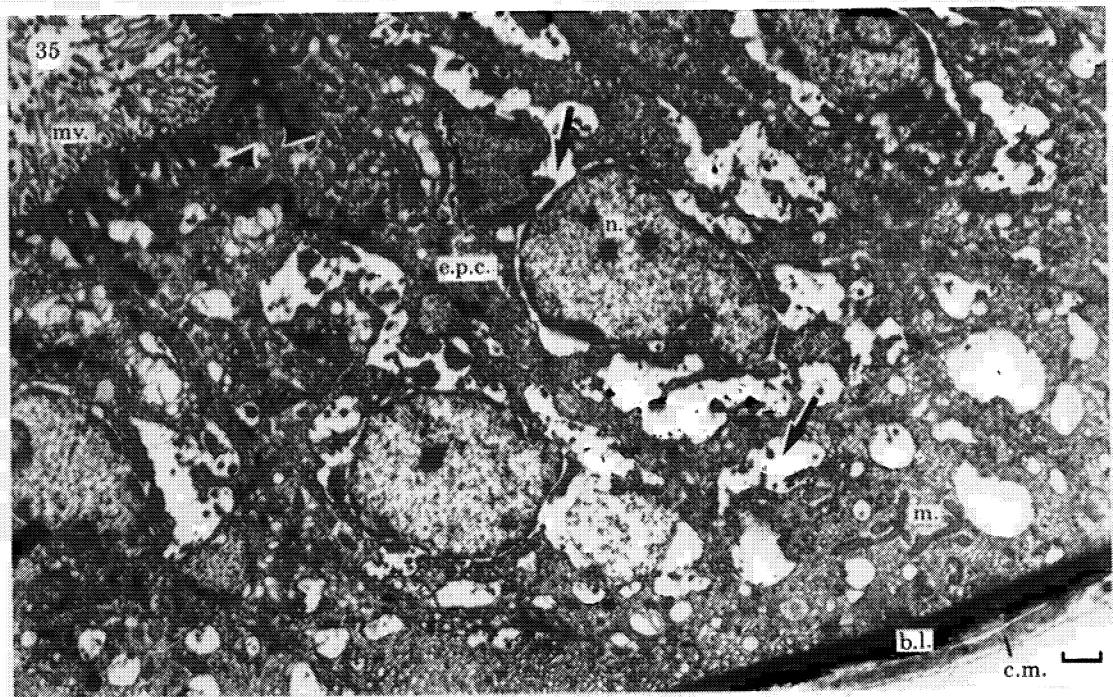
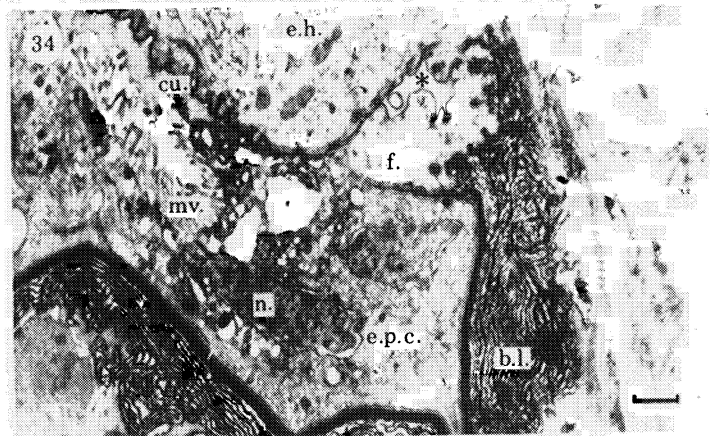
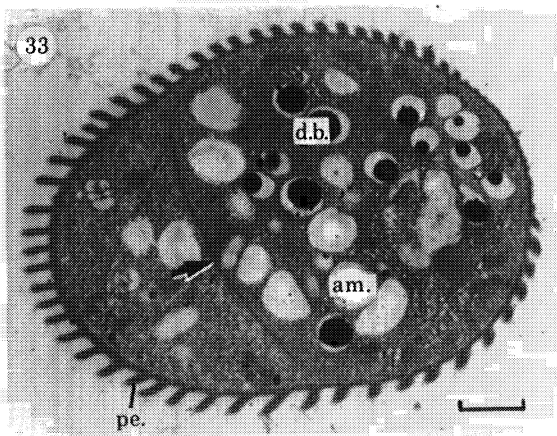
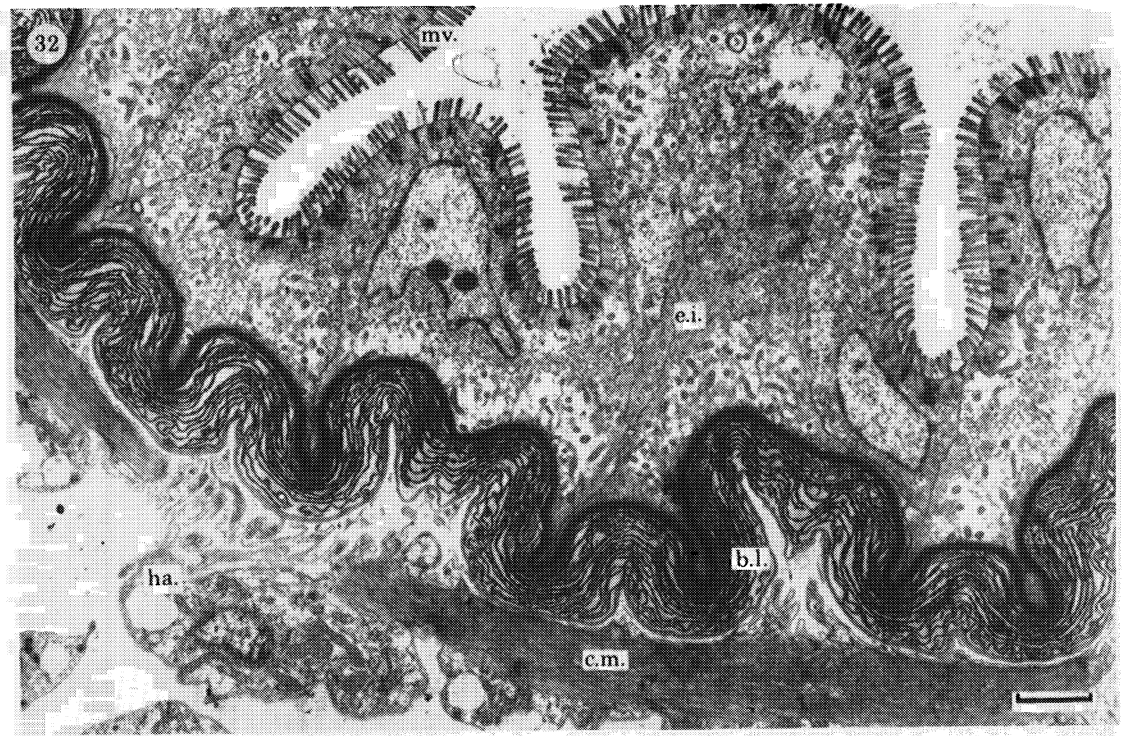


FIGURES 24 AND 25. For description see p. 57.



FIGURES 26-31. For description see p. 57.





FIGURES 32-35. For description see p. 57.

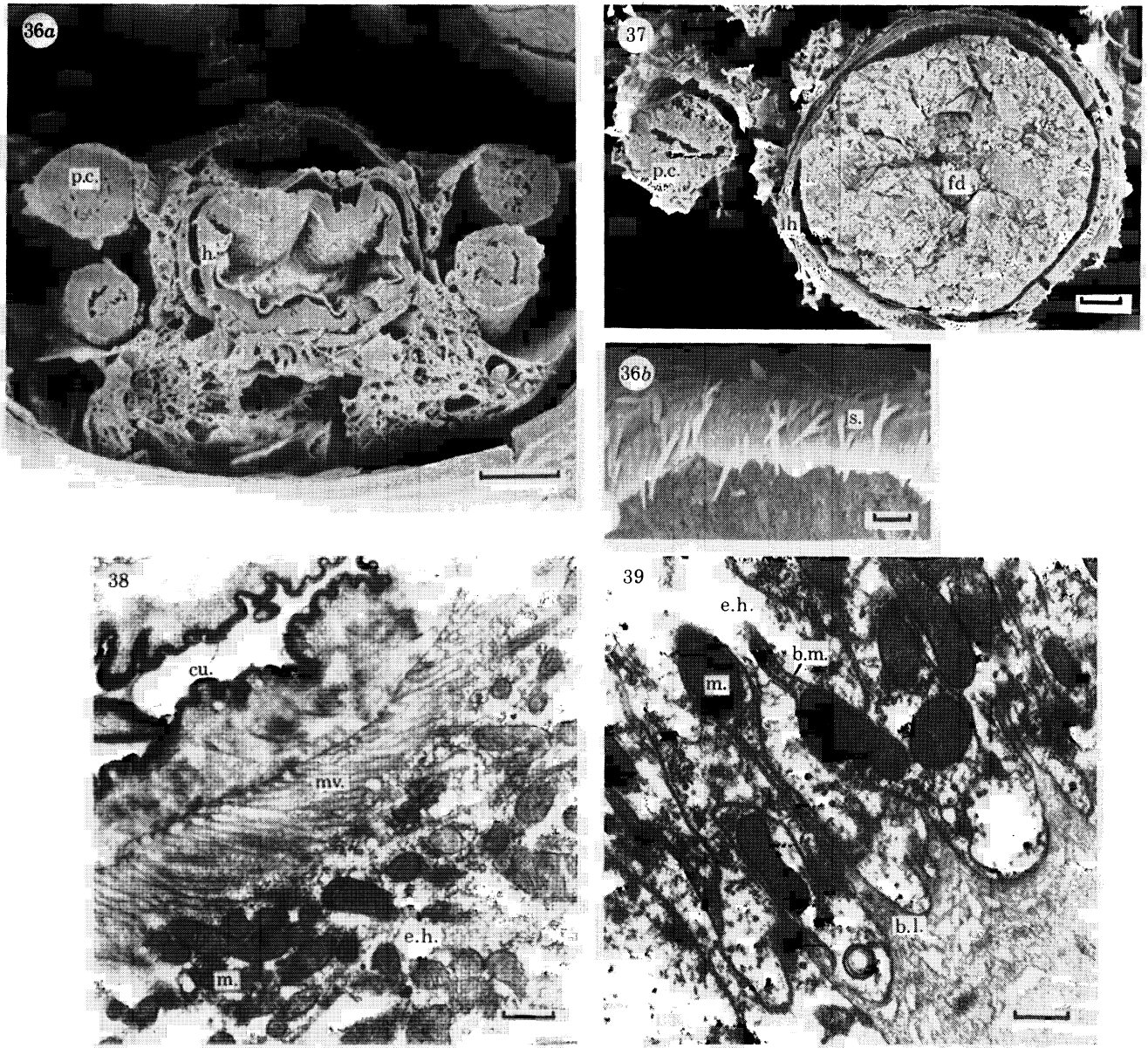


FIGURE 36. (a) Transverse fracture of an empty hindgut (h.) with flanking posterior caeca (p.c.) which are folded back on each other. Scale bar = 50  $\mu\text{m}$ . (b) Setation (s.) on the cuticular lining in figure 36a. Scale bar = 2  $\mu\text{m}$ , s.e.m.

FIGURE 37. Transverse fracture of a full hindgut (h.). Scale bar = 20  $\mu\text{m}$ , s.e.m.

FIGURE 38. Microvilli (mv.) underlie the cuticular lining (cu.) of the hindgut (e.h.). Scale bar = 0.5  $\mu\text{m}$ , t.e.m.

FIGURE 39. Basal cell membrane (b.m.) of the hindgut (e.h.) has folds associated with mitochondria (m.) to form 'ion pumps'. Scale bar = 0.5  $\mu\text{m}$ , t.e.m.

surface of the particles is filtered into channels and transported to the ventral caeca. The residual particles are transported posteriorly along the intestine and eventually released as faeces from the hindgut. In the ventral caeca, material is digested by the secondary process and the products are absorbed by the epithelium. The tissues in the posterior region of the gut are involved in excretion and reabsorption. Evidence for these conclusions is provided in this paper and by further work to be described in another publication.

### 5. MOUTH AND OESOPHAGUS

The mouthparts are arranged vertically with the mandibles (md. in figure 3*a*) forming the uppermost elements adjacent to the mouth (mo.). The oesophagus (o. in figure 2*a*) extends dorsally from the mouth to the stomach (cd.st.) and has longitudinal folds (f. in figure 5, plate 1) in the wall which produce an I-shaped section for the lumen in the mid-region.

The cuticle lining the walls of the mouth and the oesophagus is densely covered with setae (s. in figure 5, plate 1) about 5  $\mu\text{m}$  in length, which are directed posteriorly.

At the junction between the oesophagus and the stomach, the walls are modified to accommodate a valve system (d.a. and l.a. in figures 2*a* and 3*b*; figure 6, plate 1). The main component takes the form of two dish-shaped folds or ampullae (l.a.), which intrude into the lumen and are arranged with the convex surface on the anterior side. These hinge onto the lateral wall and can open towards the oesophagus like a pair of doors. A reduction in the thickness of the lateral walls of the oesophagus conforms to the shape of the ampullae when

### DESCRIPTION OF PLATES 6, 7 AND 8

FIGURE 24. Further development of B cells shows an increase in the number of apical vacuoles and the appearance of pinocytotic activity at the apical membrane (small arrow). Microvilli (mv.) are reduced further in height and are still characterized by the long fibrous roots (arrowhead). Neighbouring R/F cell (R/F) degenerates with vesicles (long arrow) forming from the microvilli. Scale bar = 1  $\mu\text{m}$ , t.e.m.

FIGURE 25. Final stage in B cell (B) development. Apically there is a single large vacuole (v.) and no microvillous border. Adjacent R/F cells (long arrows) show advanced degeneration. Scale bar = 2  $\mu\text{m}$ , t.e.m.

FIGURE 26. Smooth endoplasmic reticulum (s.e.r.) at base of an R/F cell in the mid-region of a ventral caecum. Scale bar = 0.5  $\mu\text{m}$ , t.e.m.

FIGURE 27. Lipid (li.) in an R/F cell in the proximal region of a ventral caecum. Scale bar = 0.5  $\mu\text{m}$ , t.e.m.

FIGURE 28. Proximal region of a ventral caecum. R/F cells (R/F) contain mitochondria (m.) and lipid (li.). B cells are absent. Scale bar = 5  $\mu\text{m}$ , t.e.m.

FIGURE 29. Proximal region of an anterior dorsal caecum (e.d.c.) with nerve cell processes containing neurosecretory granules (n.g.). Scale bar = 1  $\mu\text{m}$ , t.e.m.

FIGURE 30. Transverse fracture of an empty intestine (i.). The volume is reduced and the epithelium is infolded (cf. figure 31). Scale bar = 10  $\mu\text{m}$ , s.e.m.

FIGURE 31. Transverse fracture of a full intestine (i.). The volume is increased and the epithelium is not folded (cf. figure 30). Scale bar = 10  $\mu\text{m}$ , s.e.m.

FIGURE 32. Transverse section of an intestine (e.i.) showing the microvillous border (mv.), thick basal lamina (b.l.) and circular muscle (c.m.). Scale bar = 2  $\mu\text{m}$ , t.e.m.

FIGURE 33. A gregarine parasite which sometimes occurs in the intestine. Note the multi-layered pellicle (pe.), amylopecten granules (am.) and dark bodies (d.b.). An arrow shows a transverse septum. Scale bar = 1  $\mu\text{m}$ .

FIGURE 34. Junction of the mid (e.p.c.) and hindgut (e.h.). Cleft (\*) in the cuticular lining (cu.) and infold (f.) of the basal lamina (b.l.) are close. Scale bar = 1  $\mu\text{m}$ , t.e.m.

FIGURE 35. Transverse section of the proximal posterior caecum (e.p.c.). Note the distension of the nuclear envelopes and the endoplasmic reticulum (arrows). Mitochondria have a dense matrix (arrowhead). Scale bar = 1  $\mu\text{m}$ , t.e.m.

they are in the open position. A row of curved setae is arranged along the free margin of these ampullae and the setae from each row interdigitate when the ampullae occlude the lumen of the gut. The line of setae from the free margin is continuous across the base of the posterior face of the ampullae. The setae change gradually from the short (*ca.* 20  $\mu\text{m}$ ), stout form (s. 1 in figure 8, plate 1) at the free margins to the long (*ca.* 50  $\mu\text{m}$ ) slender, setulated form (s. 2) at the base. Also, the base has a row of short fine setae (s. 3) alongside the row of long setae. This arrangement produces a 'basket-like' structure (figure 8, plate 1).

The valve also has two hinged, dorsal ampullae (d.a. in figure 6, plate 1) which are slightly posterior to the lateral ampullae. The free margins of the dorsal ampullae bear a row of flattened, setulated setae. In addition, the lumen between the dorsal and lateral ampullae is obstructed by fine setae (s. in figure 8, plate 1) about 10  $\mu\text{m}$  in length.

Ventral to the ampullae (figure 3*b*; figures 6 and 7, plate 1) the lumen between the oesophagus and the stomach is screened by setae (s) which cover a complex arrangement of internal, longitudinal folds (f) in the walls of the gut.

#### 6. GENERAL FEATURES OF THE STOMACH

The stomach is separated into the cardiac (cd.st.), pyloric (pl.st.) and funnel (fu.st.) regions (figure 2*a*; regions are divided by dotted lines in figure 3, inset). The cardiac or anterior region is separated from the pyloric region by discontinuities in some of the epithelial ridges and in the main linear arrangements of setae. There is also complete discontinuity in the arrangement of the musculature between the two regions (figure 2*b*). The funnel or posterior region of the stomach takes the form of a comparatively simple tube, devoid of setae. Longitudinally, the lumen of the stomach is divided into the food (fo. in figure 3), circulation (cl.) and filtration channels (fl.). The food and circulation channels extend the length of the stomach, but the filtration channels terminate at the entrance of the ventral caeca. The circulation channels also connect with the ventral caeca via a valve (figure 3*h*) having gradually changed position along the length of the pyloric stomach, but the food channel has no direct contact with these caeca.

#### 7. CARDIAC STOMACH

In the cardiac stomach, the food channel dominates the lumen (figure 3*c*); the circulation channel is located dorsally, the filtration channels ventrally.

Adjacent to the ampullar system, the circulation channel occupies the full width of the stomach and is separated from the food channel by two rows of setae (s.cl. in figure 3*c*; figure 10, plate 2), which arise from the folds in the dorsolateral walls of the gut and are directed posteriorly and ventrally. A gap of 1  $\mu\text{m}$  separates the setae. Towards the posterior end of the cardiac stomach (figures 3*d, e*), the circulation channel (cl.) divides into two channels, situated dorsolaterally. The screen between the circulation and food channels is maintained by the setae (s.cl. in figure 2*a*) which change progressively in orientation along the dorsolateral folds. The final setae in each row are directed dorsally at the roof of the stomach. Ventral to the circulation channels, the lateral walls of the food channels are covered by dense groups of short (*ca.* 5  $\mu\text{m}$ ), posteriorly directed setae (s. in figures 10 and 11, plate 2).

The ventral region of the food channel is separated from two filtration channels (fl.) by two rows of setae (s.fl. in figure 3*c*; figure 9, plate 1 and figure 10, plate 2) arising from the ventrolateral walls. At the anterior of the stomach, the rows run parallel to the floor of the

gut, but towards the posterior end of the cardiac stomach they curve dorsally and terminate close to the circulation channels (long arrow(s) in figure 2*a*; figure 11, plate 2). Anteriorly, the distal ends of the setae interdigitate to form a screen or filter, (s.fl. in figure 9, plate 1 and figure 10, plate 2). A gap of 2  $\mu\text{m}$  separates the bases of the setae, which is wider than the gap between the setae limiting the circulation channels. The filtration channels are separated by the ventral cardiac ridge (c.r.) which arises from the floor of the stomach along the midline (figure 3*c*; figure 9, plate 1 and figure 10, plate 2). The apex of the ridge has short, fine setae (s. in figure 9, plate 1) which interdigitate with the setae (s.fl.) separating the food and filtration channels. Posteriorly the setae (s.fl.) gradually change in orientation from a medial to a posterior direction and the screen between the food and filtration channels is maintained by overlapping ventrolateral folds (f.fl. in figures 2*a* and 3*d*) which arise from the lateral walls. The ventral cardiac ridge (c.r.) does not extend into this region of the stomach (figure 2*a*).

The boundary between the cardiac and pyloric regions occurs ventrally at the termination of the cardiac ridge and extends dorsally along the line of setae (long arrow in figure 2*a*) which, anteriorly, separates the food and filtration channels (s.fl.); it continues to the terminal setae of the screens separating the food and circulation channels at the posterior end of the cardiac stomach (arrowhead in figure 2*a* and figure 11, plate 2). Finally, the boundary terminates dorsally at the ridge (\* in figures 2*a*, *b*) which crosses the roof of the stomach. The three types of channel in the cardiac stomach continue into the pyloric stomach.

#### 8. PYLORIC STOMACH

The volume of the food channel in the pyloric stomach is restricted by a massive intrusion of the ventral pyloric ridge (p.r., or vx and bs, in figures 2*a*, 3*e*, *f*, *g*; figure 11, plate 2 and figure 16, plate 4) which arises from the floor of the gut. This ridge varies considerably in structure along its length but, essentially, it is differentiated into the basis (bs), which completely divides the filtration channels, and the vertex (vx), which substantially divides the lumen of the food channel. The ridge terminates towards the posterior end of the pyloric region (figures 2*a*, 3*h*; figure 17, plate 4) at the confluence of the circulation and filtration channels with the openings of the ventral caeca (en. v.c.). In this region the ridge is extended posteriorly to form a spigot for a valve (sp. in figure 2*a*).

The lateral walls of the food channel, ventral to the circulation channels, are covered with setae which have a similar structure and arrangement to those described for the same region in the cardiac stomach (s. in figure 11, plate 2). Dorsal to the circulation channels, setae are sparse and unevenly distributed.

The channels change position gradually along the length of the pyloric stomach. Anteriorly, the circulation channels (cl.) are situated dorsolaterally (figure 3*f*), but become progressively more lateral at the posterior end (figure 3*h*; figures 16 and 17, plate 4), where they are interposed between the food and filtration channels. Large outfolds in the lateral wall of the gut accommodate each circulation channel. As in the cardiac stomach, a row of setae separates the circulation channel from the food channel but eventually curves medially across the floor of the food channel, anterior to the termination of the ventral pyloric ridge (s.cl. in figure 16, plate 4). In this region, the individual setae are directed posteriorly (s.cl. in figure 17, plate 4) alongside the spigot (sp.) that extends from the ridge, thereby maintaining the screen between the food and circulation channels.

The food channel of the pyloric stomach is separated from the filtration channels by a pair

of ventrolateral folds in the walls of the gut (f.fl. in figures 3*e, f, g*; figure 11, plate 2 and figure 16, plate 4), which extend directly from the cardiac stomach. The folds are separated by the intrusion of the vertex (vx) of the ventral pyloric ridge into the lumen of the food channel. The setae of the vertex form a screen or filter between the food channel and the filtration channels, where the apices of the folds run parallel to the sides of the vertex (figures 3*e, f*; figure 11, plate 2). This screen forms the first filter (f. I) of a double filtration system in the pyloric stomach and is essentially continuous with the filter in the cardiac stomach. At the anterior of the pyloric stomach, the vertex has a dense array of fine setae of variable length (figure 11, plate 2). Towards the posterior, where the ridge attains its full height, the density of the setae on the vertex is maintained, but they become more uniform in length, lanceolate and bear setules (arrow in figure 12, plate 3).

The second filter (f. II) of the double filtration system is located within the filtration channels of the pyloric stomach (figure 3*e, f*; figure 11, plate 2). On each side of the basis (bs) of the ventral pyloric ridge, there are two 'filter membranes' (f. II) which effectively delimit two final, adjacent channels (fn.fl. in figure 3*e, f*, figure 11, plate 2). These 'filter membranes' are formed by a row of setae on the ventral margin of each channel, which are attached to each other at regular intervals along their length (figure 13*a*, plate 3) which extends to the dorsal margin of each channel. Each seta within the membrane has two rows of short setules (figures 13*b*, 14*a, b*, plate 3) facing the channel of the first filter (fl.). The distal ends of each row of setules are in contact with those from the neighbouring setae (figures 13*b*, 14*a, b*, plate 3). The gaps between the setules form the pores of the filter which are *ca.* 0.06  $\mu\text{m}$  in width (figure 14*a*, plate 3).

Within the filtration channels, both the first and second filters are elaborated further by the setation of the lateral walls of the gut (double arrowheads in figure 11, plate 2 and figure 15, plate 3). The setae are *ca.* 8  $\mu\text{m}$  in length with a dense arrangement (figure 15, plate 3). Their orientation varies with the curvature of the walls but, essentially, they are directed dorsally. Their distal ends can have direct contact with the setules of the 'filter membrane' of the second filter (f. II). In addition, towards the posterior of the second filter system, the setae in the extreme dorsal row on the walls are differentiated further (arrow in figure 15, plate 3). Each seta is much longer (*ca.* 15  $\mu\text{m}$ ) and thicker than those in the more ventral rows, and has short setules located on the surface exposed to the channel of the first filter (fl.). The modified setae are located slightly dorsal to the second filter (f. II) and are directed towards the first filter (f. I).

The second filter system is terminated by the fusion of each 'filter membrane' to the lateral walls of the gut. The channels of the filter (fn.fl. in figure 3*e, f*; figure 11, plate 2 and figure 16, plate 4) extend and open into the confluence of the circulation channels (cl.) and the ventral caeca (en.v.c. in figure 3*h*; figures 16 and 17, plate 4). The first filter is restricted by an increase in the width of the ventral pyloric ridge (arrow in figure 3*g*; figure 16, plate 4) which abuts the lateral walls, ventral to the apices of the ventrolateral folds (f.fl.) that occur between the food and filtration channels.

At the confluence, the spigot of the valve (sp. in figures 2*a*, 3*h, i*; figures 17 and 18, plate 4) separates the circulation channels (cl.) from the filtration channel (fn.fl.) and the opening to the ventral caeca (en.v.c.). In transverse section, the spigot has a rounded keel and flattened lateral extensions (sp. in figure 18, plate 4) and the whole structure is tapered and curved slightly in a dorsal direction (sp. in figure 2*a*). The spigot fits into a fissure in the ventral wall of the gut. Setae (s. in figures 17 and 18, plate 4) occur on the surface of the spigot and the

margins of the fissure. Where the ventral caeca open into the confluence beneath the valve, the epithelium of the midgut between the caeca and the intestine is separated along the midline by a tongue of cuticularized epithelium (to.) arising anteriorly from the foregut (figure 3*h, i*; figure 17, plate 4). Posterior to the confluence, the epithelium from the midgut becomes continuous across the midline, ventral to the tongue of epithelium from the foregut (figure 3*i*). This tongue has a dorsal ridge which extends along its length. The posterior end of the pyloric stomach is marked by the termination of both the spigot (sp.) and the tongue (to. in figure 2*a*).

The anterior dorsal caeca (d.c.), originating from the midgut, are located dorsolateral to the stomach (figure 3*f, g*; figures 16 and 17, plate 4). The posterior regions of the caeca make contact with and open against the outer surface of the pyloric stomach (figure 3*i*). Where the stomach surface is open to the caecal lumen, it is lined with cuticle since here the stomach wall is folded to produce a double layer of epithelium, with cuticle on both internal and external surfaces. Both layers of cuticle are continuous with the cuticle lining the internal and the external surface of the funnel (fu.st. in figure 3*j, k*).

At the junction of the foregut and midgut (figure 19*a, b*, plate 5), there is a cleft (\*) lined with cuticle (cu.) in the terminal cell of the foregut. Furthermore, there is a massive, pleated fold (f. in figure 19*b*, plate 5) in the basal lamina which extends into the epithelial layer between the tissues of the foregut and the midgut and lies in close proximity to the cleft. Only a restricted layer of cytoplasm lies between the cuticle and the basal lamina.

#### 9. FUNNEL REGION OF STOMACH

The funnel (fu.st. in figure 1) is longer than the combined lengths of the cardiac and pyloric regions of the stomach. From its terminal region the epithelium is folded back, externally, to give it a double wall with cuticle on both inner and outer surfaces (fu.st. in figure 3*j, k*). It is enclosed completely by the lumen and epithelium of the intestine (i.).

The funnel has a large, central food channel, flanked by two circulation channels. Anteriorly (figure 3*j*) the circulation channels (cl.) are located dorsolateral to the food channel and are defined by longitudinal ridges in the wall of the gut. There are no setae separating the food and circulation channels. Two ridges in the roof of the food channel merge with the dorsal ridges of the circulation channels towards the posterior end of the funnel (figure 3*k*).

In the ventral region of the funnel (figure 3*j*), there is a fissure (arrow), continuous with that of the valve in the pyloric stomach. The fissure margins are modified to form a barrier which prevents the bulk of the food material from entering the lumen of the midgut encompassing the funnel. At the anterior end of the funnel, the margins along the fissure are folded to form a longitudinal groove which is flanked by two ridges (arrow in figure 3*i*). The margins abut each other and one ridge from each margin is located in the groove of the opposing margin. Along the length of the funnel, the ridges external to the grooves expand laterally and those inside them are reduced in size (arrow in figure 3*j*). Finally, the margins of the fissure overlap completely when the gut is empty, and they can extend to the circulation channels in the dorsolateral regions of the gut (figure 3*k* and \* in figure 20, plate 5). However, the volume of the funnel lumen is increased by the presence of food (figure 21, plate 5), a change accommodated by the reduction in the degree of overlap (\*), to the extent that the margins approach the ventral midline of the gut.

The cuticle of the food channel, ventral to the circulation channels has a series of folds which

give the wall a corrugated appearance (f. in figures 20 and 21, plate 5). The number of corrugations increases along the length of the channel as the ventral margins of the wall extend laterally.

#### 10. GENERAL FEATURES OF THE MIDGUT

The blind ends of all the caeca in the midgut are packed with small cells. Along the length of the caeca and the intestine, these cells are differentiated to form a single layer of columnar epithelium with a microvillous border. All regions of the midgut have a thick basal lamina.

#### 11. VENTRAL CAECA

Each ventral caecum (v.c.) is joined to the foregut by a short tube (en.v.c. in figure 3*h*) of midgut epithelium which has a fine structure similar to that of the anterior intestine (i.) and the differentiated regions of the anterior dorsal caeca (d.c.) described below.

The range of cell types which occur can be described according to the classification proposed by Hirsch & Jacobs (1928) for the hepatopancreatic caeca of the crayfish *Astacus leptodactylus*. By this scheme, the cells are classified as 'embryonic' cells (E), 'Retzell' cells (R), 'fibrillar' cells (F) and 'Blasenzell' cells (B). This nomenclature has been applied in most of the recent studies of the hepatopancreatic caeca of the Malacostraca (Stanier *et al.* 1968; Moritz *et al.* 1973; Schultz 1976; Barker & Gibson 1977, 1978). However, there are exceptional cell types known, particularly in certain isopods where R and F cells are considered to be the same type (Vernon *et al.* 1974).

In *C. volutator*, the epithelium varies in thickness and takes the form of a series of longitudinal ridges and troughs which extend most of the length of the caeca. At the blind distal end, there are only small E cells but away from this region the adjacent cells show some initial differentiation (figure 22, plate 5). The cytoplasm of individual cells shows differences in density which can be mainly attributed to variations in the number of free ribosomes. However, in the mature cells there are no consistent differences in structure and density that can define the distinction between R and F cells which occur in other Malacostraca. For the purpose of this presentation, they will be considered as one type of cell and termed R/F.

R/F cells have a centrally located nucleus (n.) and a dense microvillous border (mv. in figures 22 and 23, plate 5 and figure 25, plate 6). Microfilaments embedded in the apical cytoplasm of the cells extend along the axes of the microvilli. The lateral membranes at the apices of the cells are linked by septate junctions of the continuous type (Satir & Gilula 1973). Other regions of the cells do not have specialized membrane junctions. The organelles of the R/F cells vary in number and distribution within the cell and, also, along the length of the caeca. In general, a mature cell has numerous mitochondria (m. in figure 25, plate 6 and figure 28, plate 7) which are mainly located ventral to the nucleus; rough (r.e.r.) and smooth (s.e.r.) endoplasmic reticulum occurs primarily in the apical (figure 25, plate 6) and basal region (figure 26, plate 7), respectively. Furthermore, most of the rough endoplasmic reticulum occurs in the distal region of the caeca. Golgi bodies (g.) are common and in mature cells have swollen cisternae (figure 25, plate 6 and figure 27, plate 7). Lipid droplets (li.) form the main storage material and occur primarily in the proximal regions of the caeca (figures 27 and 28, plate 7).

Many R/F cells along the length of a caecum have features that are characteristic of degeneration (long arrows in figures 24 and 25, plate 6). In these cases, the nucleus (n.) has a dense nucleolus and the chromatin is aggregated. The cytoplasm is dense and lacks Golgi



bodies and endoplasmic reticulum. In addition, the microvilli (mv.) become vesicular (figure 24, plate 6) and, finally disintegrate completely (figure 25, plate 6).

The epithelial ridges of the caeca contain B cells which have a single large vacuole and a restricted amount of dense marginal cytoplasm. The B cells are arranged in rows along the apices of the ridges which occupy approximately three-quarters of the length of a caecum. Towards the distal end of a caecum, the rows of cells are continuous, but this is not necessarily so proximally. There can be considerable variation in the relative lengths of 'continuous' and 'discontinuous' sections. There are no B cells at either end of a caecum.

Towards the distal end of a caecum, there are cells intermediate in structure between R/F and B cells; the cytoplasm varies in density and contains supra-nuclear vacuoles (v. in figure 23, plate 5) which appear to coalesce, forming the large vacuole of the B cells. Pinocytotic activity is evident at the apical membrane of the B cells (short arrow in figure 24, plate 6) and this probably contributes to the contents of the vacuole. The microvillous border is reduced in thickness and density (mv. in figure 23, plate 5 and figure 24, plate 6) and the associated microfilaments (arrowhead in figure 23, plate 5 and figure 24, plate 6) become prominent. Also, the contact between the cell membrane and the basal lamina of the epithelium is reduced. The irregular shaped nucleus (n.) is confined to the basal region of the cell (figure 25, plate 6) together with free ribosomes and rough endoplasmic reticulum. Distal to the large vacuole, mitochondria (m. in figure 24, plate 6) and numerous smaller vacuoles of varying size form the 'apical complex'. With increasing maturity, the large vacuole of the B cell increases in size and the volume of the apical complex is reduced until, eventually, the microvilli are lost. At this stage, the entire contents of the cell and the adjacent, disorganized R/F cells are released into the lumen of the caecum (figure 25, plate 6). There is an apparent association between B cells and the adjacent R/F cells which is manifested by a gradual ageing of the R/F cells as the B cells develop.

The epithelium of the ventral caecum is encompassed by a basal lamina (b.l. in figure 26, plate 7) which takes the form of a single thick band (*ca.* 2  $\mu\text{m}$ ) of fine granular material. At the proximal end, where the tube of epithelium unites the ventral caecum and the stomach, the basal lamina (b.l. in figures 19*a, b*, plate 6) becomes similar to that of other regions of the midgut (see below).

## 12. ANTERIOR DORSAL CAECA AND INTESTINE

The small undifferentiated cells at the blind ends of the anterior dorsal caeca increase in volume and develop a dense microvillous border as they migrate proximally. The microvilli (mv.) have a central core of fibrils which are embedded in a dense band of amorphous material situated in the apical region of the cell (figure 32, plate 8). Also, apically, a septate junction of the continuous type (Satir & Gilula 1973) occurs between the lateral membranes of adjoining cells. Ventral to the septate junction, the lateral membranes are straight and unspecialized.

In section, neighbouring cells of the anterior dorsal caeca have marked differences in density which can be attributed primarily to variations in the number of free ribosomes (figure 29, plate 7). In addition, mature cells have numerous cisternae of smooth endoplasmic reticulum (arrow) which occur primarily in the basal region (figure 29, plate 7).

The basal lamina (b.l. in figure 29, plate 7), which encompasses the epithelium of the anterior dorsal caeca and the intestine, is a layered structure; a thick band of dense material, which is consistently 0.2  $\mu\text{m}$  in thickness, abuts the basal membrane of the epithelial cells and is surrounded by dense bands which have an aggregate thickness ranging from 0.3–1  $\mu\text{m}$ . In

transverse section, the dense bands appear beaded (figure 29, plate 7), except towards the posterior end of the intestine where they are smooth (figure 32, plate 8). In regions where the caeca are attached to the cuticle of the funnel, the bands increase in number and undergo massive folding. Here the aggregate thickness of the layers of the basal lamina increases to around 2  $\mu\text{m}$ .

Fine nerve processes containing neurosecretory granules (n.g. in figure 29, plate 7) occur in the basal region of epithelium, at the proximal end of the caeca.

The epithelium of the intestine is continuous with that of the anterior dorsal caeca. Posterior to the funnel, the volume of the intestine lumen changes according to the absence or presence of food; when empty, the lumen is reduced and the epithelium is folded to form villi (figure 4a, figure 30, plate 7 and figure 32, plate 8). However, when full, the lumen is expanded and the epithelium forms a thinner, unfolded lining (figure 31, plate 7). The fine structure of the epithelium at the anterior end of the intestine is similar to that described for the columnar epithelium of the anterior dorsal caeca. However, towards the posterior end of the intestine there is a progressive reduction in the differences in density between neighbouring epithelial cells (figure 32, plate 8). This is associated with the domination of smooth endoplasmic reticulum in all the cells and the reduction in the number of free ribosomes and rough endoplasmic reticulum. Occasionally, a cephaline gregarine occurs in the lumen of the intestine (figure 33, plate 8).

At the posterior end of the intestine the cuticularized epithelium of the hindgut (h.) protrudes anteriorly along the midline of both the dorsal and ventral regions of the gut wall (figure 4b). Posteriorly, the dorsal protrusion of the hindgut progressively expands until it restricts each half of the midgut tissue to the ventrolateral margins (figure 4c). Finally, these remnants of the midgut separate from the hindgut to form the posterior caeca (figure 4b, c, d).

The fine structure of the junction of the midgut and hindgut is similar to that between the foregut and the midgut. There is a deep cleft (\* in figure 34, plate 8) in the layer of cuticle (cu.) which runs close and parallel to an infold (f.) of the thick band of dense material of the basal lamina (b.l.). The thin dense bands of the basal lamina are not infolded.

### 13. POSTERIOR CAECA

The cells of the posterior caeca have the microvillous border (mv.) and the septate junctions characteristic of the midgut, but the array of microvilli is less regular (compare figures 34 and 35, plate 8 with figure 22, plate 5; figure 25, plate 6; figure 28, plate 7 and figure 32, plate 8). In the mid-region, neighbouring, differentiated cells can show marked differences in density which result from variations in the content of smooth endoplasmic reticulum, mitochondria, free ribosomes and dense bodies. Towards the proximal end of the caeca, the cells (e.p.c. in figures 34 and 35, plate 8) are uniform in density and the cytoplasm in the basal region is dominated by smooth endoplasmic reticulum. Many mitochondria, particularly those underlying the microvillous border, have a dense matrix (arrowhead in figure 35, plate 8). In contrast to other regions of the midgut which have been fixed under the same conditions, there is extensive vacuolation around the nuclei and throughout the cytoplasm (arrows in figure 35, plate 8). It is presumed that optimum conditions for fixation differ from those for other tissues of the midgut. The basal lamina (b.l.) which has dense beaded layers, is similar to that of the anterior dorsal caeca.

## 14. HINDGUT

The hindgut (h.) varies in shape along its length when empty. Essentially, opposing walls of the gut come together to produce a lumen which is flattened in transverse section. However, this effect is produced, anteriorly, by the dorsal and ventral walls (figure 4*c, d*; figure 36, plate 9) and, posteriorly, by the lateral walls (figure 4*e, f*). When the lumen is full, the wall is unfolded (figure 37, plate 9) and becomes circular in transverse section.

The epithelium is lined with cuticle which is continuous with the external surface. Apart from the posterior regions, this cuticle is covered with short stout setae (figure 36*b*, plate 9). At the telson (t. in figure 1), the sides of the gut are breached (figure 4*g*) and the hindgut merges with the anus, which takes the form of a horizontal opening at the posterior end of the telson.

The epithelium has a microvillous border (mv.) abutting the cuticle (cu.) of the gut (figure 38, plate 9). In some cells, the numerous mitochondria (m.) are substantially larger than those in other regions of the alimentary canal but endoplasmic reticulum and Golgi bodies are less numerous. Some of the mitochondria are associated closely with extensive infoldings of the basal cell membrane (b.m. in figure 39, plate 9). The epithelium in the region of the telson has relatively undifferentiated cells.

The basal lamina (b.l.) of the hindgut is of variable thickness and consists of diffuse granular material (figure 39, plate 9); it is thickest in regions where the epithelium is folded into the gut lumen.

## 15. MUSCULATURE OF THE ALIMENTARY CANAL

The foregut and hindgut have both extrinsic and intrinsic, striated muscles, while the midgut has only intrinsic, striated muscles. The extrinsic type connect the gut to the exoskeleton, while the intrinsic type link different regions of the gut. The muscles of the foregut and the anterior midgut are illustrated in figure 2*b*. Also, some of the muscles are shown in figure 3, and are specified in the text below. The muscles of the posterior midgut and hindgut are shown in figure 4, and are also specified in the text.

*(a) Foregut*

The oesophagus is encompassed by circular muscles (i.o. in figure 3*a*) and has numerous extrinsic muscles (ex.o. 1, 2, 3). Some of these (ex.o. 1 in figure 3*a*) extend most of the length of the dorsal wall and in the anterior region of the oesophagus separate from each other and the gut and originate on the cuticle within the labrum. The extrinsic muscles of the lateral wall (ex.o. 2) and those on the ventral wall (ex.o. 3) originate at the base of each second antenna, and a cuticular infolding or apodeme at the base of the mouthparts, respectively.

At the entrance to the stomach, there is a system of extrinsic and intrinsic muscles which operate the valve system. One pair (ex.v. 1 in figure 3*a*) inserts on the dorsolateral margins of the gut above the lateral ampullae, and another, more substantial pair (ex.v. 2 in figure 3*b*), inserts on the dorsolateral margins of the gut above the dorsal ampullae. The lateral ampullae have a pair of large extrinsic muscles (ex.v. 3) which originate at the base of the second antennae and insert on the mid-region of the ampullae. In addition, a pair of intrinsic muscles (i.v. 1 in figure 3*b*) extend posteriorly from the dorsal region of the ampullae to the roof of the gut. The ridges on the external surface of the gut, ventral to the lateral ampullae have two pairs of extrinsic muscles (ex.v. 5 in figure 3*b*; also ex.v. 6 in figure 2*b*) which originate on the

apodeme at the base of the mouthparts. The floor of the gut, at the entrance to the stomach, is encompassed by intrinsic muscles (i.v. 2 in figure 3*b*) and is connected by a pair of extrinsic muscles (ex.v. 4) to the same apodeme.

The cardiac stomach (cd.st.) is suspended dorsally, at the anterior and posterior ends, by pairs of muscles (ex.c. 1, 2) which run directly from the gut to the carapace, and ventrally by a pair of muscles (ex.c. 3) which run from the gut to the apodeme. A band of intrinsic muscle (i.c. 1 in figure 3*c*) encircles the floor of the stomach in the region of the ventral cardiac ridge and is anchored to the dorsolateral margins of the stomach, posterior to the dorsal ampullae. In addition, a sheet of muscle (i.c. 2 in figure 3*d, e*) which inserts on the dorsolateral margin of the gut originates on the ridge which marks the external transition between the cardiac and pyloric stomach.

Inserting anteriorly on the pyloric stomach (pl.st.) is a pair of muscles (ex.p. 1 in figure 3*d*) which originate at the base of the antennae. Also, a pair of muscles (ex.p. 2) which insert at the level of the circulation channels, originate on the cuticular infold at the base of the mouthparts. The filtration region of the pyloric stomach has an intricate musculature; longitudinal muscles (i.p. 1 in figure 3*e, f, g* but not shown in figure 2*b*) at the mid-ventral line and are overlaid perpendicularly by a sheet of muscle (i.p. 2 in figure 3*d, f, g*) which runs across the floor of the stomach. Finally, bands of muscle (i.p. 3 in figure 3*e*) encircle the entire filtration region and are attached to the ridges on the external surface of the gut at the transition between the cardiac and pyloric stomach. Towards the posterior end of the pyloric stomach, a muscle on each side (i.p. 4 in figure 3*g*) is inserted immediately anterior to the confluence with the ventral caeca. These extend dorsally and originate at the sides of the gut at the level of the circulation channels.

#### (*b*) Midgut

The ventral caeca (v.c. in figures 3*h, i, j, k* and 4*a, b, c*) are invested by a meshwork of longitudinal (l.m.) and circular (c.m.) muscles. Circular muscles occur around the tube of epithelium which unites the ventral caeca and the stomach (en.v.c. in figure 3*h*). The proximal region of the anterior dorsal caeca (d.c. in figure 3*i*) has strands of longitudinal muscles which are encompassed by circular muscles that merge with those of the intestine (i. in figures 3*j, k* and 4*a*). The bands of muscles are packed closely to form a continuous sheet. The longitudinal muscle terminates posterior to the funnel of the stomach and the circular muscle terminates at the junction of the intestine and hindgut. The posterior caeca (p.c. in figure 4*b, c, d*) have a meshwork of narrow bands of longitudinal (l.m.) and circular (c.m.) muscle which do not extend to the blind ends of the caeca.

#### (*c*) Hindgut

Thick strands of longitudinal muscles (l.m.) extend along the anterior region of the hindgut (h. in figure 4*d, e*) and are surrounded by thick bands of circular muscle (c.m.) which form a continuous sheet that terminates adjacent to the anus. Within the last abdominal segment and the telson, dilator muscles originating on the lateral exoskeleton insert on the sides of the hindgut (ex.h. 1 in figure 4*f, g*). Other dilators are present dorsally and ventrally (ex.h. 2 in figure 4*f, g*).

## 16. AN INTERPRETATION OF THE FUNCTION OF THE GUT FROM ITS STRUCTURE

## (a) Foregut

Detrital material selected by the mouthparts is transferred to the entrance of the stomach where the lateral ampullae act as a valve. When the valve is open, food is collected from the oesophagus by the 'basket-like' arrangement of setae on the ampullae (figure 8, plate 1). At the same time, the setae on the posterior face of each ampulla (s. 2, s. 3) prevent reflux of material already transported to the stomach. When the valve closes, the contents of the basket are delivered into the stomach and the setae on the free margin (s. 1 in figure 8, plate 1) prevent reflux into the oesophagus. The lumen, both dorsal and ventral to the valve, is occluded by setae (figure 6 and 7, plate 1).

The digestive process in *C. volutator* is based on the close association between the stomach and the ventral caeca. In many 'higher' Crustacea, these caeca or their equivalent produce most of the digestive enzymes and are involved, also, in the final processes of digestion (see review by Gibson & Barker (1979)). Within the stomach, the bulk of the food is restricted to the food channel which has no direct contact with the ventral caeca. However, the circulation and filtration channels connect the food channel with the entrance of the ventral caeca. This entrance is protected by the spigot of the valve (sp. in figure 2a; figures 17 and 18, plate 4). When the spigot is raised dorsally, the circulation channels make direct contact with the entrance. At the same time, the continuity between the filtration channels and this entrance is restricted because the lateral walls of the stomach are flexed against the basis of the ventral pyloric ridge (bs in figure 16, plate 4). In contrast, when the spigot seals into the fissure, the entrance to the ventral caeca has continuity with the filtration channels and no connection with the circulation channels. Thus, the mode of operation of the valve indicates that the two types of channel transport separate materials, a view which is supported by differences in the filter system. The circulation channels are screened along the length of the cardiac and pyloric stomach by single rows of setae; the filtration channels are screened similarly in the cardiac stomach but in the pyloric stomach there is an elaborate two part filter system.

From the structure of the stomach, it is evident that the ventral caeca can supply fluids and enzymes along the circulation channels to the ingested detritus in the food channel at the anterior end of the stomach. These materials are mixed together by the contractions of the musculature in the cardiac stomach, which cause the ventral cardiac ridge (c.r. in figures 2a and 3c) to separate the ingested material into two halves (figure 10, plate 2). In the pyloric stomach this separation is enhanced by the intrusion of the vertex of the ventral pyloric ridge (vx in figure 17, plate 4) into the lumen of the food channel. Furthermore, in the pyloric stomach there is a marked reduction in the area of the transverse section of the food channel. These features bring a greater proportion of the food in direct contact with the wall of the gut and facilitate the access on enzymes. Therefore, in the pyloric stomach, soluble material and fine particles are probably extracted more efficiently than in the cardiac stomach where there is less contact between the food and the structures of the gut.

Material with a diameter of 2  $\mu\text{m}$  or less can pass from the food channel into the filtration channels, either through the single layer of setae on the cardiac stomach or through the dense array of setae that forms the first filter of the two part filter in the pyloric stomach (f. I in figure 11, plate 2). All the material drawn into the filtration channels is filtered further through the setulose membranes of the second filter (figure 14a, b, plate 3). Only particles less than 0.06  $\mu\text{m}$

in diameter can reach the entrances of the ventral caeca. Setae and folds on the ventral pyloric ridge and the walls of the stomach, between the food and filtration channels, prevent contamination of the final filtrate (figure 16, plate 4). The valve at the entrance to the ventral caeca also prevents contamination of the final filtrate by material from the circulation channels which are confluent with this region of the gut.

Contractions of the muscles, which encompass the base of the pyloric stomach, bring the dense setae on the lateral walls of the gut (figure 15, plate 3) into contact with the 'filter membrane' of the second filter. Thus, material retained on the filter is swept dorsally by the brushing action of these setae. Eventually this residual material is probably returned to the food channel by the movement of the long, thick, setulate setae (arrow in figure 15, plate 3), dorsal to the dense setae.

Enzymatic digestion of residual material in the food channel can continue in the funnel of the stomach, posterior to the entrance of the ventral caeca. Products of digestion in this region may be transferred anteriorly along the circulation channels and eventually enter the ventral caeca for further processing.

(b) *Midgut: ventral caeca*

The ventral caeca are larger and structurally more complex than the other components of the midgut. They are the principal site for the production of digestive enzymes (Agrawal 1963*c*) and, since they receive most of the products of primary digestion from the stomach, they are the major site for secondary digestion. The epithelium shows progressive differentiation and growth starting from the distal end of each caeca, where E cells develop into R/F cells. The R/F cells have rough endoplasmic reticulum which is probably involved in the production of digestive enzymes and they can contain numerous lipid droplets indicating that they also absorb and store materials. It is probable that the function of the R/F cells varies with their position along the length of the caecum. Thus at the distal end where rough endoplasmic reticulum predominates in the cytoplasm (figure 25, plate 6), the cells primarily produce enzymes; at the proximal end, where lipid predominates (figure 28, plate 7) the cells process the final products of digestion. In addition, Icelly & Nott (1980) have shown that R/F cells in animals taken from a site contaminated with mine waste can incorporate copper within granules. Similar to the lipid, most of these granules are stored in the proximal region of the caeca, where they are aggregated within multivesicular bodies.

Some of the R/F cells in the distal region of the ventral caeca differentiate further to produce B cells. These are dominated by a single large vacuole and have only a restricted volume of cytoplasm (figure 25, plate 6). It is clear, therefore, that the B cells are not involved primarily in the production of enzymes nor in the storage of the products of digestion. The vacuoles increase in size towards the proximal region of the caecum and their contents are released into the lumen by holocrine secretion. This process is not associated with those periods of the digestive cycle when the requirement for enzymes is greatest. Furthermore, any function ascribed to the B cells has to account for the active 'apical complex' located distal to the vacuole (figure 24, plate 6). Pinocytosis occurs along the apical cell membrane, which indicates that material can be accumulated from the lumen of the caecum; some of this must contain the products of primary digestion. It is therefore probable that B cells effect intracellular digestion and that the products are transported to the adjacent cells and the blood. The residual material is accumulated in the vacuole and is eventually secreted into the lumen.

(c) *Midgut: anterior dorsal caeca, intestine and posterior caeca*

In common with the ventral caeca, the epithelium of the anterior dorsal and posterior caeca is regenerated from small, relatively undifferentiated cells at the distal ends. From the position and the morphology of the anterior dorsal caeca and posterior caeca, it is evident that they have different functions.

Essentially, the differentiated cells of the anterior dorsal caeca have a normal complement of organelles (figure 29, plate 7), but they are not as highly differentiated as the cells of the ventral caeca. They probably make a minor contribution to the digestive processes. However, there is experimental evidence that the posterior caeca (figure 35, plate 8) are not involved in digestion (Icely 1981). They and the posterior region of the intestine, have characteristics of epithelia that transport ions and water. These include a dense microvillous border, extensive development of smooth endoplasmic reticulum, and numerous mitochondria which often have a dense matrix. These tissues are able to synthesize only a limited amount of material since they have few free ribosomes and no rough endoplasmic reticulum.

The food bolus within the intestine is held together by a mucoid substance which acts presumably as an alternative to the peritrophic membrane, lubricating the passage of the bolus and protecting the epithelium from abrasive action. The food also produces a marked increase in the volume of the gut which is limited by the basal lamina. The basal lamina is much larger and more complex than it is in the ventral caeca. The function of the fine nerve cell processes which occur between the cells in the epithelium of the anterior dorsal caeca (n.g. in figure 29, plate 7) is unknown.

(d) *Hindgut*

The transport of material along the hindgut is effected by the substantial muscles which encompass this region. The movement of material is also assisted by the short stout setae which are directed posteriorly and cover the cuticle in the anterior and middle region (s. in figure 36*b*, plate 9). Apart from the posterior region of the hindgut, the fine structure of the epithelium is similar to the 'ion pump' system which has been described in insects (Wall & Oschman 1975). In this system, mitochondria are closely associated with extensive folds of the basal cell membrane and an apical microvillous border underlying the cuticle (figures 38 and 39, plate 9). This pump may serve to maintain the normal ionic concentration of the blood. Faeces are ejected by the combined contractions of the intrinsic and extrinsic muscles at the posterior of the hindgut.

## 17. DISCUSSION

(a) *Comparison with an earlier study on the gut of C. volutator*

This interpretation of the function of the gut in *C. volutator* contradicts the main conclusions of Agrawal (1963*a*) on the same species. He states that 'The structure of the cardiac stomach provided as it is with a variety of spined, toothed and hooked ridges and plates, suggests that it is adapted for further trituration of food'. As evidence for this suggestion, he states that 'Transverse sections of the cardiac stomach in adult individuals show that the lumen is full of large food particles while the gut behind it contains finer particles'. However, fractured tissue in this study shows that the various spined ridges are organized to act as screens between the

longitudinal channels linking the cardiac, pyloric and funnel regions of the stomach. Although the musculature of the stomach kneads the food against these setal screens, as well as the setae on the walls of the food channels and the vertex of the ventral pyloric ridge, only friable material is broken up; solid particles remain intact. Also, the size distribution of ingested particles is consistent at all stages along the length of the gut (compare figure 9, plate 1; figure 10, plate 2; figure 17, plate 4; figure 21, plate 5; figure 31, plate 7 and figure 37, plate 9).

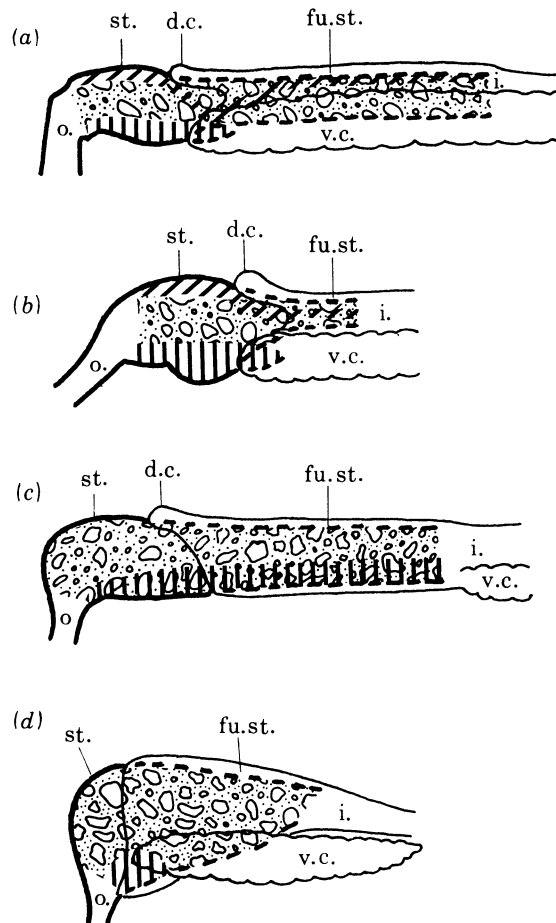


FIGURE 40. Foregut organization in the Gammaridea (a), Caprellidae (b), Cyamidae (c) and Hyperiidea (d). Figure 40a is modified from figure 1 in the current study; (b) is modified from figure 1 in Keith (1974); (c) is drawn from micrographs in Keith (1974) and from plates 12, 13, 14 in Agrawal 1966; (d) is modified from figure 4a in Shaeder & Evans (1975). The stippling of diagonal lines represents a circulation channel, the dots and irregular circles, a food channel and the vertical lines, a filtration channel. The drawings are not to scale.

(b) *Comparison with the general features of the gut in other amphipods*

The Order Amphipoda is divided into the Gammaridea, Caprellidea and Hyperiidea. The morphology of the gut has been examined in at least 50 species (see table 2.6 in Icery (1981)), including examples from all three suborders. The foregut of *C. volutator* (figure 40a) is similar to that of other gammarids (Agrawal 1964, 1966). In the caprellid family Caprellidae, the foregut (figure 40b) has the channels and the filter system (Mayer 1882; Agrawal 1966; Keith 1974), characteristic of the Gammaridea, but there are marked differences in structure. However, in the caprellid family Cyamidae, the stomach (figure 40c) is separated only into



food and filtration channels with no circulation channels or second filter system. Similarly, the stomachs (figure 40*d*) of many species of the Hyperideiida (Claus 1879; Dunbar 1946; Bowman 1962; Agrawal 1966; Shaeder & Evans 1975) have only food and circulation channels and no second filter system, although the lumen is enlarged considerably. In some hyperiids, the foregut comprises only an oesophagus (Evans & Shaeder 1972; Brusca 1981).

In contrast to the foregut, the midgut (see paragraph above for references) differs in structure between species of the Gammarideiida. There are differences in both the number and sizes of the caeca although the arrangement is similar to that of *C. volutator*. In the Caprellidae, the arrangement of the midgut is similar to that of the Gammarideiida, but there are fewer variations; the posterior caeca are vestigial. The midgut of the Cyamidae has only an intestine and a pair of ventral caeca arising from the posterior end of the foregut. The midgut of many hyperiids also comprises only an intestine and a pair of ventral caeca but, in contrast to the Cyamidae, the caeca are shorter and arise from the foregut immediately posterior to the oesophagus, while the anterior region of the intestine is enlarged considerably. In some parasitic hyperiids this region of the intestine is not enlarged (Evans & Shaeder 1972; Brusca 1981).

The hindgut has not been described for many amphipods. However, comparisons between the present work on *C. volutator* and other British species, indicate differences in size and degree of folding within the gut wall (Agrawal 1964, 1966).

Agrawal (1964, 1966) suggests that differences in the structure of the gut are usually associated with differences in the size of the food particles. Presumably, the availability, diversity and nutritional value are also of importance. Thus, the relatively complex gut in the Gammarideiida and Caprellidae enables the animals to extract nutrients from bulky food of relatively poor nutritional value in comparison with the simple, reduced gut of parasitic amphipods including the Cyamidae (Keith 1974) and some hyperiids (Evans & Shaeder 1972; Brusca 1981). The enlarged stomach and anterior intestine of carnivorous hyperiids enable prey to be stored during digestion (Shaeder & Evans 1975).

The various combinations of anterior, dorsal and ventral caeca in gammarids are not readily attributable to differences in diet or habitat. However, the posterior caeca differ in length according to the habitat (Graf 1968), being much shorter in marine animals than in brackish water, freshwater or terrestrial animals. The other sub-orders are exclusively marine and have either vestigial or no posterior caeca. Differences in the structure of the hindgut may also be related to habitat differences.

(c) *Comparison with detailed studies on the foregut*

Detailed studies on the morphology and function of the foregut in amphipods are limited to gammarids *Synurella ambulans* (Thiem 1941), *Marinogammarus obtusatus* (Martin 1964) and *Bathyporeia sarsi* (Kannerworff & Nicolaisen 1969). Although these have many features in common, there are marked differences in the structure of the double filter system in the pyloric stomach. As in *C. volutator*, the first filter in *B. sarsi* (Kannerworff & Nicolaisen 1969) is formed by the setae on the apical region of the ventral pyloric ridge. However, unlike *C. volutator*, the covering of setae is restricted because the ridge does not extend into the lumen of the food channel. In *S. ambulans* (Thiem 1941) and *M. obtusatus* (Martin 1964) the first filter is the same as that in the cardiac stomach of all four species, taking the form of two rows of setae arising from the ventrolateral walls of the gut. As well as these differences in the first filter, the 'filter membrane' of the second filter in *C. volutator* is much finer (pore size 0.06  $\mu\text{m}$ ) than that

reported for *B. sarsi* (0.9  $\mu\text{m}$ ) and *S. ambulans* (1.3–1.4  $\mu\text{m}$ ). The small pore size of *C. volutator* results from the meshwork of setules on the 'filter membranes'. However, there is a possibility that similar setules occur in the other two species but are too fine to have been resolved with the light microscope. No size is given for the pores of the second filter in *M. obtusatus* (Martin 1964).

It is probable that the above differences in morphology reflect differences in diet. Although both *C. volutator* and *B. sarsi* ingest particulate matter, the fine particles of mud in the gut of *C. volutator* (Fenchel *et al.* 1975) form a more compact mass than the coarser particles of sand in the gut of *B. sarsi* (Kannerworff & Nicolaisen 1969). Presumably nutrients can be extracted from the sand particles without breaking up the food bolus.

*S. ambulans* (Thiem 1941) and *M. obtusatus* (Martin 1964) feed on plant material which is probably more easily screened from the filtration channels than particulate material. Indeed, these species have the least elaborate first filter system. The fine indigestible particles in the diet of *C. volutator* could explain why it has the smallest pores in the second filter.

(d) *Comparison with detailed studies on the ventral caeca*

The main studies on the histology of the ventral caeca of amphipods are summarized in table 1. These are essentially similar to those in *C. volutator*, where there are E cells which differentiate to form R/F cells and some of these differentiate further to form B cells. In *Orchestia platensis*

TABLE 1. STUDIES ON THE CYTOLOGY OF THE VENTRAL (HEPATOPANCREATIC) CAECA OF THE AMPHIPODA

	cytology of the caeca†	reference
Gammaridea		
<i>Gammarus fluviatilis</i>	Reservezellen (R), Leberzellen (F), Fermentzellen (B)	Weber 1880
<i>Marinogammarus obtusatus</i>	reserve (R and F or R/F), secretory (B)	Martin 1964
<i>Gammarus lacustris lacustris</i>	non-vacuolated (R and F or R/F), vacuolated (B)	Schmitz 1967
<i>Gammarus minus</i>	R, F, B	Schultz 1976
<i>Orchestia platensis</i>	R, F, B	Moritz <i>et al.</i> 1973
<i>Talorchestia martensii</i>	non-vacuolated (R/F), vacuolated (B)	Shyamasundari & Hanumantha Rao 1977
<i>Hyaella azteca</i>	R, F, B	Schmitz & Scherrey 1983
Caprellidea		
<i>Protella phasma</i>	non-vacuolated (R and F or R/F), vacuolated (B)	Mayer 1882
Hyperidea		
<i>Parathemisto gaudichaudi</i>	non-vacuolated (R and F or R/F), vacuolated (B)	Shaeder & Evans 1975

† Only the mature cells of the epithelia are described.

and *Gammarus locusta* (Moritz *et al.* 1973) and *Gammarus minus* (Schultz 1976), the E cells differentiate into distinct R and F cells; in these species B cells develop apparently from F cells. There is no evidence for the restitution of the B cells after the contents have been extruded.

In common with *C. volutator* (Agrawal 1963c; Icelly 1981) the cells in the ventral caeca of *Marinogammarus marinus* (Agrawal 1963b) and *M. obtusatus* (Martin 1964) produce most of the

digestive enzymes. In *C. volutator*, only the R/F cells have the organelles for forming enzymes. However, in *G. locusta* and *O. platensis* (Moritz *et al.* 1973) and *G. minus* (Schultz 1976), the cells are differentiated further into R and F types, and both Moritz *et al.* (1973) and Schultz (1976) imply that the F type secretes the enzymes. In decapods, the R and F cells are even more structurally distinct and it is generally accepted that the extensive rough endoplasmic reticulum and free ribosomes in the F cells produce the digestive enzymes (see review by Gibson & Barker (1979)).

Again, in common with *C. volutator*, lipid has been observed in the R/F or in the R cells of most of the species mentioned in table 1. Where R and F cells form distinct types, lipid occurs also in the F cells but at much lower concentrations than in R cells (Moritz *et al.* 1973; Schultz 1976). In decapods, lipid is found only in R cells (Loizzi 1971; Barker & Gibson 1977, 1978; Hopkin & Nott 1980). Recent studies on the ventral caeca of *Stegocephaloides christianiensis* (Moore 1979), *C. volutator* (Icely & Nott 1980) and *M. marinus* (G. Polanca & B. E. Brown, cited in Brown (1982)) show that the epithelium can store metals. Whether storage occurs only in amphipods from bathypelagic habitats, like *S. christianiensis*, and in those from polluted sites, like *C. volutator*, requires further investigation. Certainly, metals stored in the digestive gland of amphipods are not as obvious as in decapods (Ogura 1959; Djangmah & Grove 1970; Martin 1973; Becker *et al.* 1974; Hopkin & Nott 1979).

The ventral caeca of all the amphipods included in table 1 contain B cells. The large vacuole, 'apical complex' and restricted cytoplasm are not only characteristics of the B cells in *C. volutator*, but have been described in *G. locusta*, *O. platensis* (Moritz *et al.* 1973) and *G. minus* (Schultz 1976). In these, material is absorbed from the lumen by pinocytosis and, apart from *C. volutator*, some lipid is stored in the cytoplasm. In addition, the cytoplasm contains the rough endoplasmic reticulum and free ribosomes necessary for producing proteins. However, the capacity of the B cells for storage and, or, production of materials must be limited because of the restricted volume of the cytoplasm. We suggest that, like *C. volutator*, the B cells in other amphipods are involved primarily in intracellular digestion, where the products are transported to adjacent cells and the residue accumulated in the vacuole and eventually excreted via the lumen. This process would account not only for the absorption of materials in the 'apical complex', but also for the digestive enzymes located in the 'complex' of *M. obtusatus* (Martin 1964) and *C. volutator* (Icely 1981). These enzymes are not apparently stored for secretion since no study on amphipods has linked the extrusion of B cells with those stages in the digestive cycle when the requirement for digestive enzymes would be greatest.

Contrasting studies on the decapods *Astacus leptodactylus* (Hirsch & Jacobs 1928), *Orconectes virilis* and *Procambarus clarkii* (Loizzi 1971), *Homarus gammarus* (Barker & Gibson 1977) and *Scylla serrata* (Barker & Gibson 1978) have linked the extrusion of B cells with the secretion of digestive enzymes. However, Hopkin & Nott (1980) have shown that B cells in *Carcinus maenas* are extruded and that this process occurs towards the end of the digestive cycle; this appears to constitute a major process for removing waste products from the gut. Whatever the function of B cells in *C. volutator* and the decapods, it is closely associated with that of the adjacent R/F cells which age at the same rate and are discharged at the same time.

*(e) Comparison with detailed studies on the anterior dorsal caeca, intestine and posterior caeca*

Apart from *C. volutator*, studies on the histology of the anterior dorsal caeca, intestine and posterior caeca in amphipods are limited to *Gammarus pulex* (Mabillot 1955), *M. obtusatus* (Martin 1964) and a number of terrestrial species (Graf 1968; Graf & Michaut 1977, 1980). Although some of these studies are more detailed than others, all indicate that the anterior and posterior regions have different functions, as in *C. volutator*. Thus, processes of digestion have been identified in the anterior dorsal caeca and the anterior region of the intestine in *G. pulex* (Mabillot 1955), *M. obtusatus* (Martin 1964) and *C. volutator*. Furthermore, the anterior dorsal caeca may produce the peritrophic membrane observed in *Talitrus saltator*, *Elasmopus rapax*, *Gammarus pulex* (Georgi 1969) and *G. lacustris* (Lautenschlager *et al.* 1978), although Martin (1964) suggests that in *M. obtusatus* it is produced by the anterior intestine.

In addition to any physiological function that the intestine might have, it also acts as a conduit, removing indigestible material from the stomach and metabolic waste from the ventral caeca. Much of this waste comprises solid material, accommodated by an expansion of the lumen. The elasticity of the intestine is provided by folds in the epithelium and the thick, layered basal lamina in *G. pulex* (Mabillot 1955), *M. obtusatus* (Martin 1964) and *C. volutator*. Basal laminae with complex structures have also been observed in the midgut of the decapods *Menippe mercenaria* and *Homarus americanus* (Factor 1981).

Studies on the posterior caeca of *Orchestia cavimana* (Graf 1968; Graf & Michaut 1977, 1980) and *C. volutator* show that they are not involved in any process of digestion. However, marked differences in morphology are evident. At intermoult, the long posterior caeca of *O. cavimana* have two morphologically distinct regions. Proximally, there are mitochondria with a dense matrix and an extensive development of smooth endoplasmic reticulum. Distally, there are mitochondria with a clear matrix, numerous ribosomes, active Golgi bodies, extensive development of rough endoplasmic reticulum and a network of extracellular channels. At premoult, both regions are dominated by extracellular channels in which calcareous inclusions are formed from the calcium reabsorbed from the cuticle. During postmoult, the inclusions are dissolved and the calcium incorporated into the new cuticle. Graf & Michaut (1980) conclude that during intermoult the posterior caeca are probably involved in mineral and water regulation and excretion whilst, during moult, they are sites for calcium storage.

The posterior caeca of *C. volutator* are shorter than those of *O. cavimana* and do not have two distinct regions. They have many features in common with the proximal region of *O. cavimana* including some mitochondria with a dense matrix and an extensive development of smooth endoplasmic reticulum; this probably contributes to mineral and water regulation but does not store calcium. The greater morphological and functional complexity of the posterior caeca in *O. cavimana* is probably an adaptation to a terrestrial habitat where minerals and water have to be conserved because they cannot be taken up rapidly from the environment. Although the posterior caeca of *C. volutator* are less complex, they are probably essential for maintaining the ionic conditions of the blood when the animals are exposed at low tide or immersed in water of low salinity.

The anterior caeca, intestine and posterior caeca in decapods, as in amphipods, have not been studied in great detail. In contrast to the amphipods, these regions in *Pachygrapsus crassipes*, *Cancer magister*, *H. americanus* and *H. gammarus* have a uniform fine structure typical of tissues transporting ions and water (Mykles 1977, 1979). However, Holliday *et al.* (1980) concluded

that the midgut caeca of *C. magister* do not have a significant function in osmoregulation or in the formation of a peritrophic membrane and that they play only a minor role in digestion.

(f) *Comparison with detailed studies on the hindgut*

'Ion pumps' in the hindgut of *C. volutator* indicate an important physiological role. In insects, similar 'pumps' in the gut can reabsorb useful metabolites (see review by Wall & Oschman (1975)) and, in some species, surplus ions can be secreted into the gut from the blood (Bradley & Phillips 1977). At present, it is not known whether the 'pumps' occur in other amphipods.

In the decapods *C. magister*, *H. americanus* and *H. gammarus*, Mykles (1979) observed numerous mitochondria within the apical cytoplasm of the hindgut. Furthermore, the lateral and basal cell membranes are highly folded but, in contrast to *C. volutator*, mitochondria are not associated with either these folds or the microvillous border. These infoldings apparently enable the epithelium to stretch when the lumen is full (Mykles 1979). Although the hindgut in decapods does not apparently have 'ion pumps', Malley (1977) has demonstrated the transport of ions across the epithelium in *Panilurus argus*. Terrestrial isopods have 'ion pump' systems (Clifford & Witkus 1971; Vernon *et al.* 1974), and Hassal & Jennings (1975) have shown that in *Philoscia muscorum* they have a dominant function in the digestion and absorption of food.

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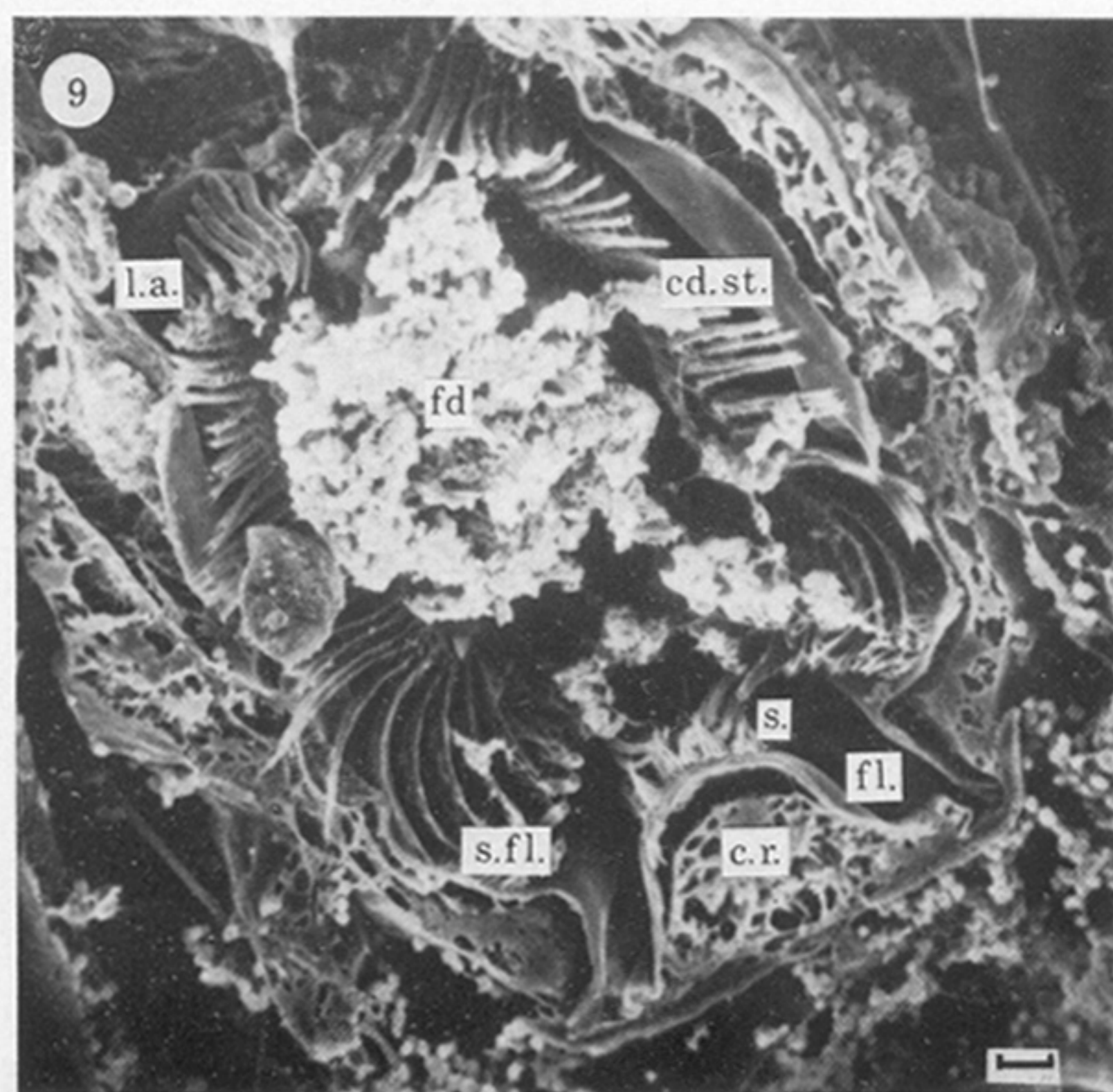
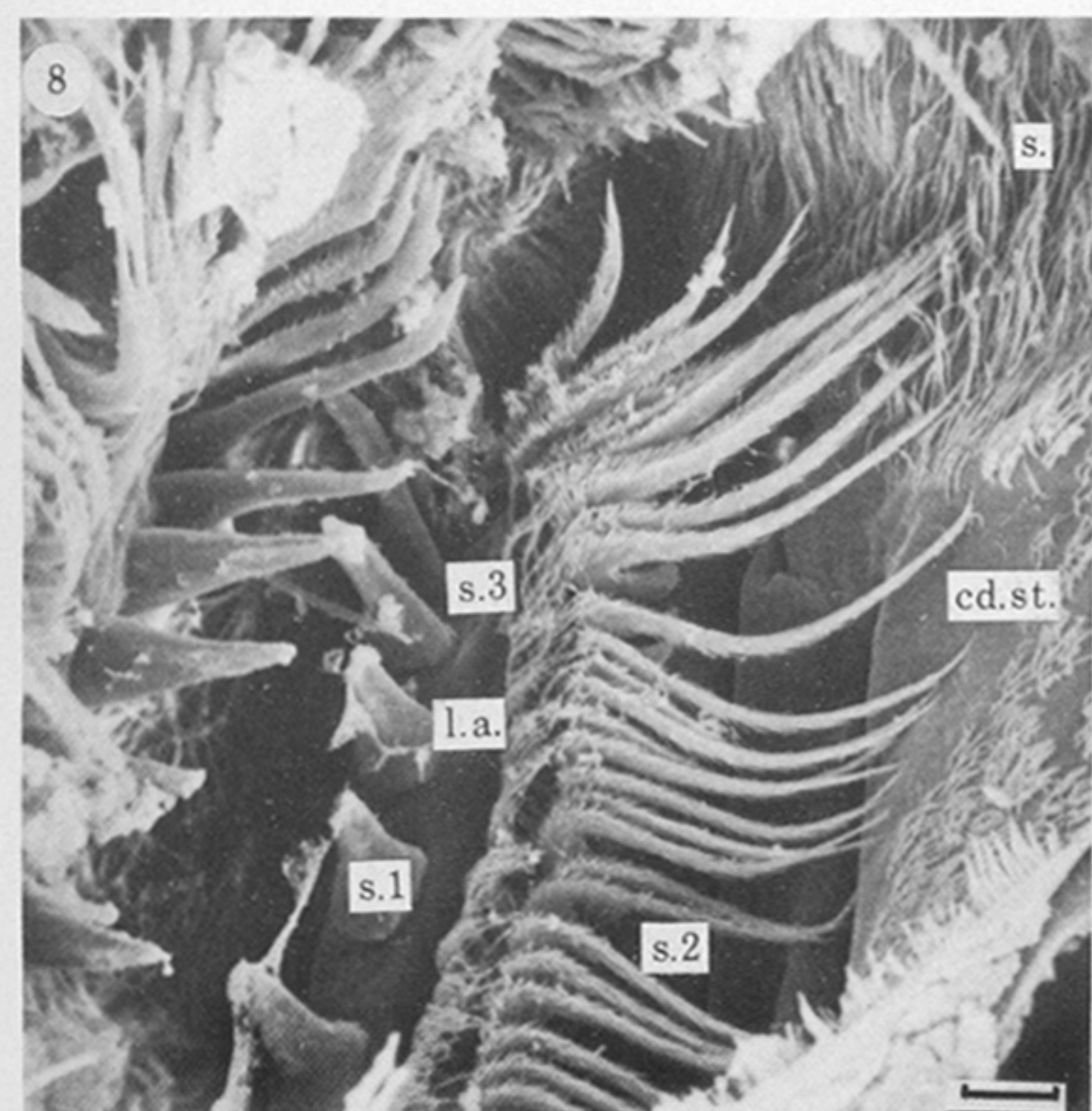
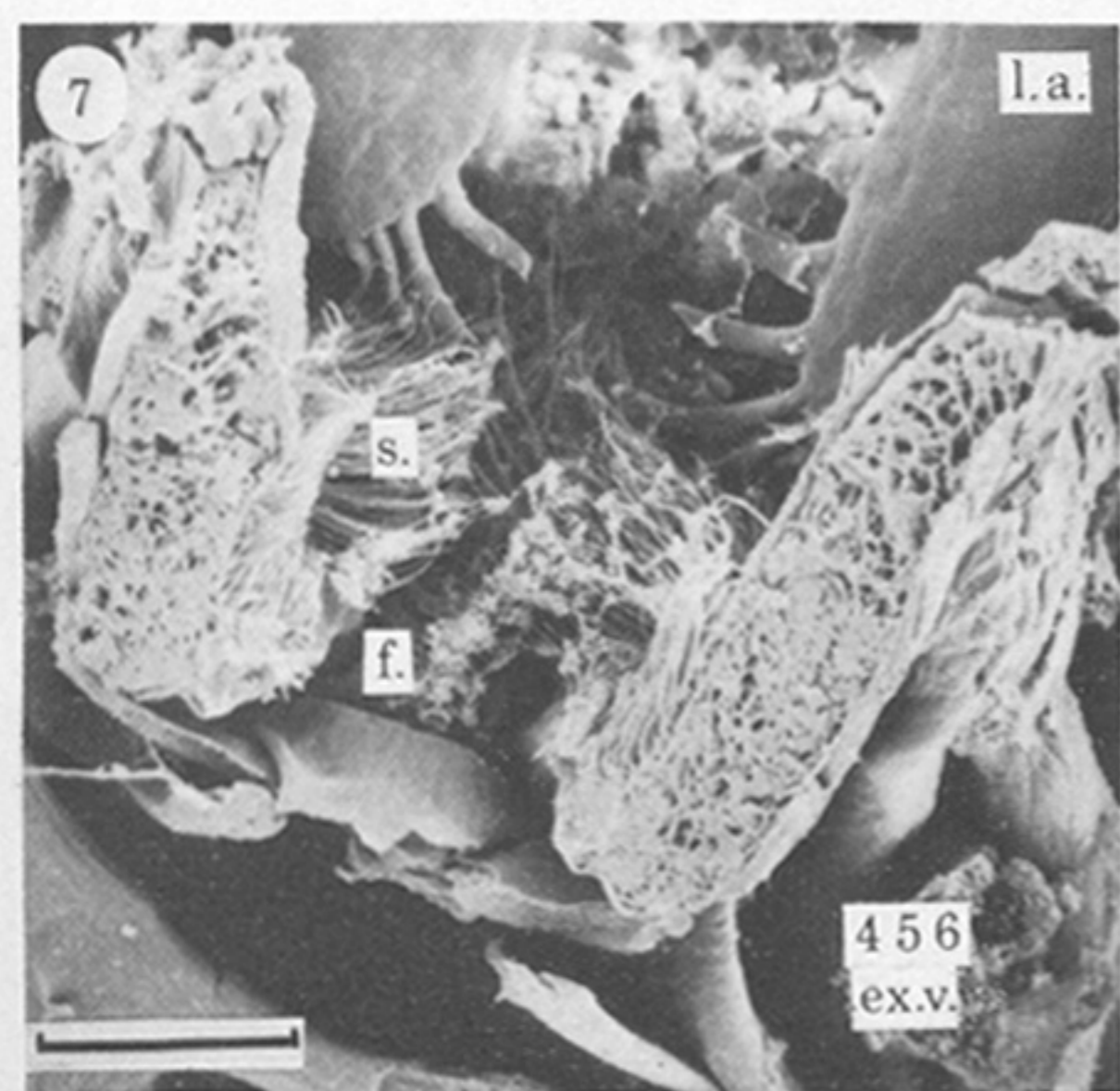
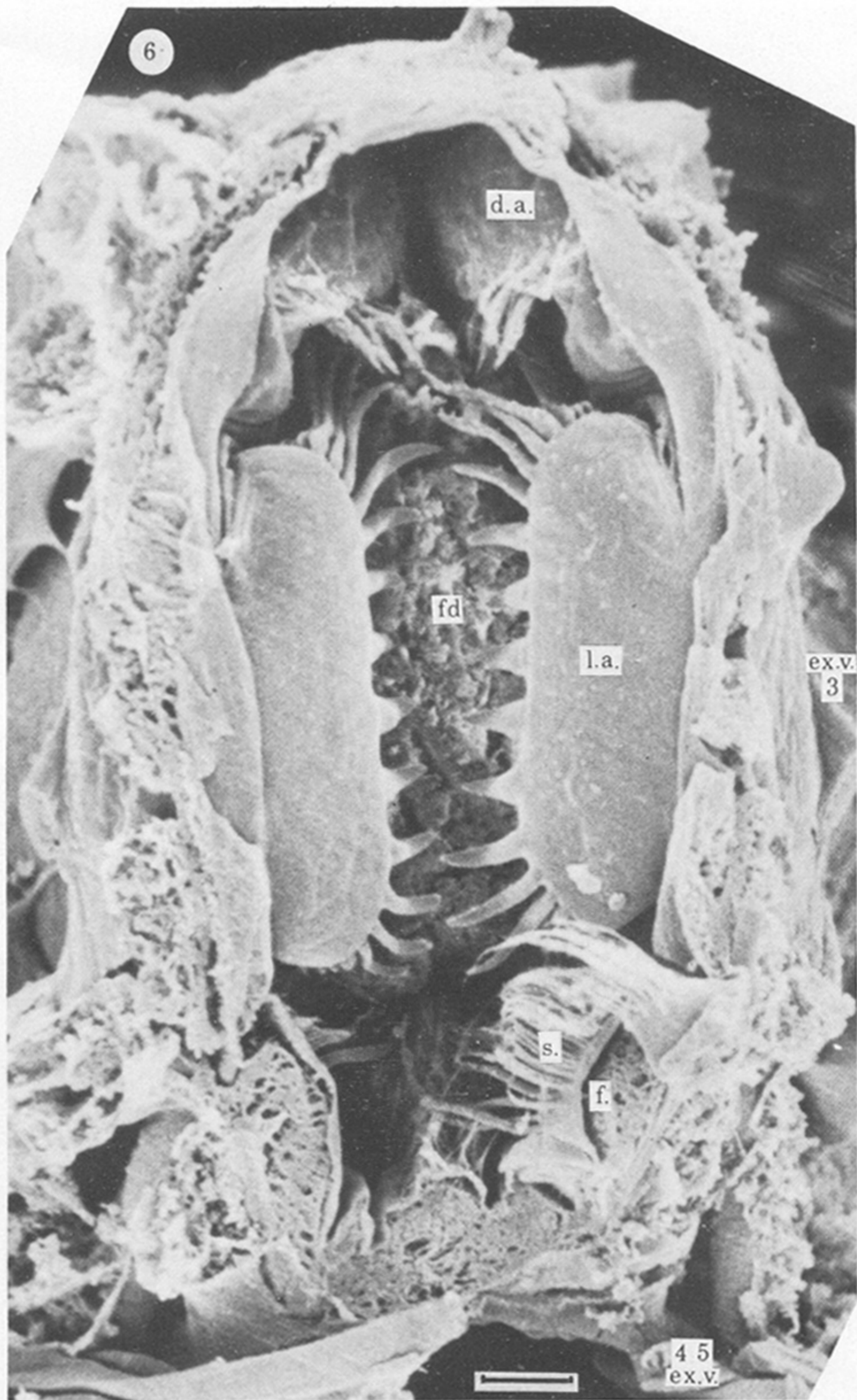
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## KEY TO ABBREVIATIONS USED IN THE FIGURES

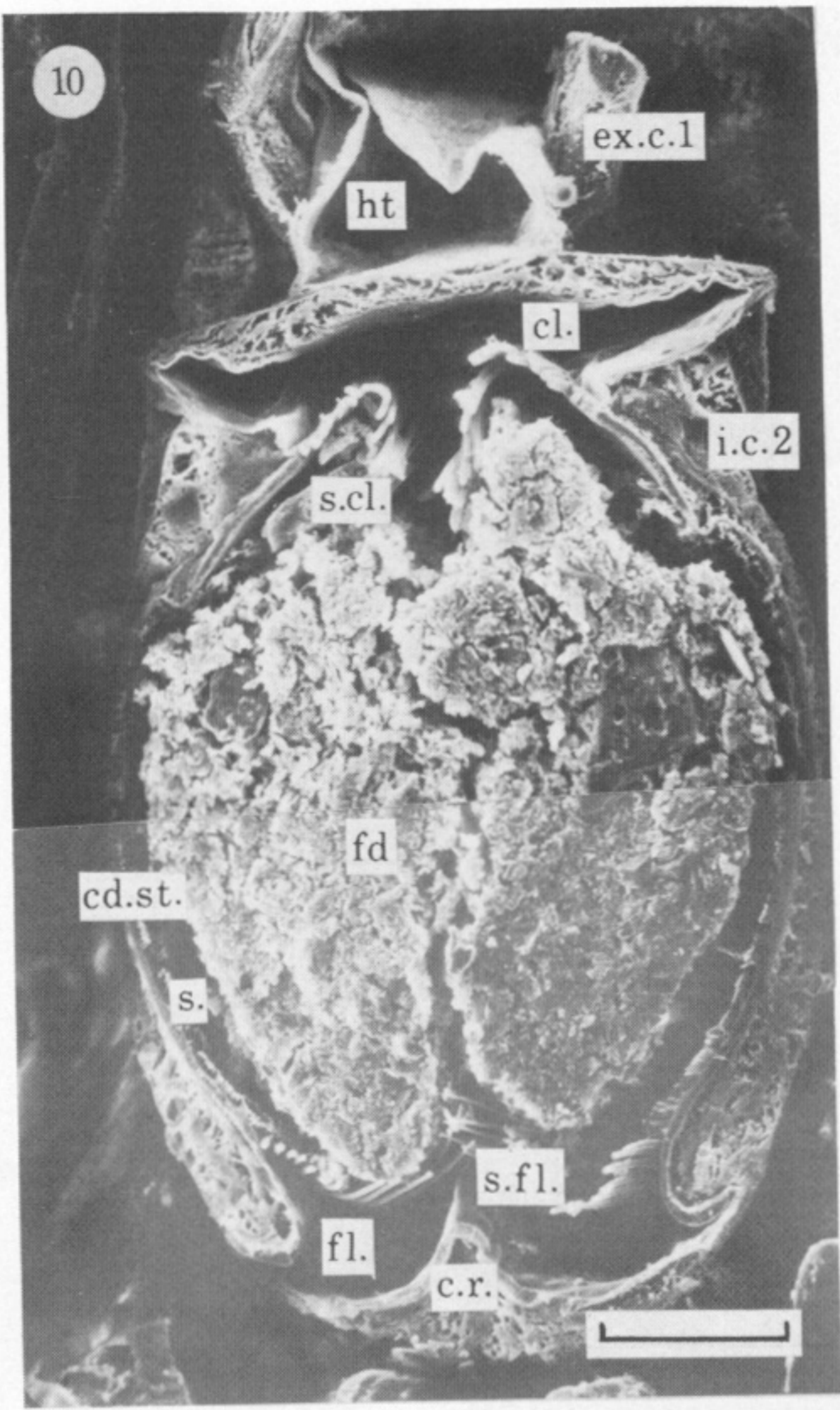
a.	anus
am.	amylopecten granules in the cytoplasm of gregarine parasite
b.l.	basal lamina
b.m.	basal cell membrane
bs	basis of ventral pyloric ridge
c.	cephalothorax
cd.st.	cardiac chamber of stomach
cl.	circulation channel of stomach
c.m.	circular muscle
c.r.	ventral cardiac ridge
cu.	cuticle
d.a.	dorsal ampulla
d.b.	dark body
d.c.	anterior dorsal caecum
e.d.c.	epithelium of anterior dorsal caecum
e.fg.	epithelium of foregut
e.h.	epithelium of hindgut
e.i.	epithelium of intestine
e.mg.	epithelium of midgut
e.p.c.	epithelium of posterior caecum
en.v.c.	entrance to ventral caecum
ex.c. 1, 2, 3	extrinsic muscles of cardiac stomach
ex.h. 1, 2	extrinsic muscle of hindgut
ex.o. 1, 2, 3	extrinsic muscles of oesophagus
ex.p. 1, 2	extrinsic muscles of pyloric stomach
ex.v. 1, 2, 3, 4, 5, 6	extrinsic muscles of valve system at entrance to stomach
f.	fold
fd	food material contained by alimentary canal
f.fl.	folds in wall of gut between food and filtration channel
fl.	filtration channel anterior to second filter of stomach
fn.fl.	final filtration channel of stomach posterior to second filter

fo.	food channel
fu.st.	funnel of stomach
f. I	first filter in pyloric chamber of stomach
f. II	second filter in pyloric chamber of stomach
g.	Golgi apparatus
h.	hindgut
ha.	haemocyte
ht	heart
i.	intestine
i.c. 1, 2	intrinsic muscles of cardiac stomach
i.o.	longitudinal and circular muscles of oesophagus
i.p. 1, 2, 3, 4	intrinsic muscles of pyloric stomach
l.a.	lateral ampulla
li.	lipid
l.m.	longitudinal muscle
m.	mitochondria
md.	mandible
mo.	mouth
mv.	microvilli
n.g.	neurosecretory granules of nerve process
o.	oesophagus
ov.	ovary
p.c.	posterior caecum
pe.	pellicle
pl.st.	pyloric chamber of stomach
p.r.	ventral pyloric ridge
r.e.r.	rough endoplasmic reticulum
s.	setae
s.cl.	setae that separate circulation channel from food channel
s.e.m.	scanning electron micrograph
s.fl.	setae that separate filtration channel from food channel in cardiac stomach
s.e.r.	smooth endoplasmic reticulum
sp.	spigot of valve at junction of stomach and ventral caecae
st.	stomach
t.	telson
te.	testis
t.e.m.	transmission electron micrograph
to.	tongue
v.	vacuole
v.c.	ventral caecum
vx	vertex of ventral pyloric ridge
B	B type cell in ventral caecum
R/F	R/F type cell in ventral caecum

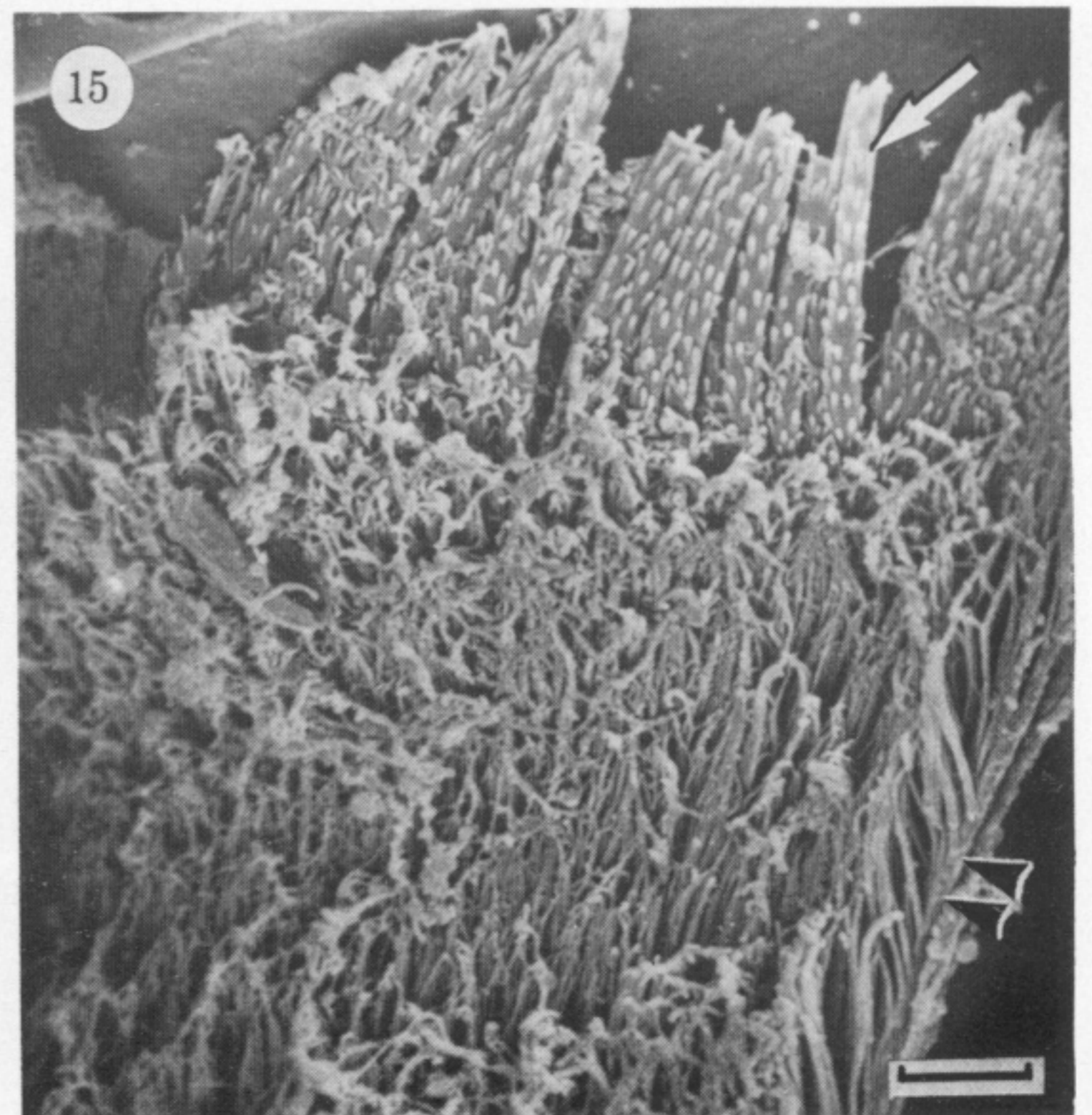
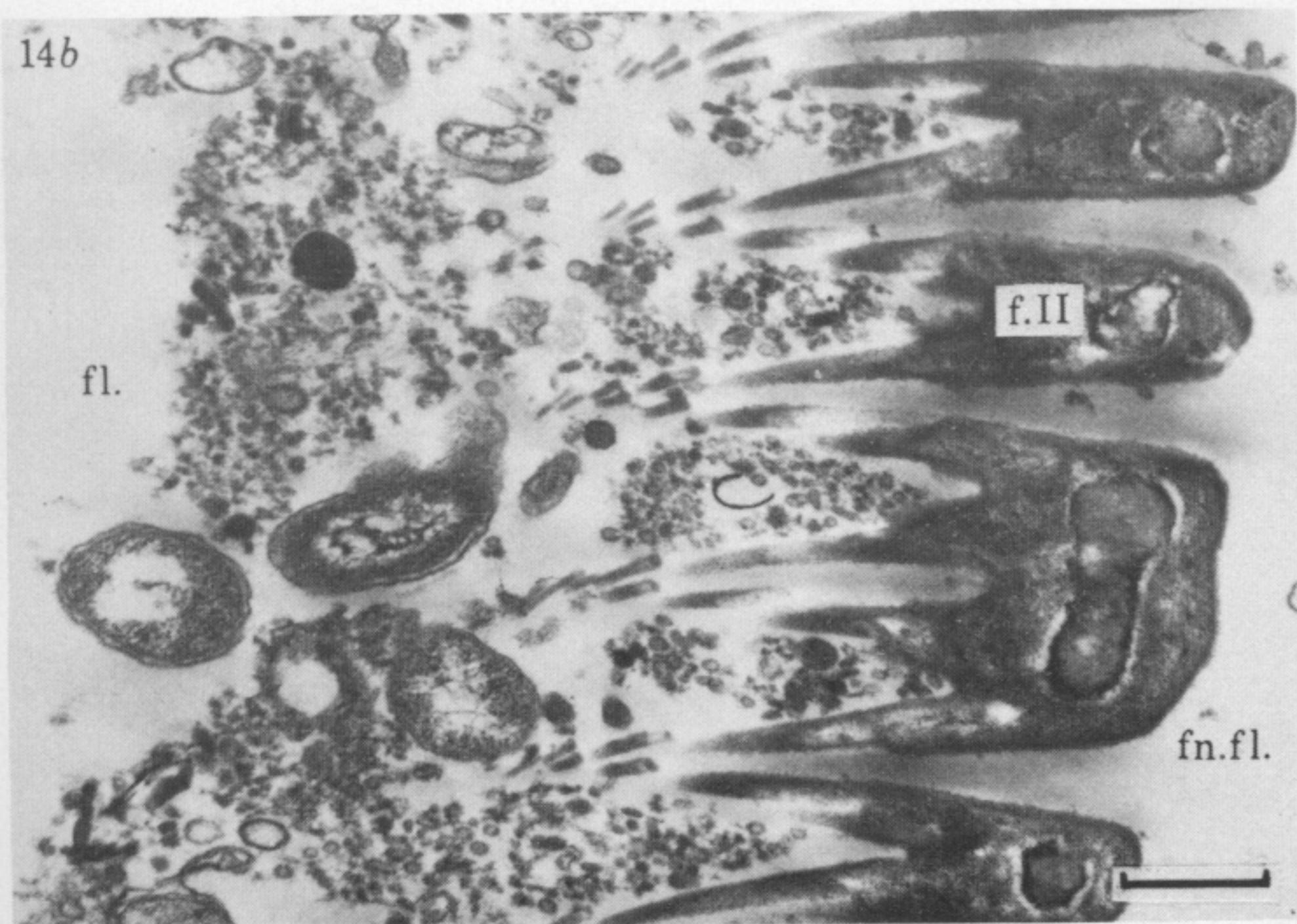
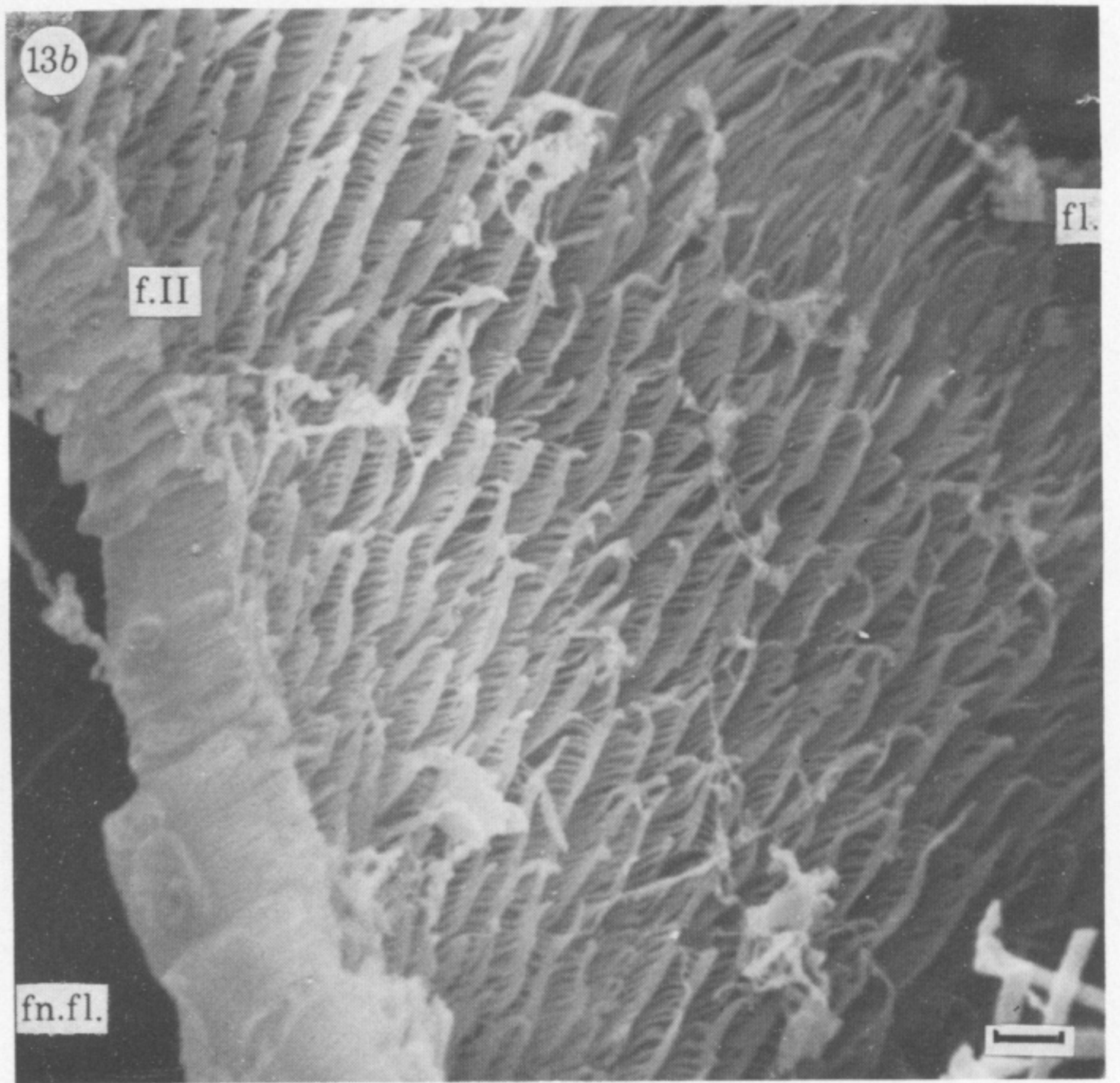
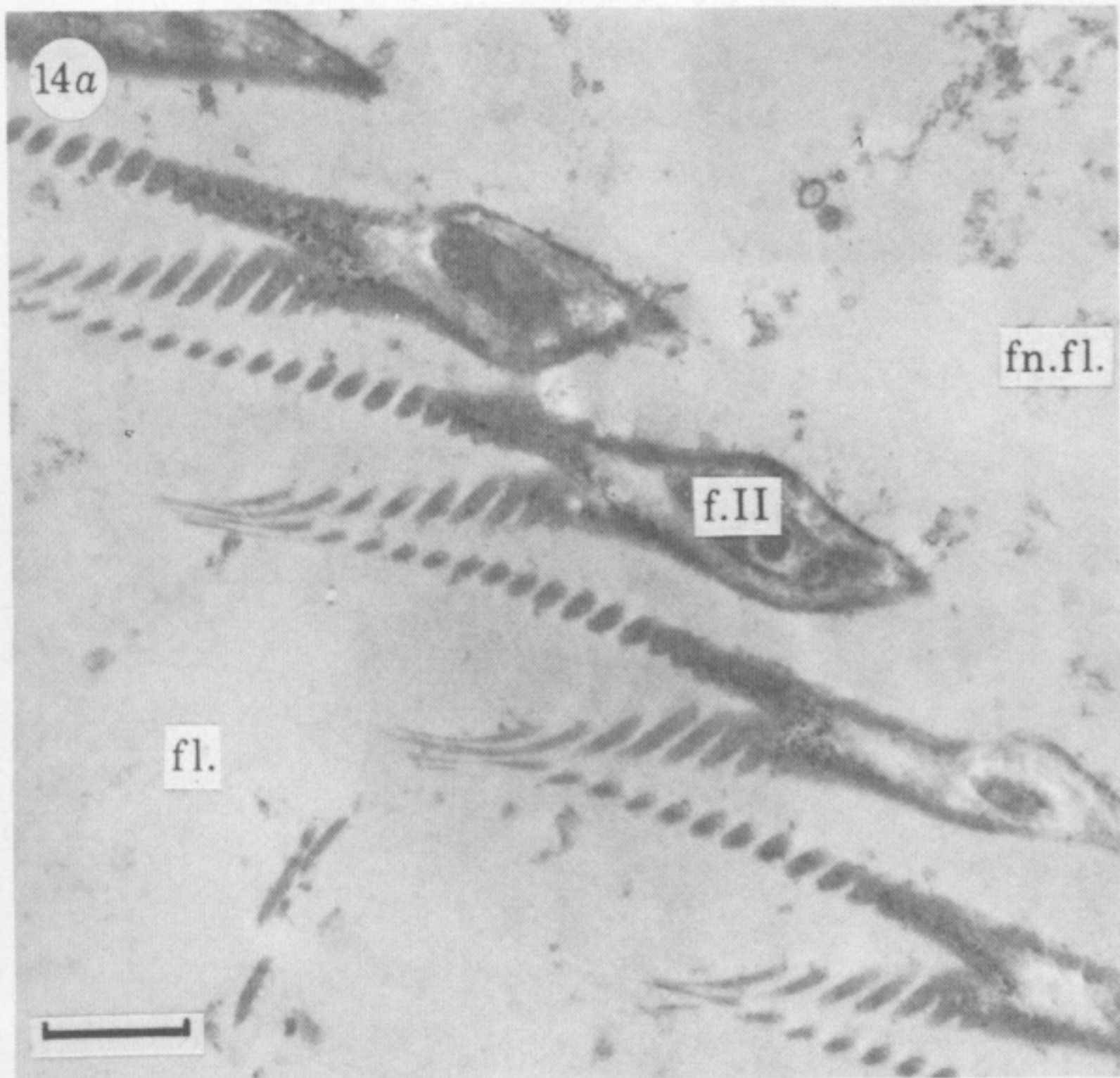
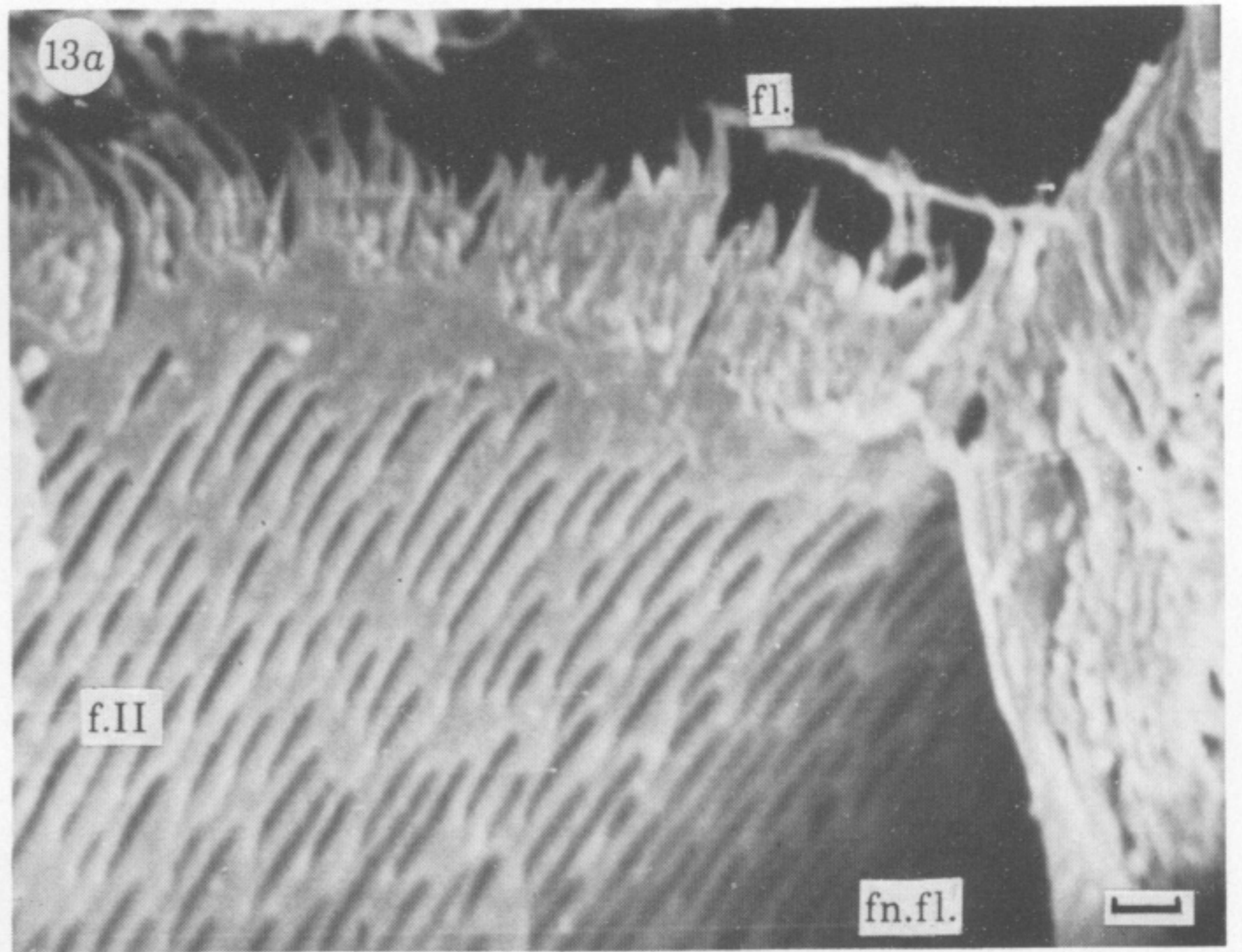




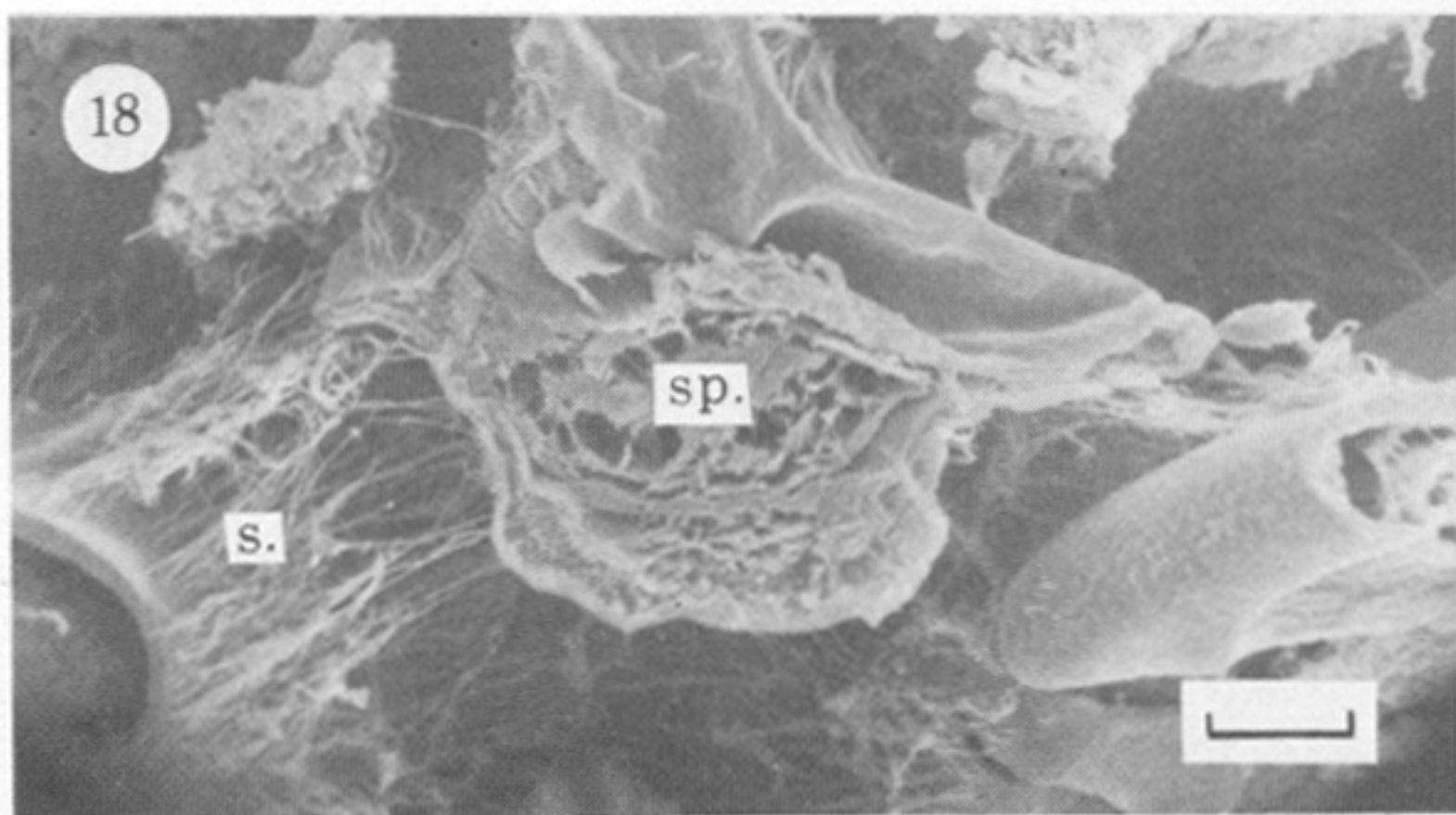
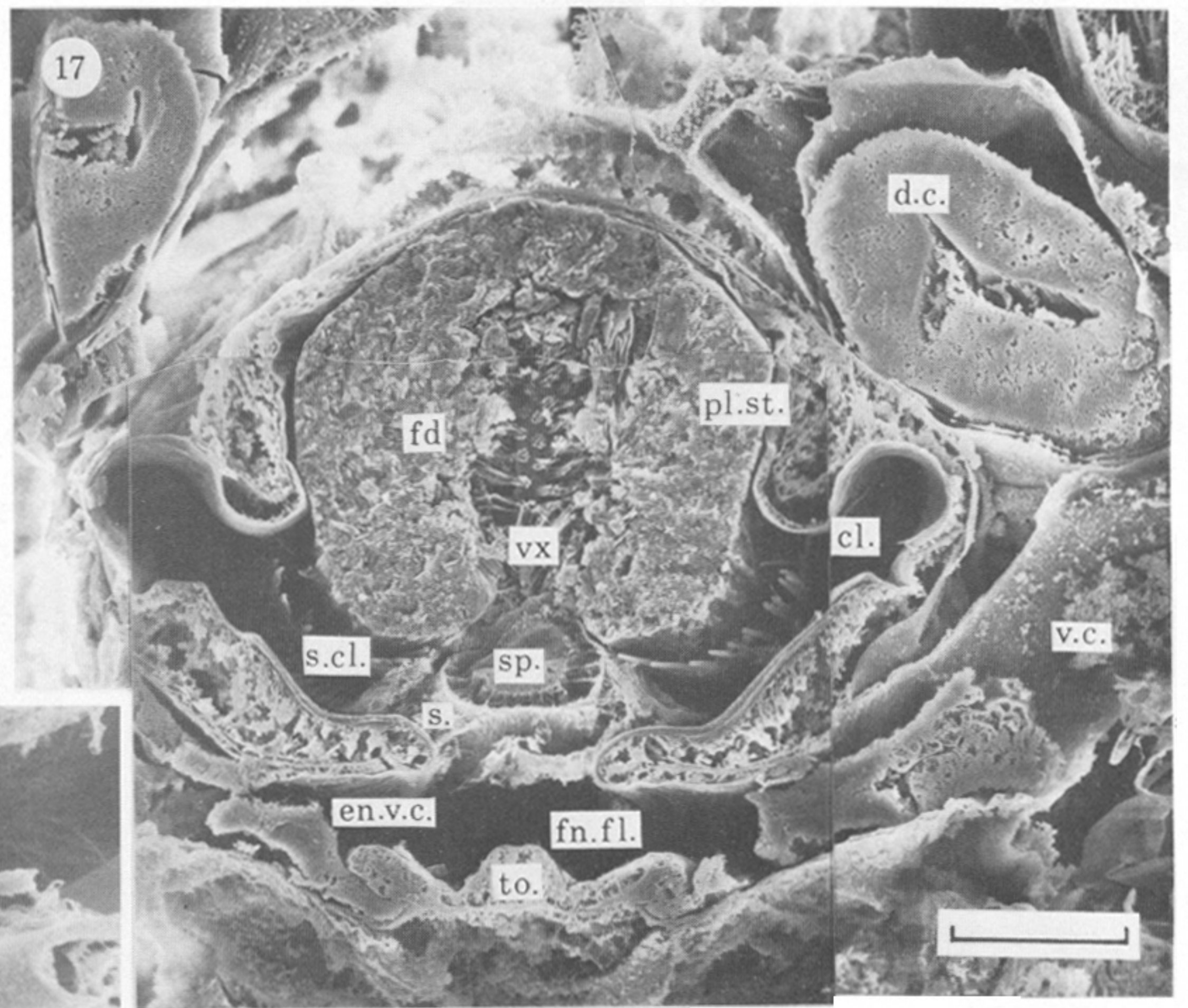
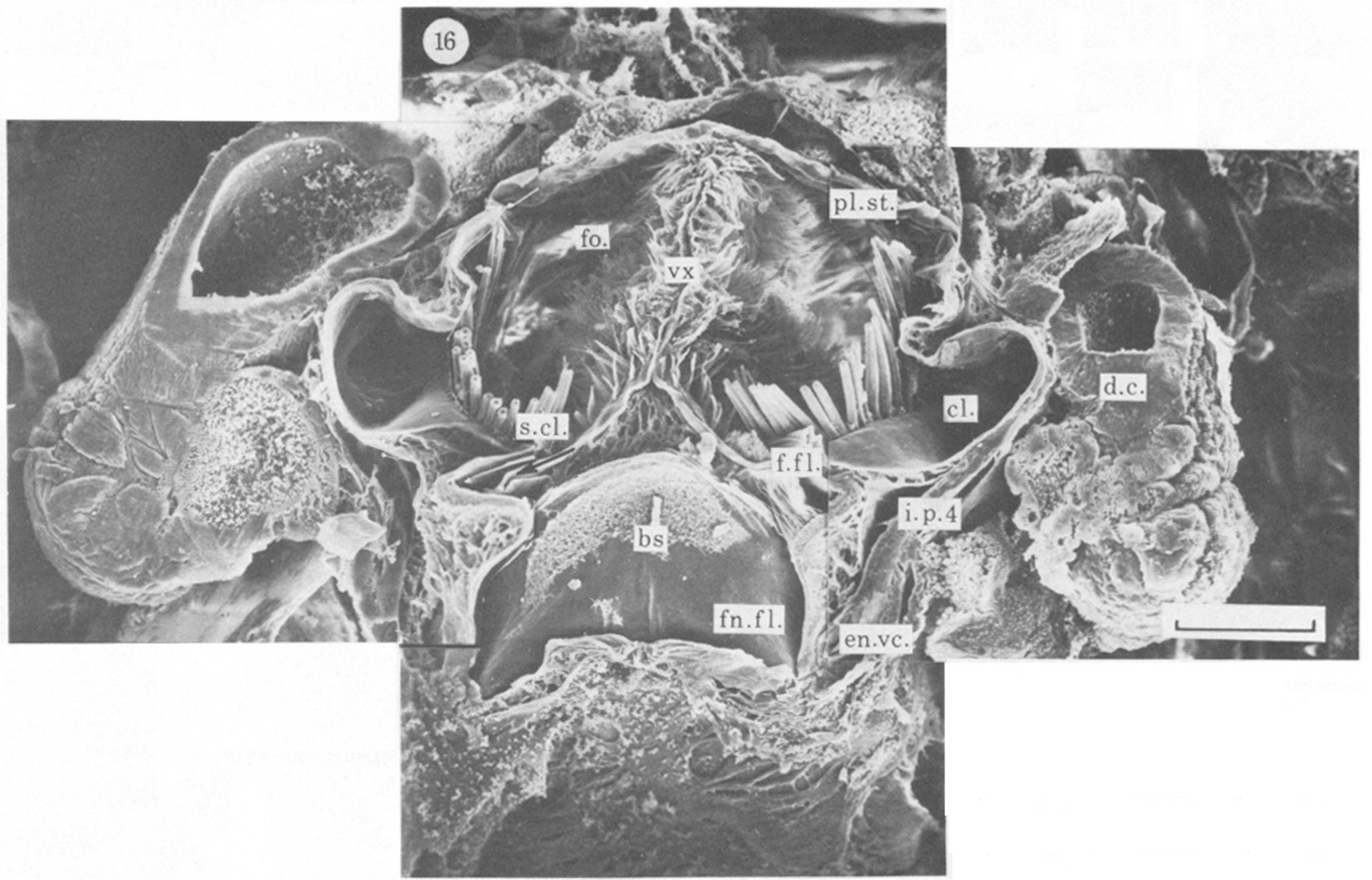
FIGURES 5-9. For description see opposite.



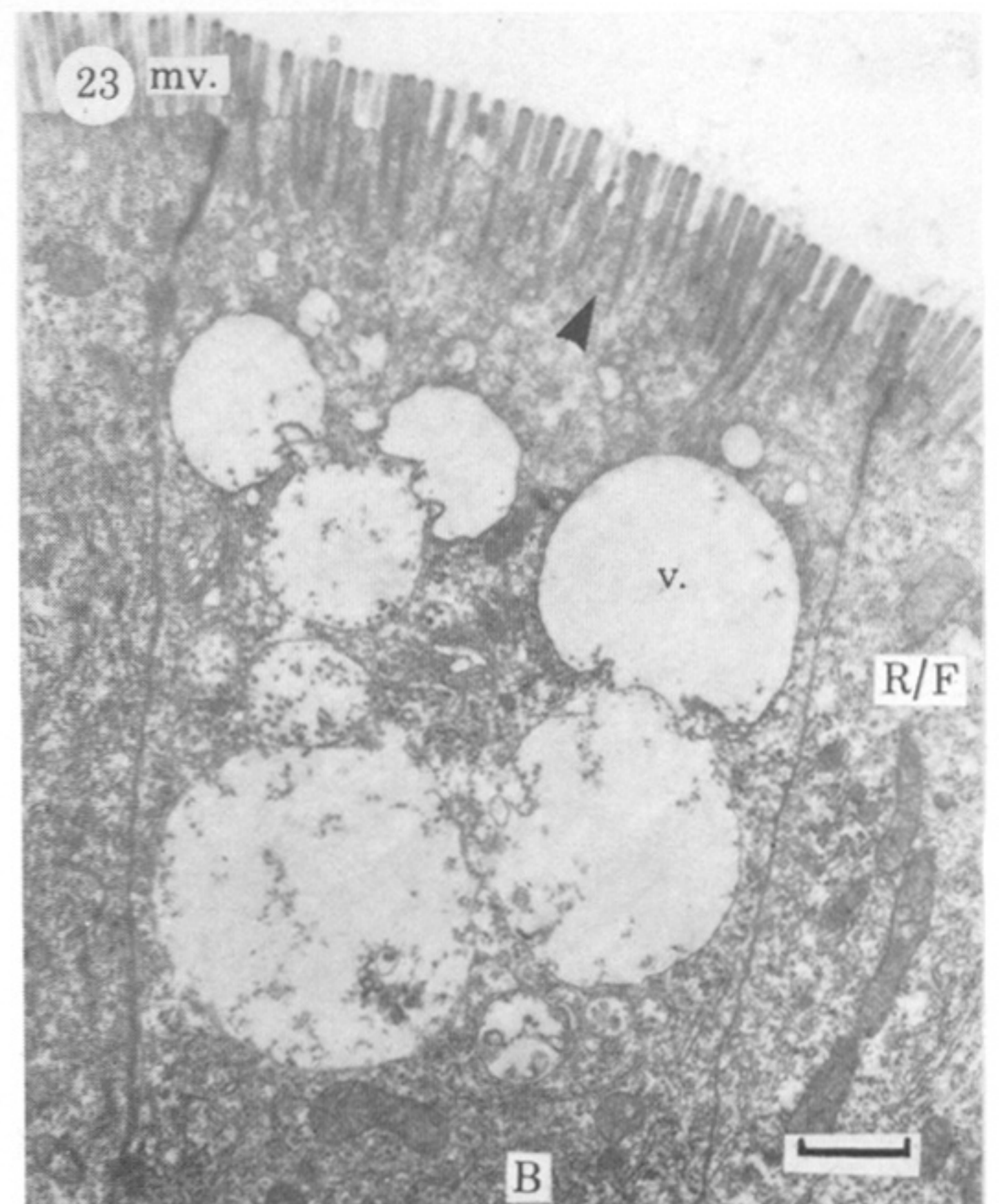
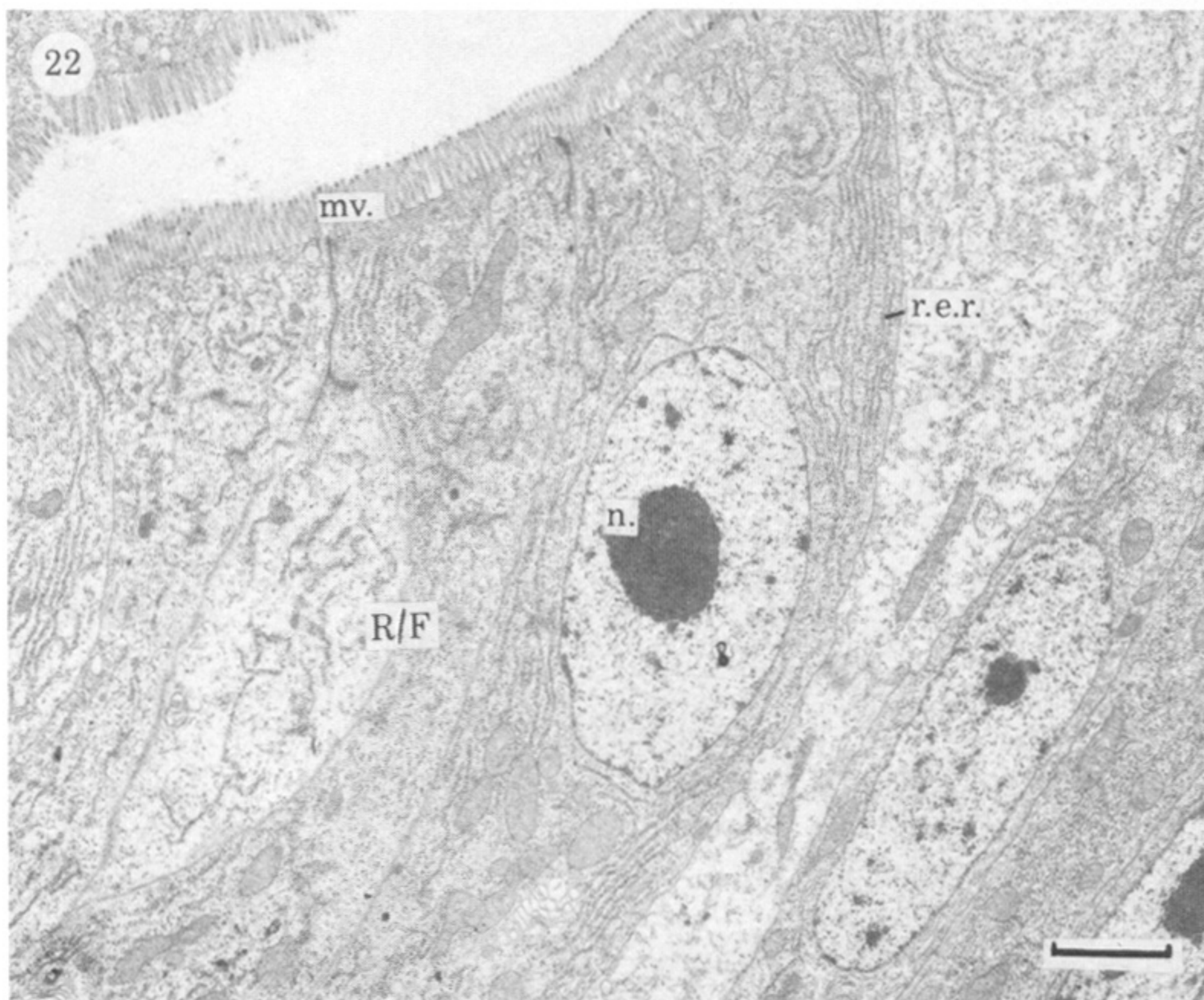
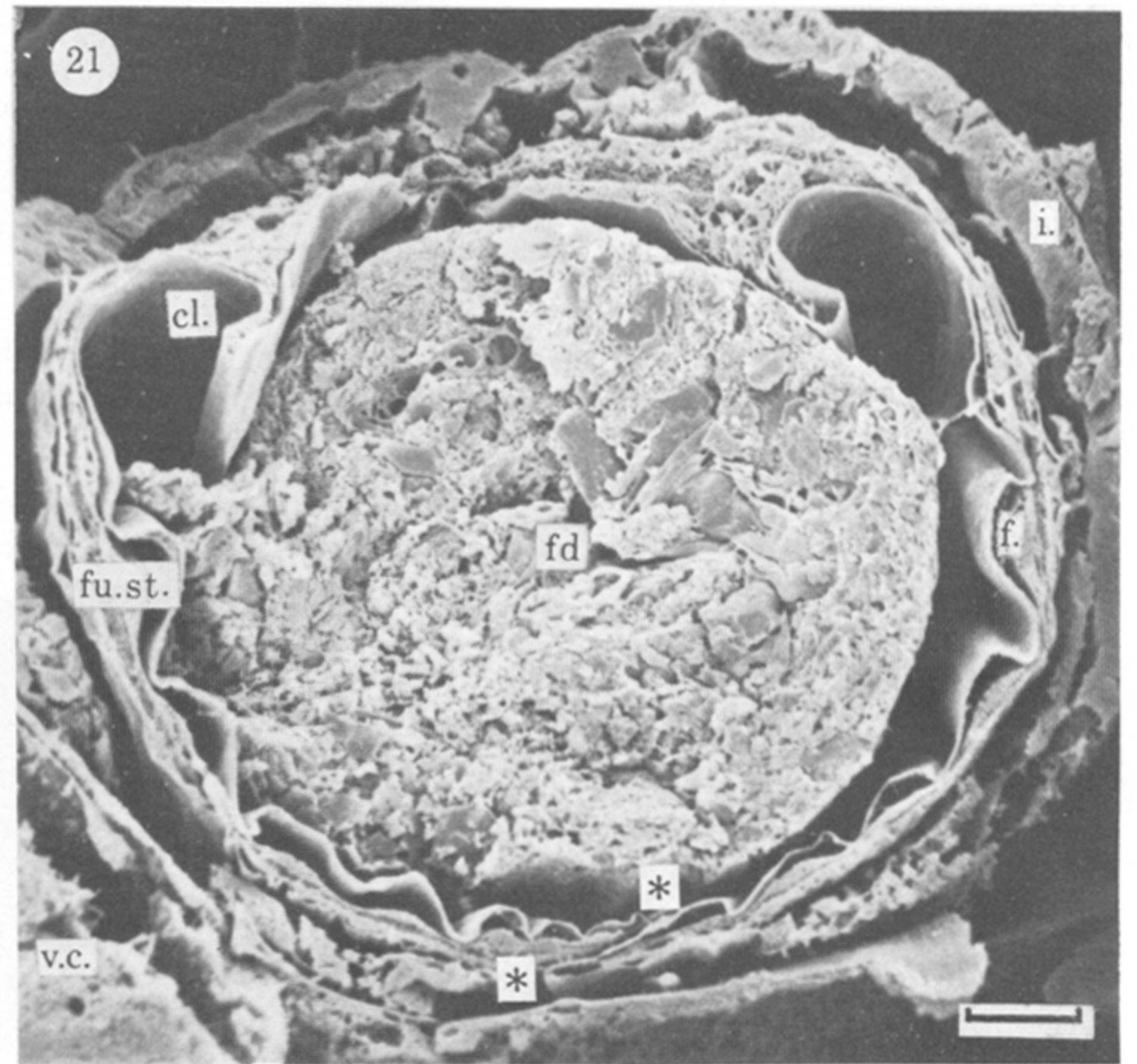
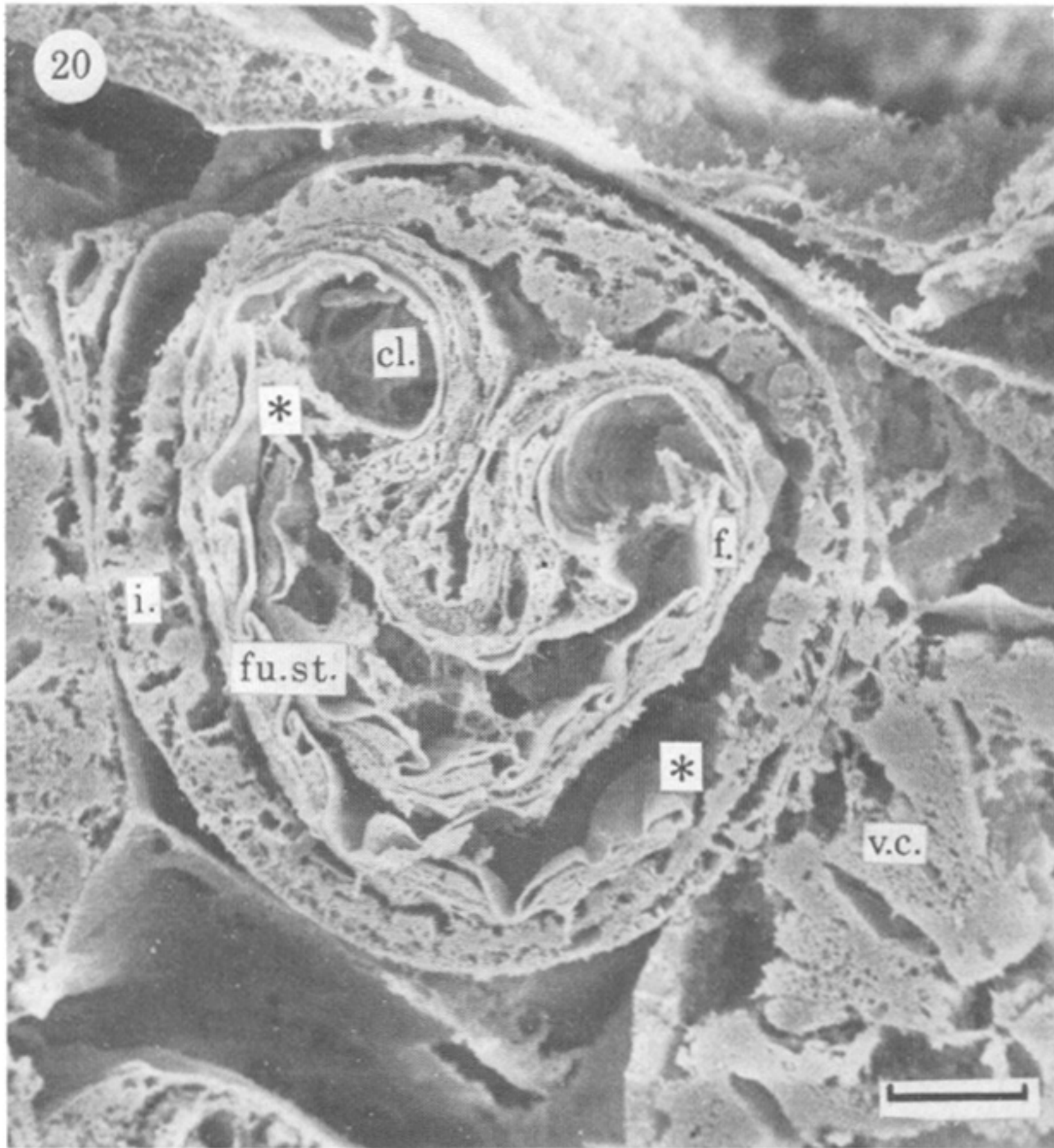
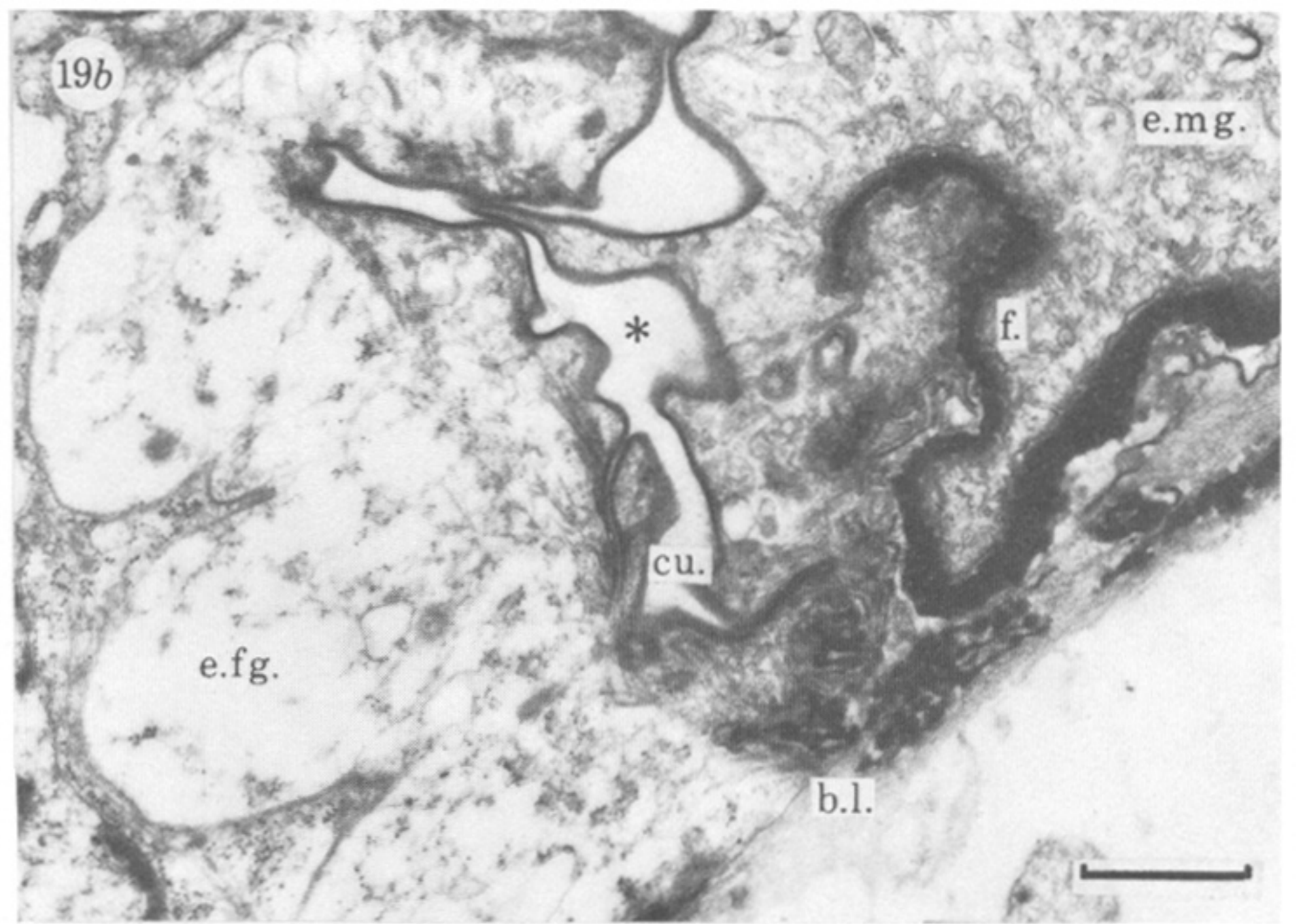
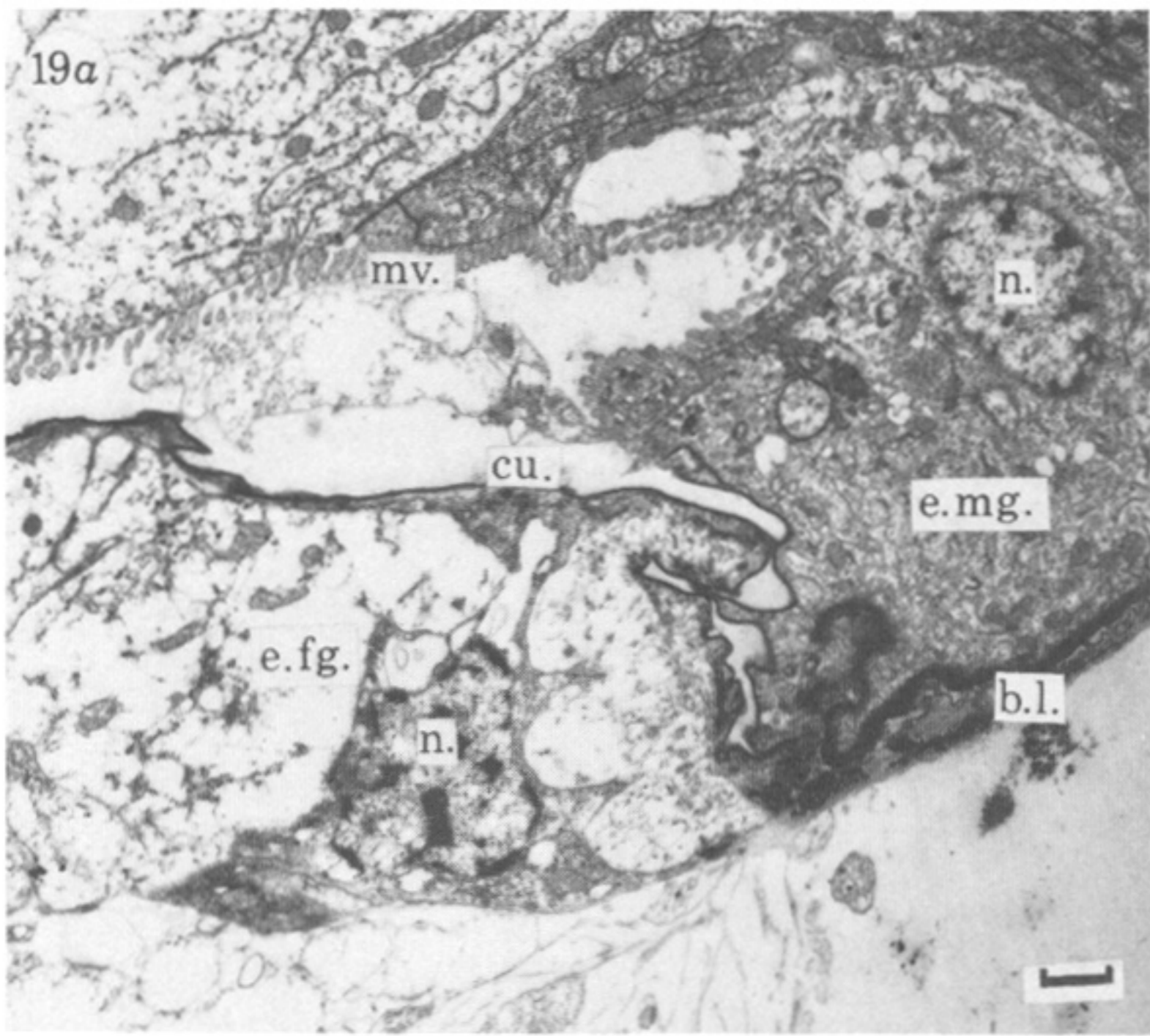
FIGURES 10 AND 11. For description see p. 56.



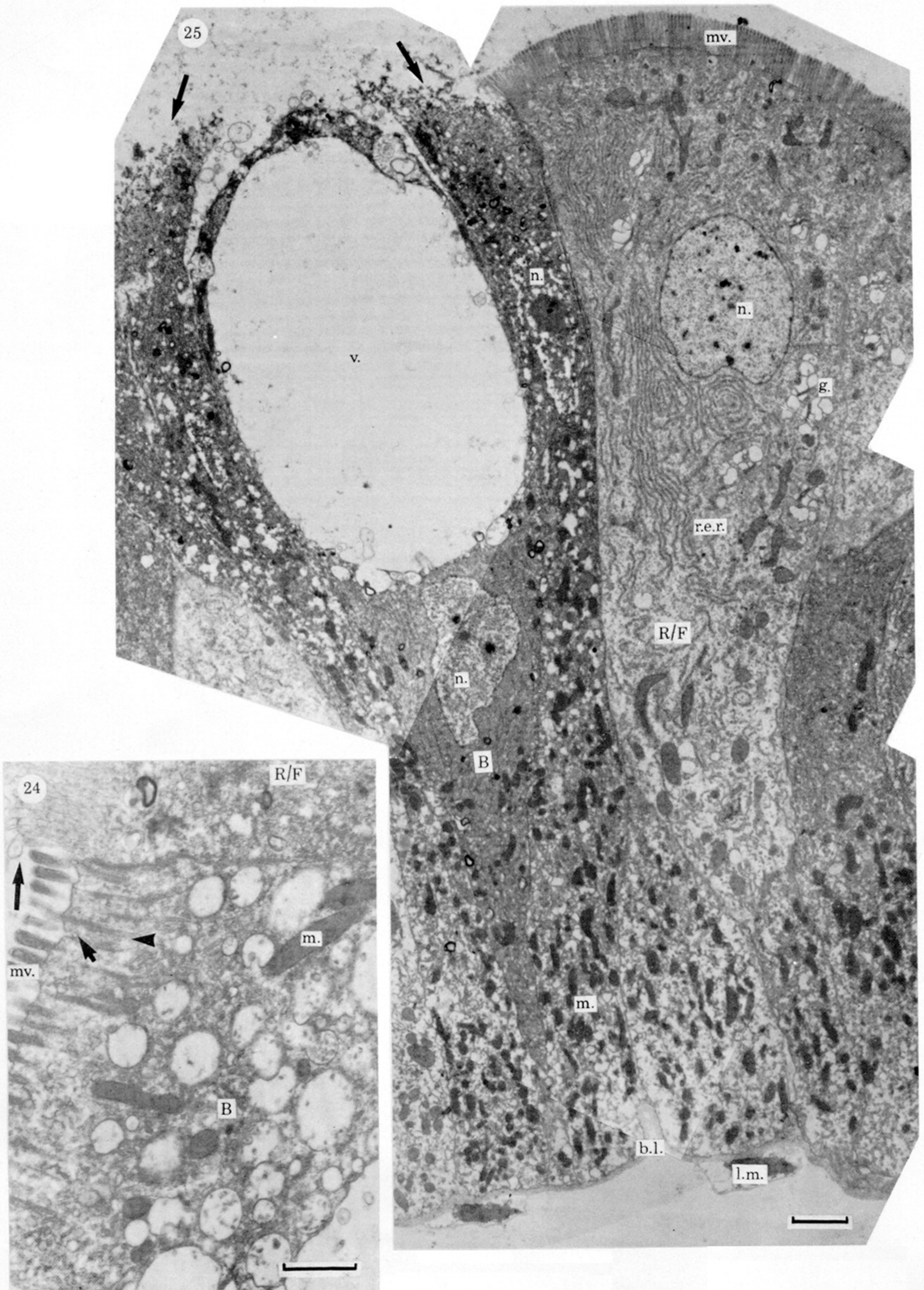
FIGURES 12-15. For description see p. 56.



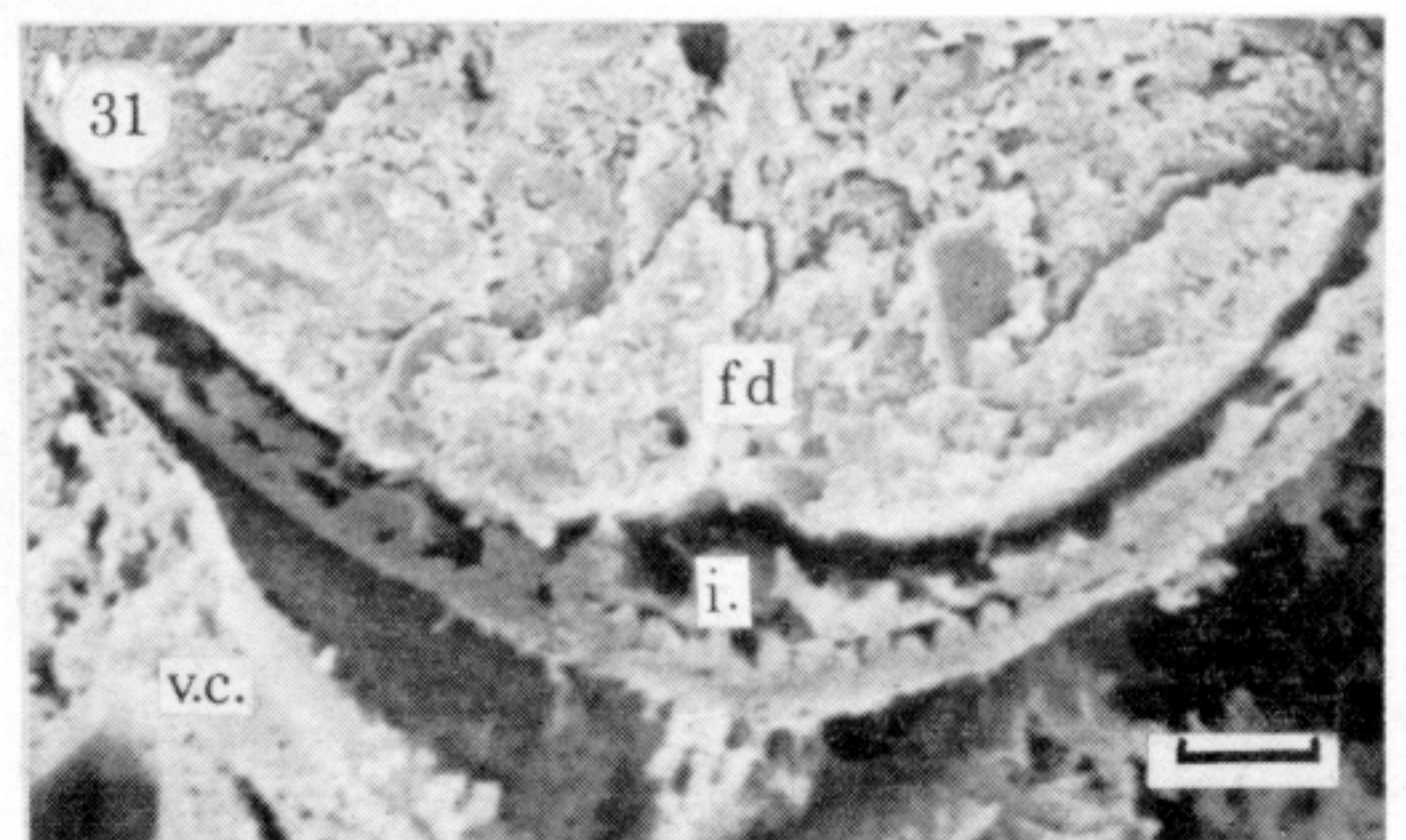
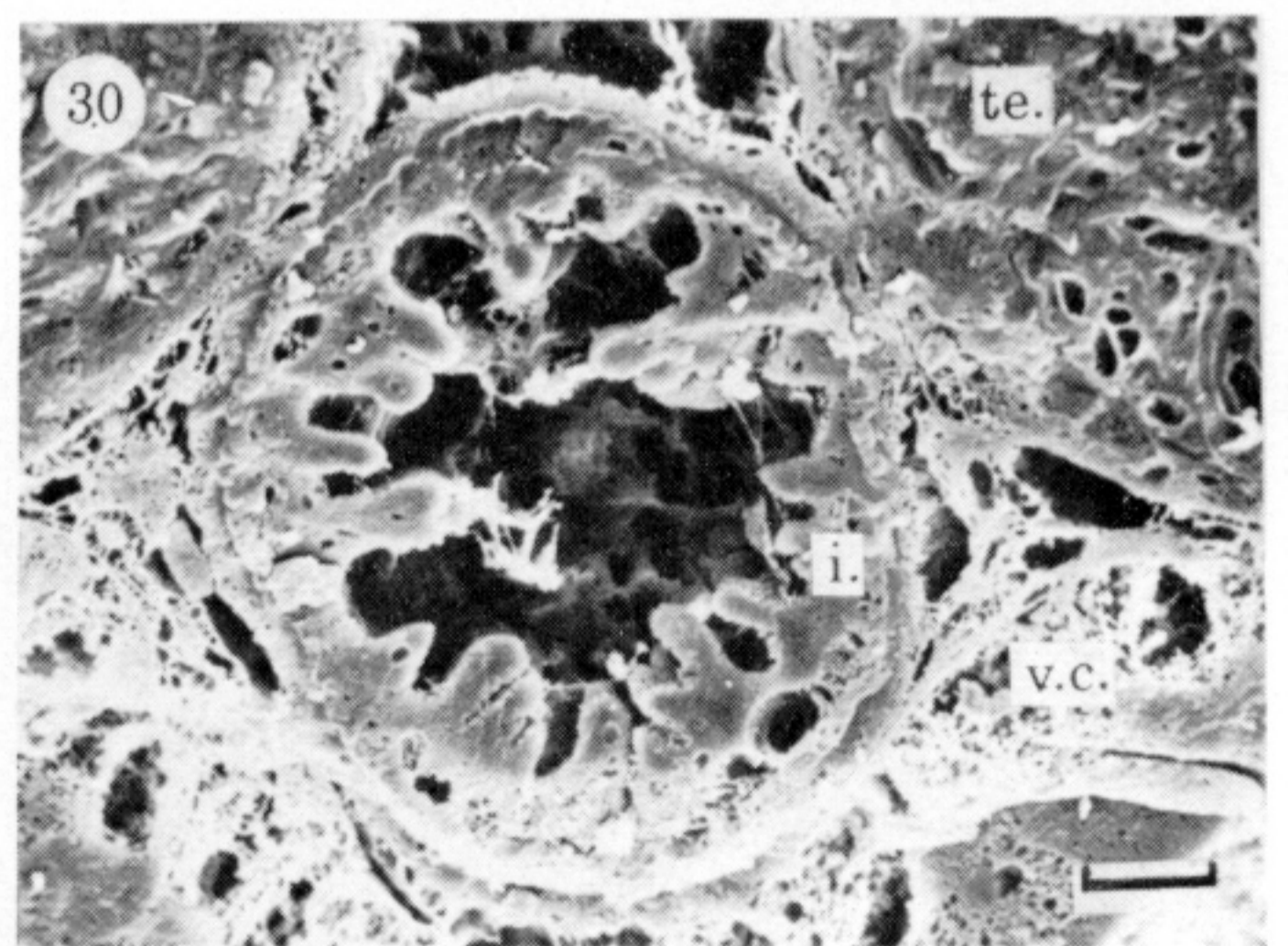
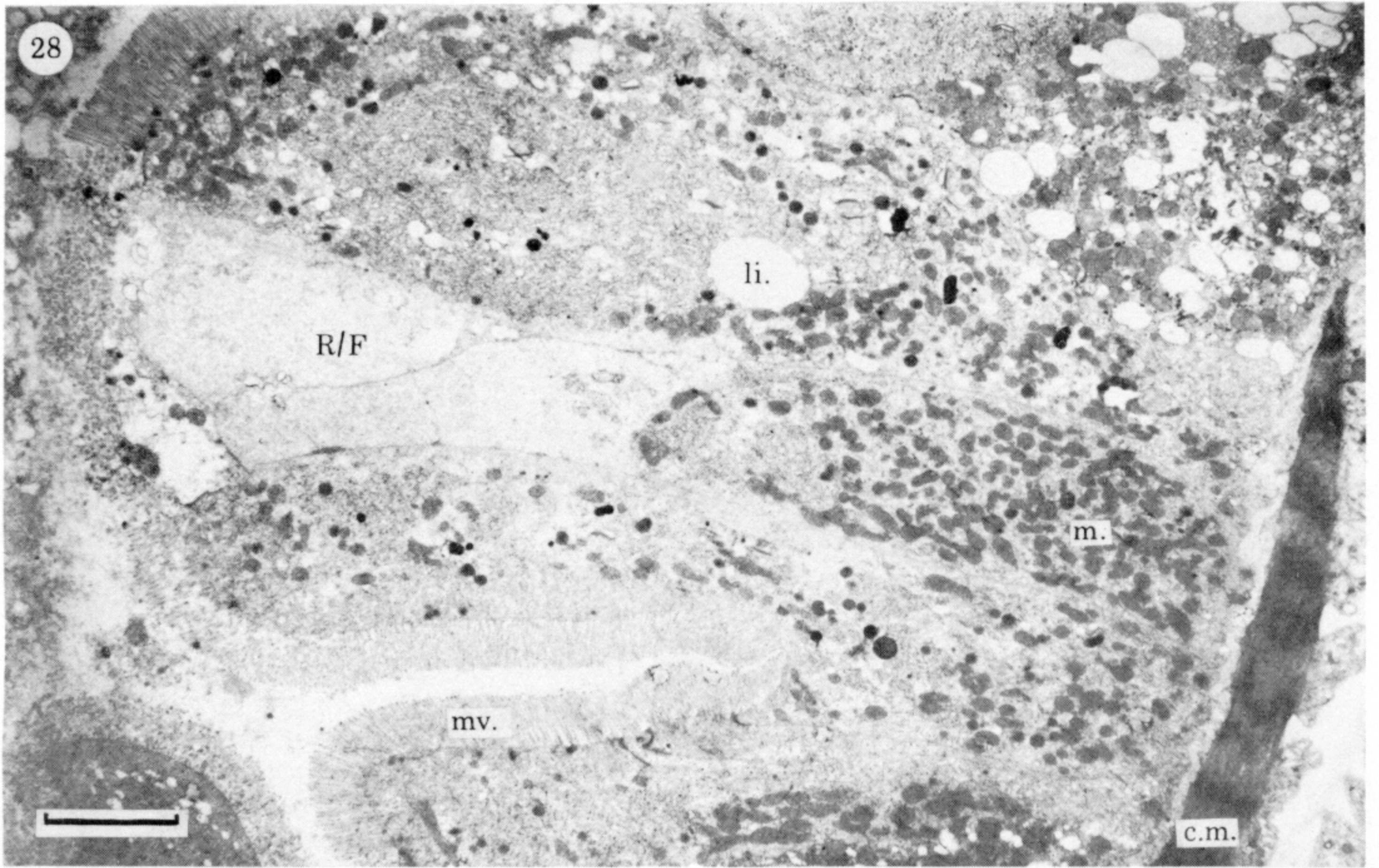
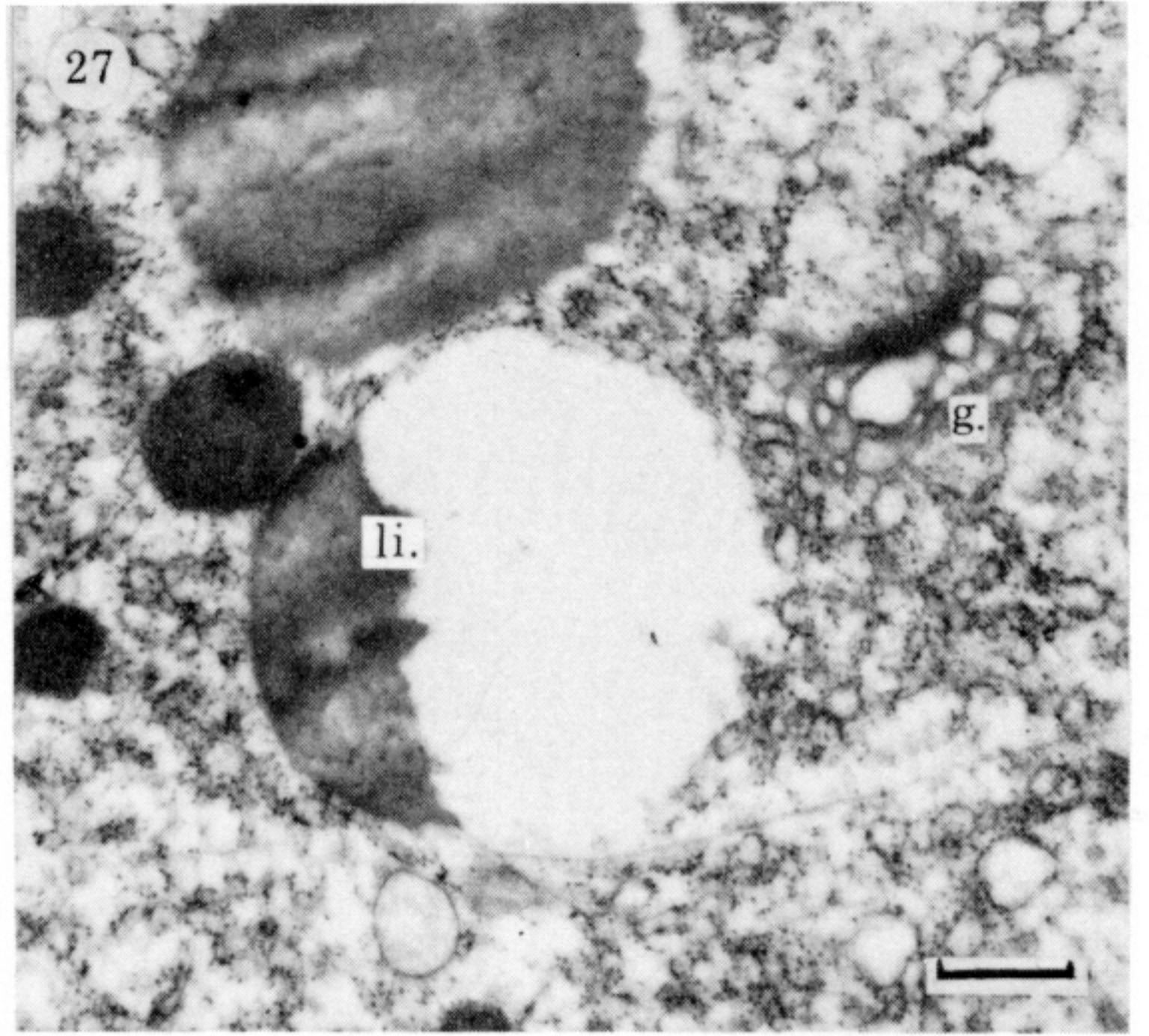
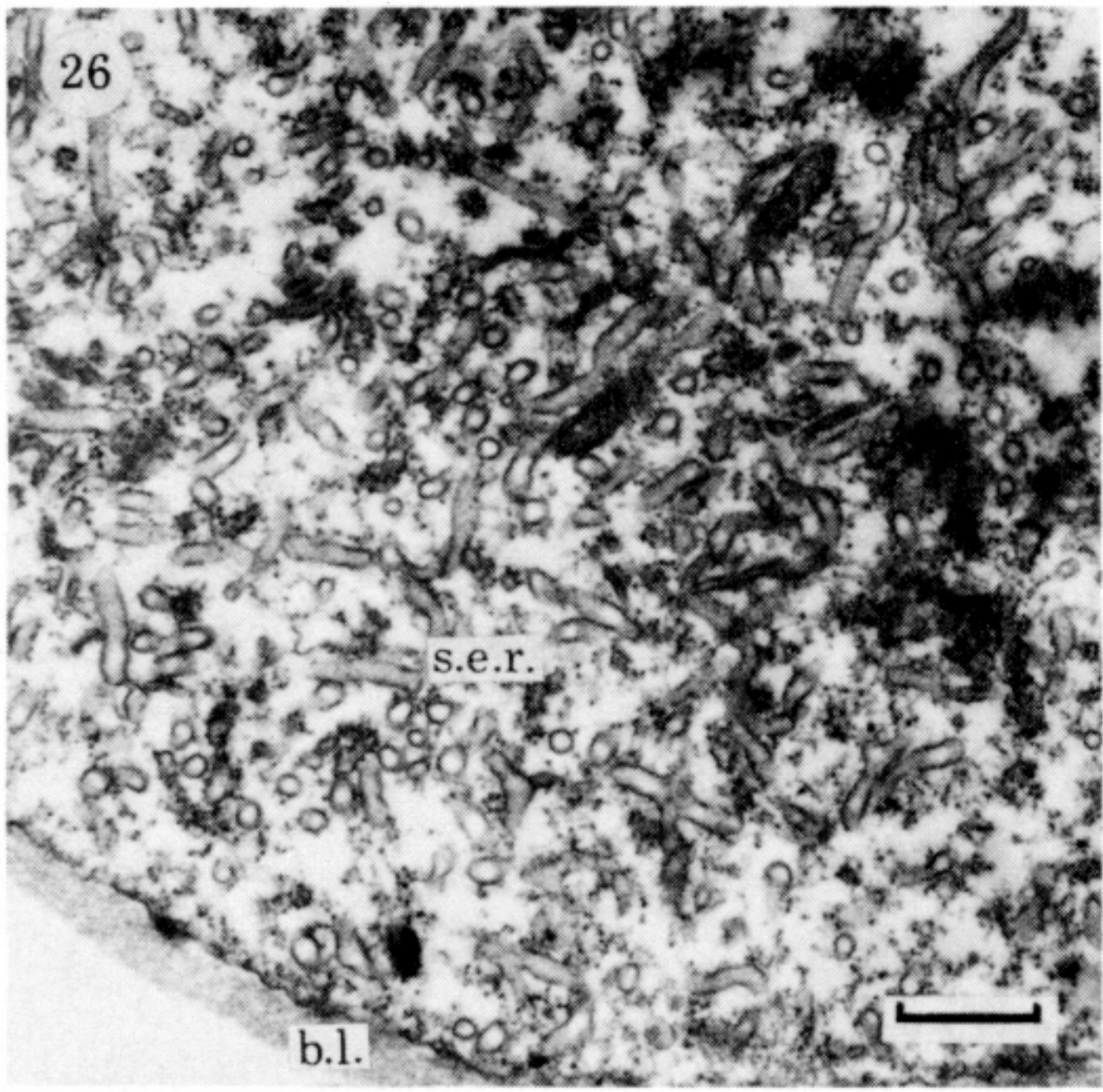
FIGURES 16-18. For description see opposite.



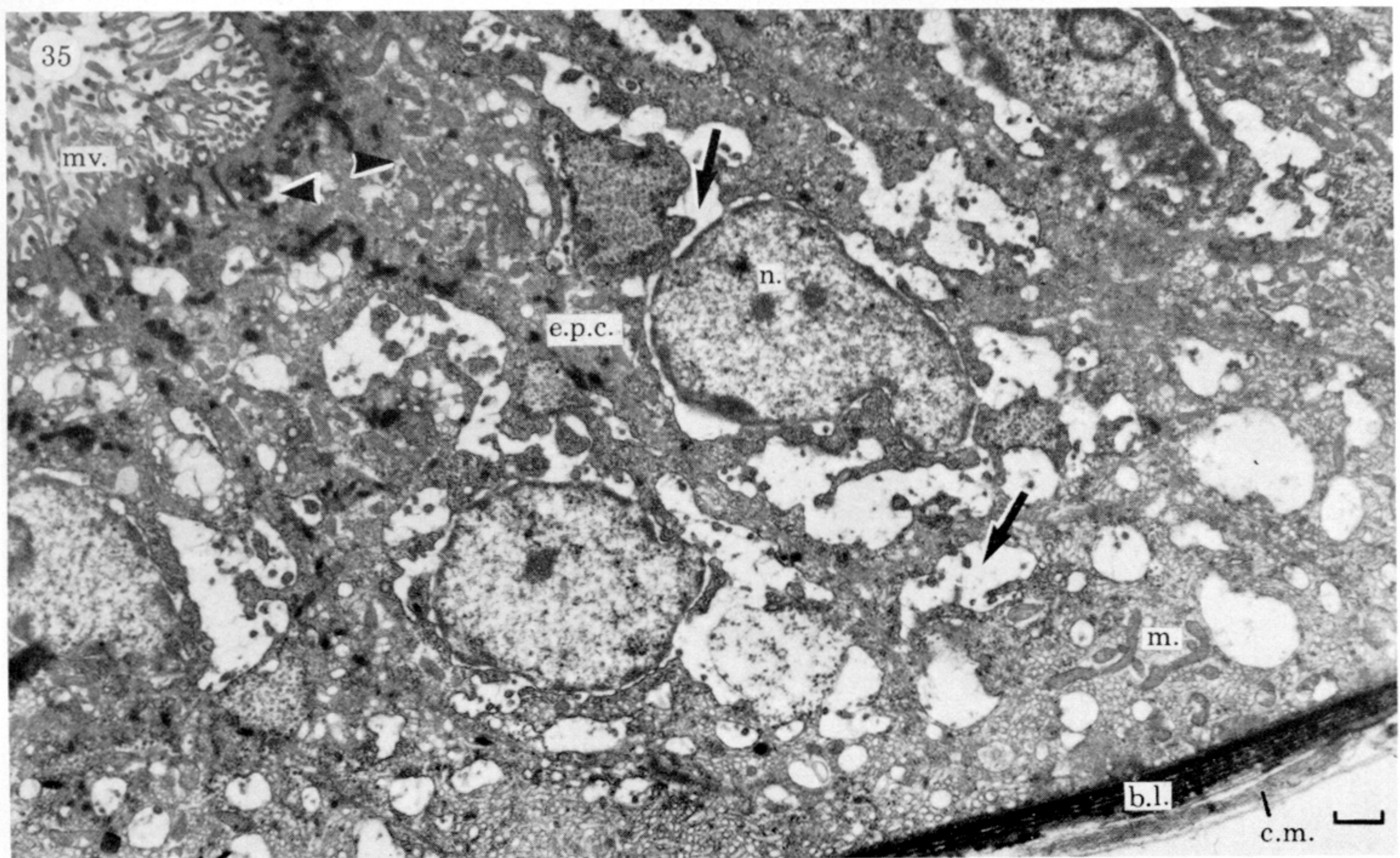
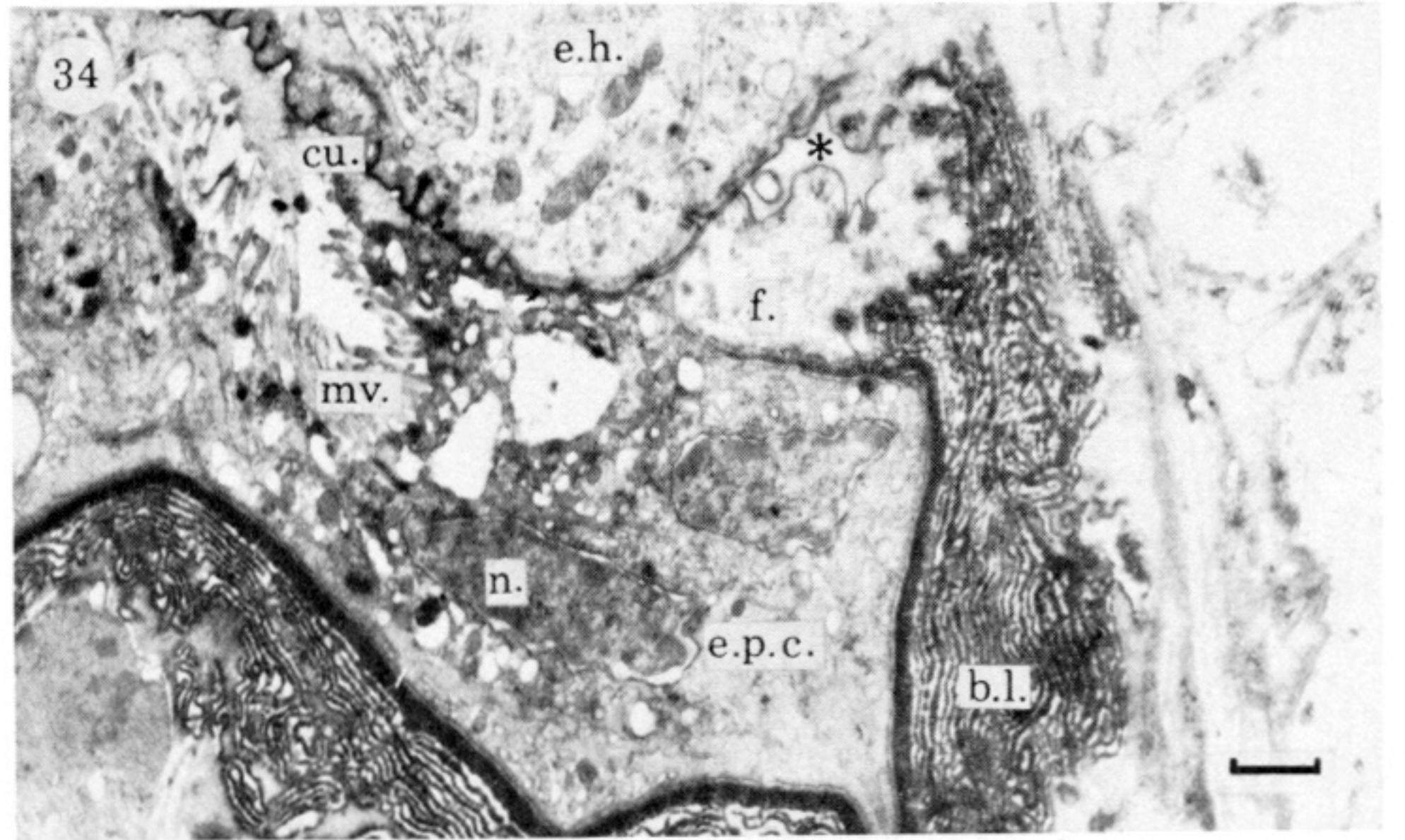
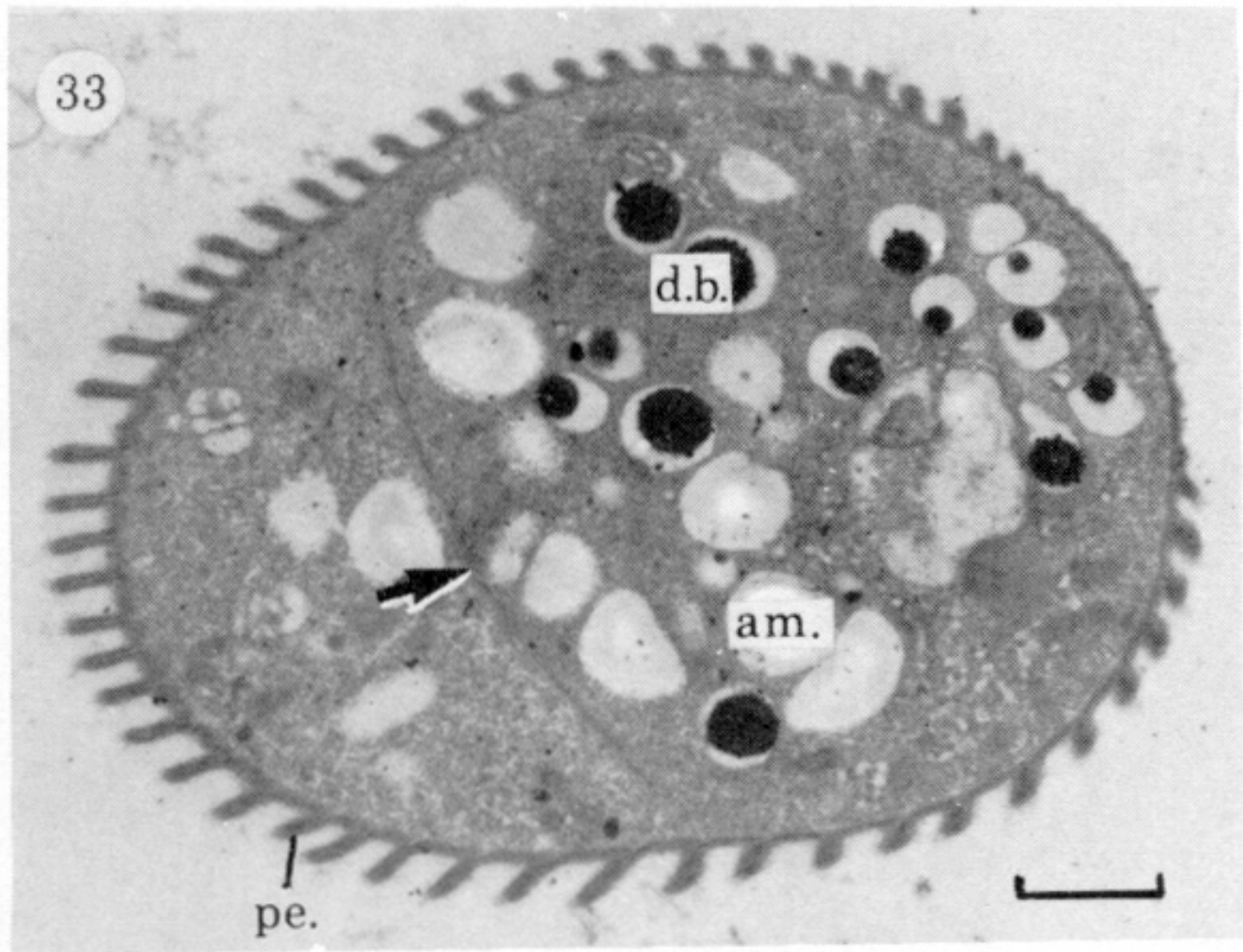
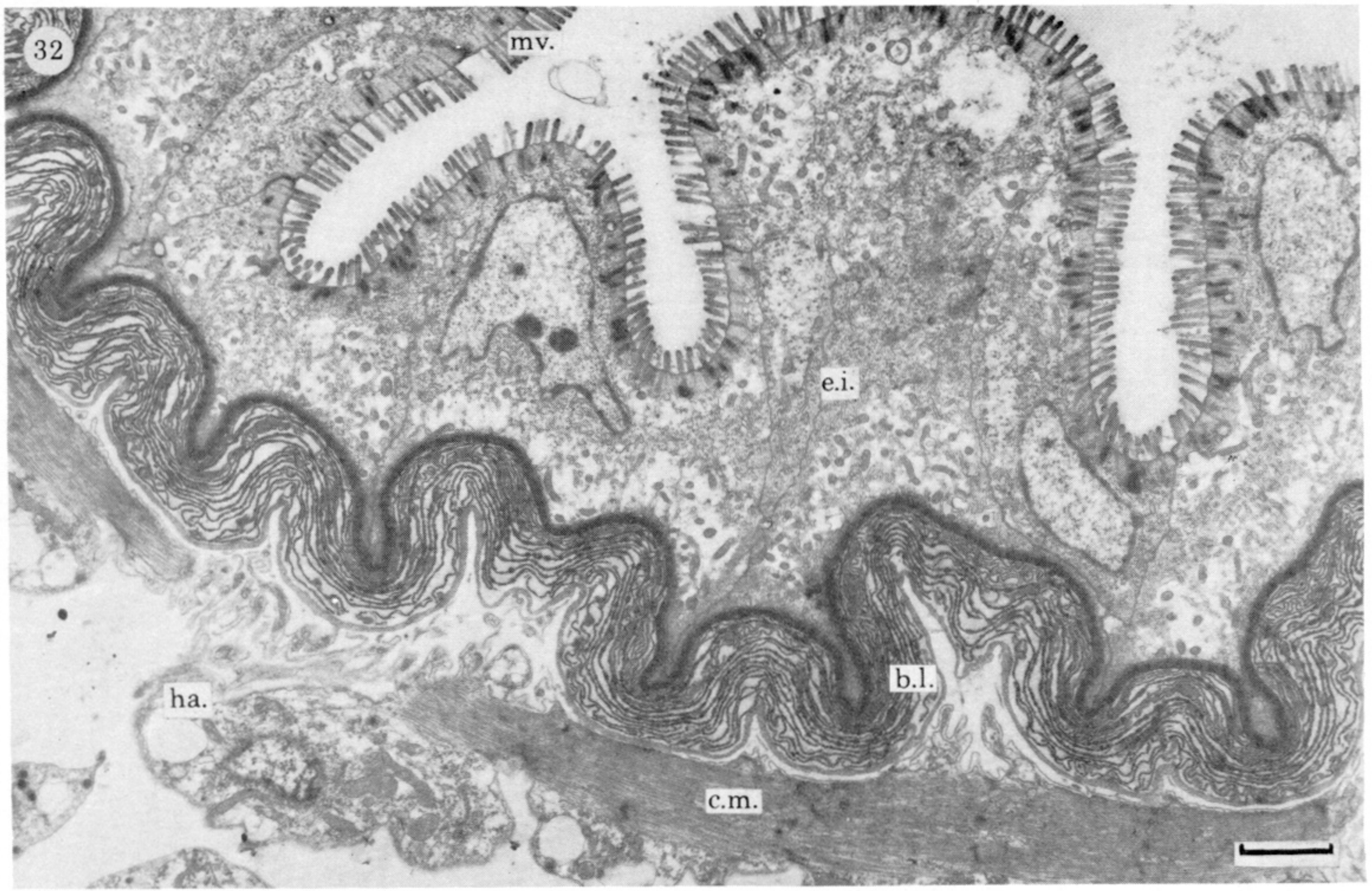
FIGURES 19-23. For description see previous page.



FIGURES 24 AND 25. For description see p. 57.



FIGURES 26-31. For description see p. 57.



FIGURES 32-35. For description see p. 57.



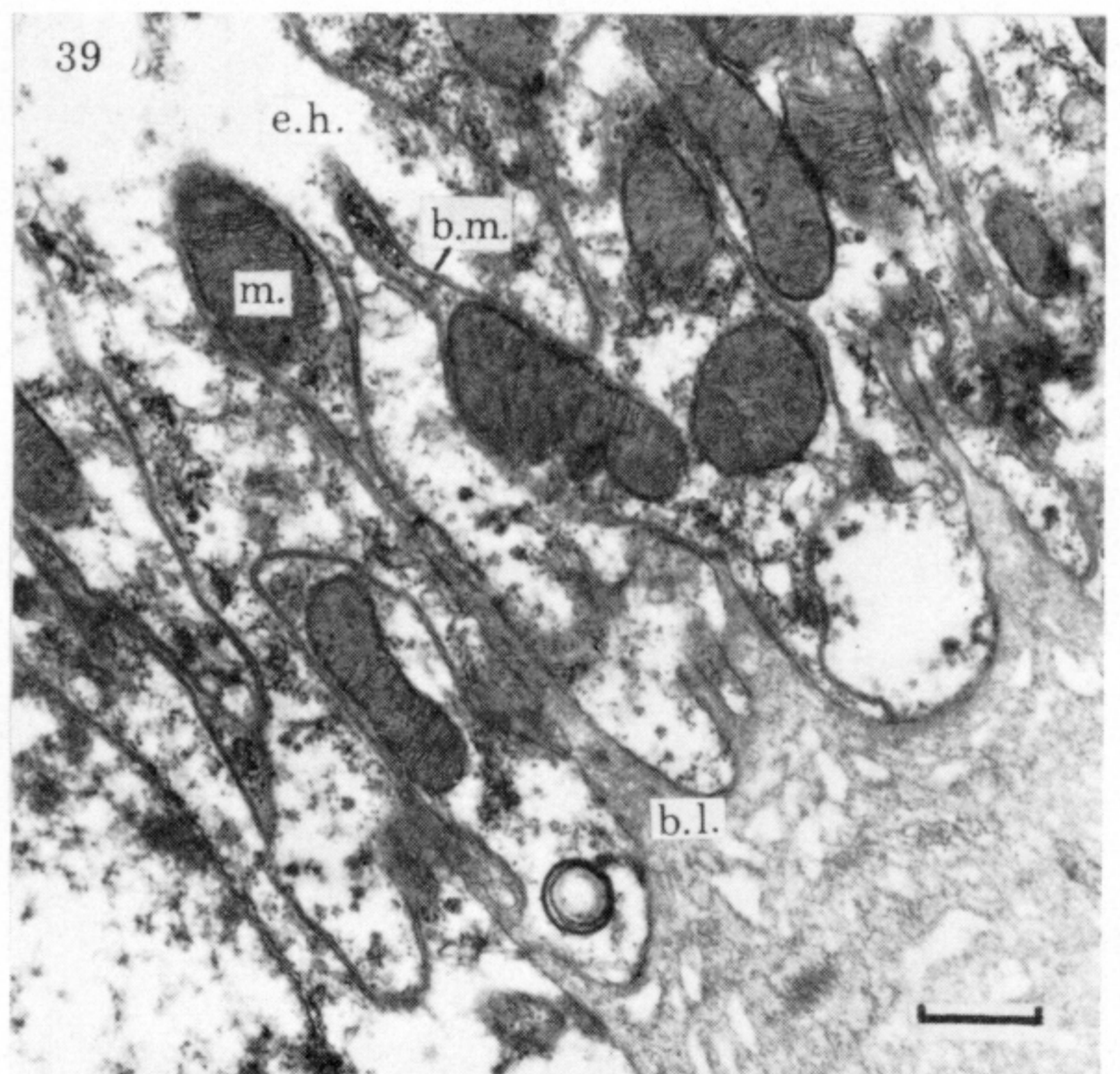
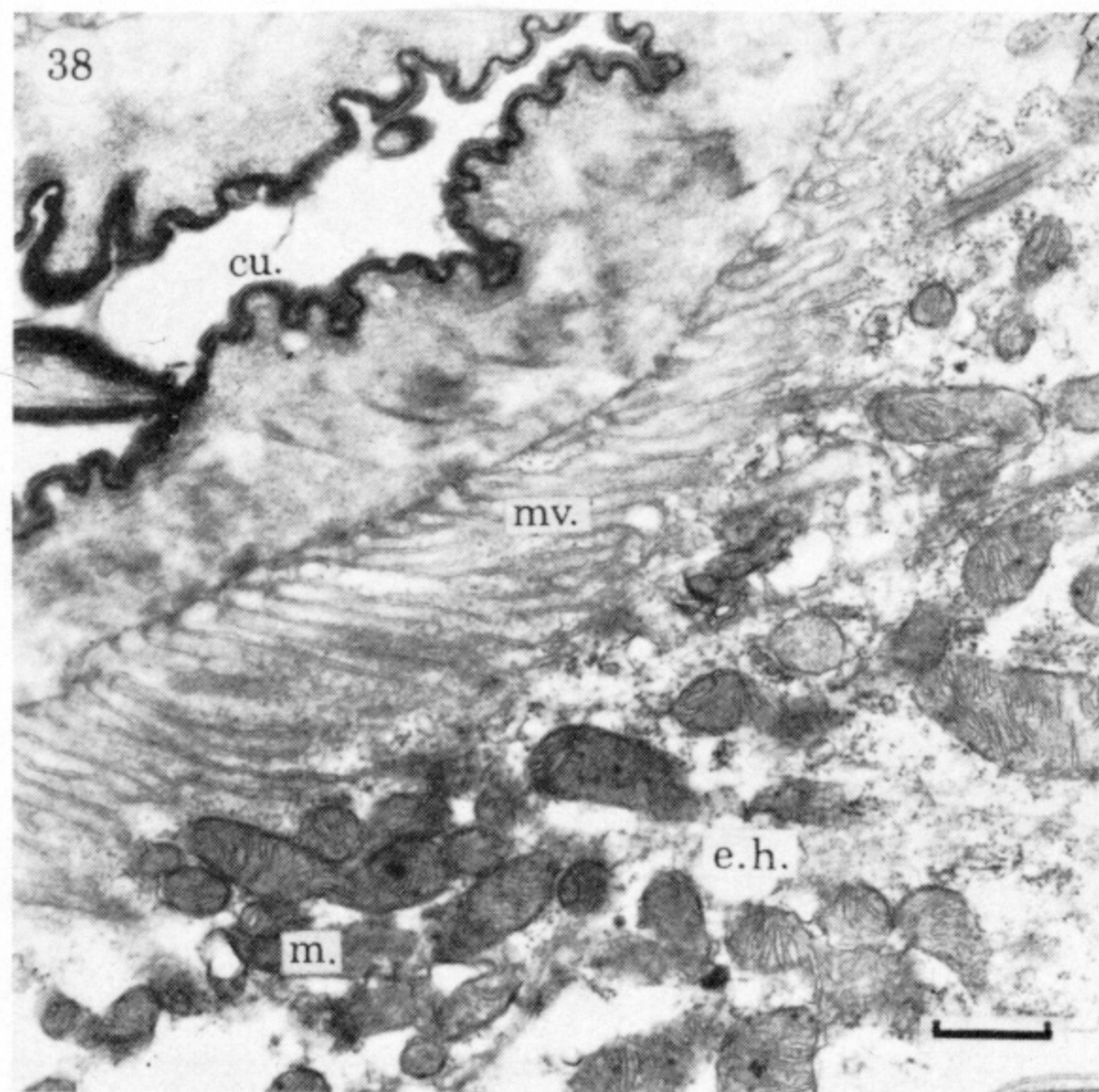
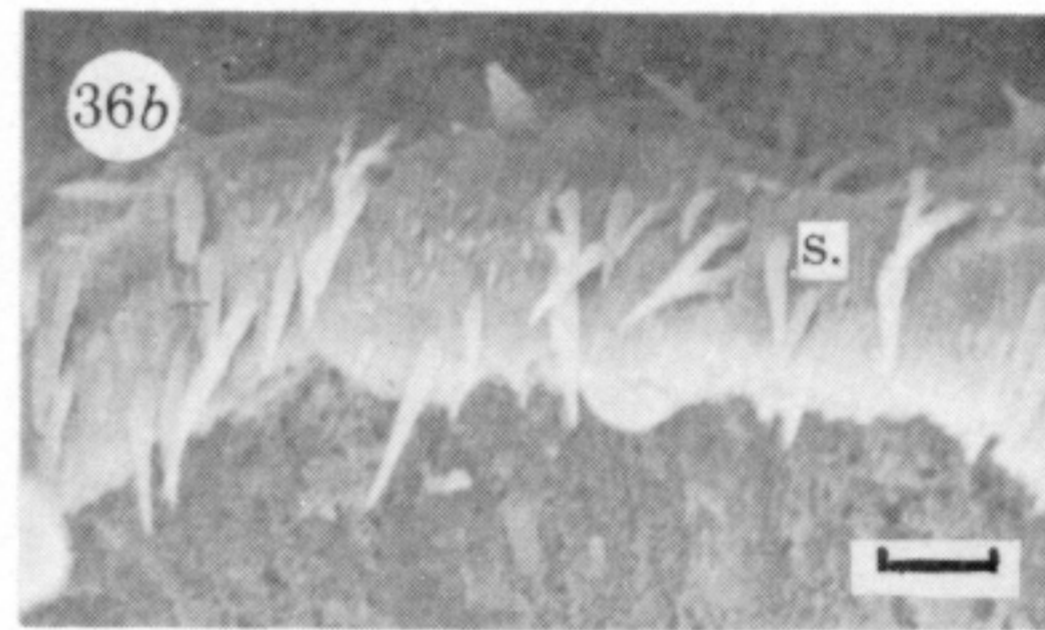
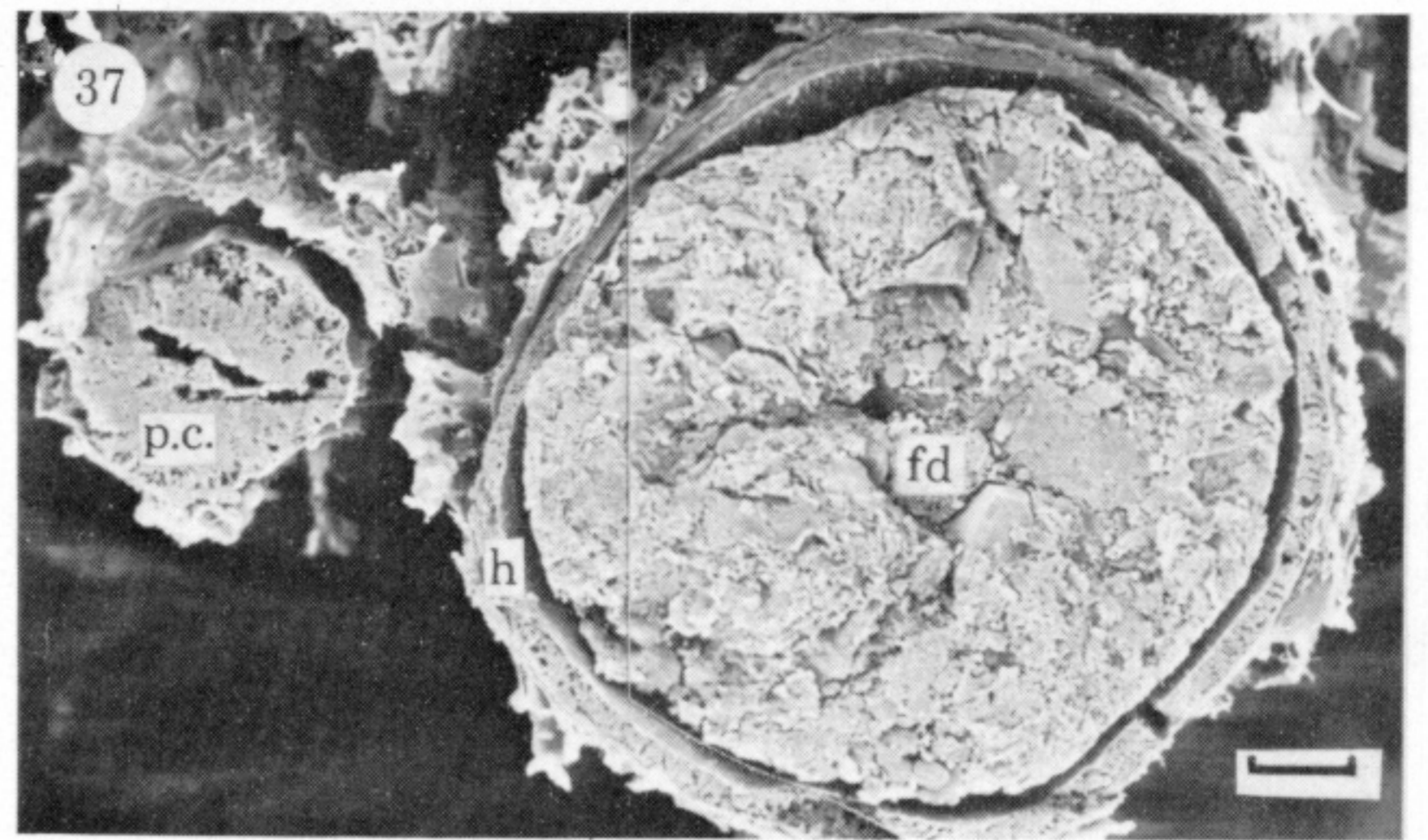
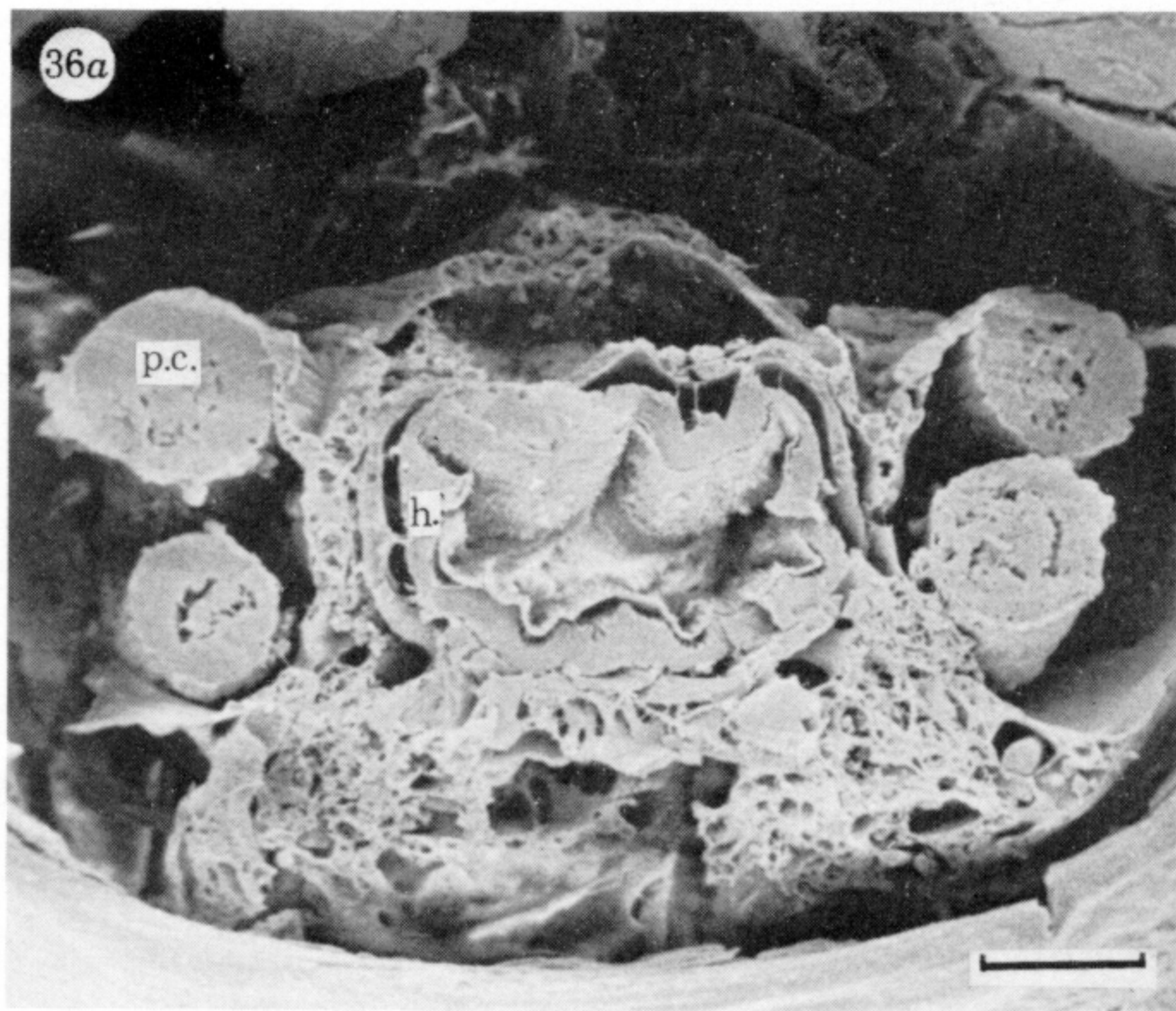


FIGURE 36. (a) Transverse fracture of an empty hindgut (h.) with flanking posterior caeca (p.c.) which are folded back on each other. Scale bar = 50  $\mu\text{m}$ . (b) Setation (s.) on the cuticular lining in figure 36a. Scale bar = 2  $\mu\text{m}$ , s.e.m.

FIGURE 37. Transverse fracture of a full hindgut (h.). Scale bar = 20  $\mu\text{m}$ , s.e.m.

FIGURE 38. Microvilli (mv.) underlie the cuticular lining (cu.) of the hindgut (e.h.). Scale bar = 0.5  $\mu\text{m}$ , t.e.m.

FIGURE 39. Basal cell membrane (b.m.) of the hindgut (e.h.) has folds associated with mitochondria (m.) to form 'ion pumps'. Scale bar = 0.5  $\mu\text{m}$ , t.e.m.