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ULTRASTRUCTURAL STUDIES ON THE FORM AND FUNCTION OF THE GASTRODERMIS OF PROTOPOLYSTOMA XENOPI (MONOGENOIDEA: POLYOPISTHOCOTYLEA)

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Studies of intestinal histology and digestive physiology have been carried out on a number of monogeneans, and the available information has been reviewed by Jennings (1968). There is a fundamental difference in the nutrition of the two sub-groups of the Monogenoidea. Representatives of the Monopisthocotylea feed on the epidermis and associated mucoid secretions of the host while the Polyopisthocotylea feed almost exclusively on the host's blood. Differences in the diet and digestive processes of these groups are reflected in the cellular organization of the gastrodermis. Much of digestive breakdown in the Monopisthocotylea is believed to be extracellular and the soluble products are absorbed by a continuous cuboidal and columnar epithelium. In the Polyopisthocotylea, on the other hand, hemoglobin degradation largely occurs intracellularly and results in the accumulation of hematin within the gastrodermal cells. This insoluble product is thought to be eliminated by the disintegration or shedding of the cell. It has been considered that the digestive process involves the constant degeneration and renewal of the so-called deciduous gastrodermis, and this gives rise to the apparently discontinuous nature of the cecal epithelium. Jennings (1968) has concluded that the consequent wastage of cellular materials during the polyopisthocotylean digestive process represents an incomplete adaptation to the blood-feeding habit.

The ultrastructure of the cecal epithelium has been investigated in only one species of polyopisthocotylean. Halton, Dermott and Morris (1968) reported that in *Diclidophora merlangi* the cecal epithelium is in fact a continuous structure composed of two distinct cell types, with pigmented "hematin cells" alternating with flat, extensive "connecting cells." The latter cover all areas of the cecal wall between the hematin cells and are so thin in section that they cannot be resolved by light microscopy.

The present paper describes the ultrastructural organization of the cecal epithelium of *Protopolystoma xenopi* (Price, 1943) Bychowsky, 1957, a blood-feeding parasite of the African clawed toad, *Xenopus laevis* (Daudin). Observations are made on the growth of the gastrodermis during the parasite's development and on the structural changes accompanying digestion; an interpretation of the functional morphology of the epithelial components is presented.

Materials and Methods

Ultrastructural observations were made on *Protopolystoma xenopi* over a range of developmental stages. Adult worms were obtained from the urinary bladder of naturally-infected *Xenopus laevis* imported from South Africa. Hosts were also

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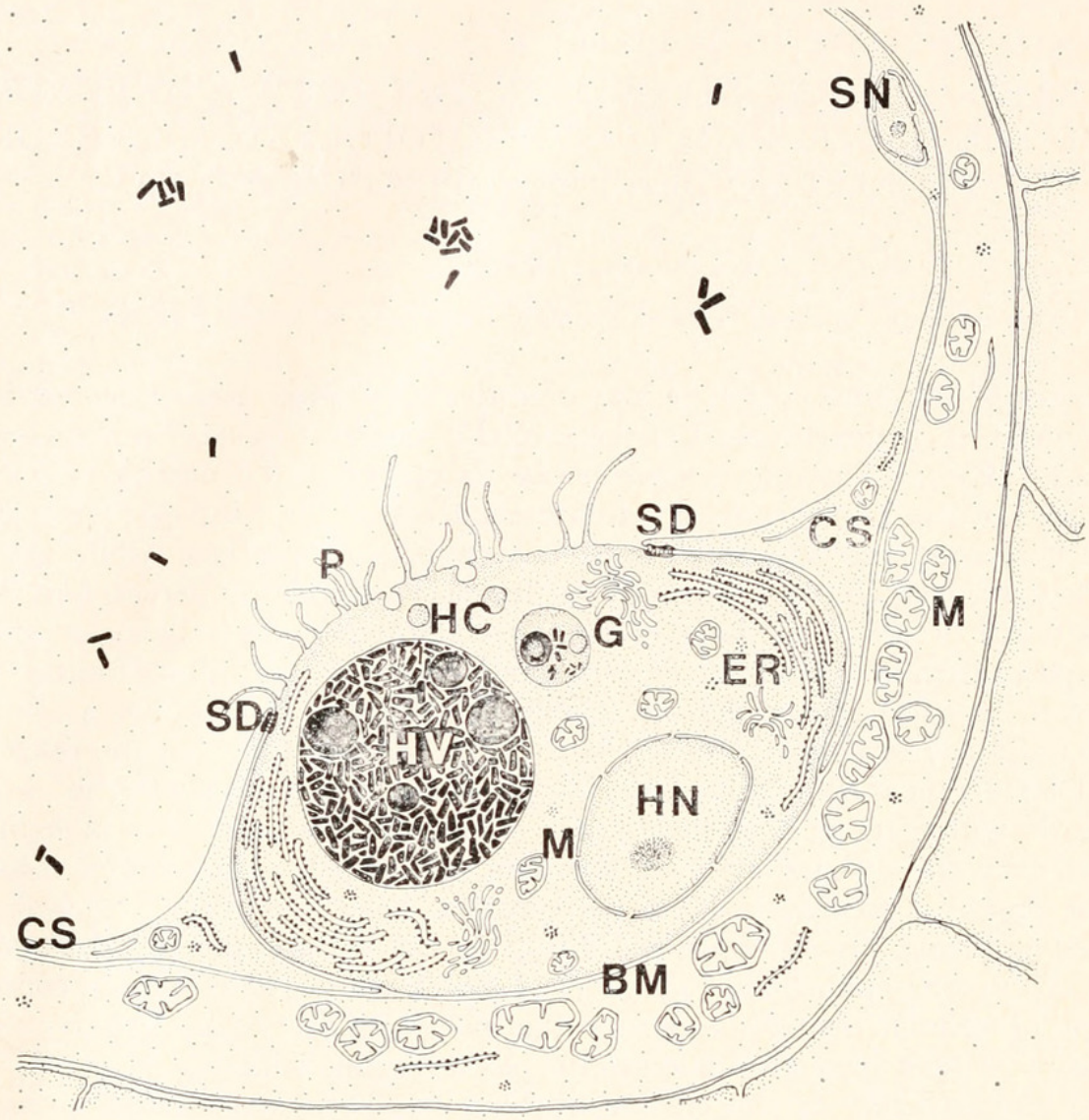


FIGURE 1. *Protopolystoma xenopi*; diagrammatic representation of the structure of the cecal epithelium. The hematin cell (HC) bears cytoplasmic processes (P) on its exposed distal border, the nucleus (HN) is basal and rough endoplasmic reticulum (ER) and associated golgi bodies (G) are situated laterally. Hemoglobin breakdown takes place within large membrane-bound vacuoles (HV) and leads to the appearance of hematin and lipid-like droplets. Mitochondria (M) are scattered in the hematin cell and densely aggregated beneath the basement membrane (BM). The sheet-like connecting syncytium (CS) surrounds the hematin cell laterally and a septate desmosome (SD) occurs at the point of maximum overlap. The nuclei (SN) and organelles of the syncytium are relatively scattered.

infected experimentally in the laboratory (Tinsley and Owen, in preparation); larval parasites were recovered from the kidneys two weeks after infection, juvenile parasites from the bladder after eight to ten weeks, and adults from the bladder after sixteen weeks.

Adult parasites were fixed at progressive intervals after feeding, specimens with bright red gut contents being regarded as very recently fed. These were fixed either immediately or after being maintained for 12, 24 and 48 hours in 33% normal strength *Xenopus* ringer.

All specimens were fixed for two hours in ice-cold 3% glutaraldehyde in 0.1 M cacodylate buffer at pH 7.2. The material was rinsed for 15 minutes in 0.1 M

cacodylate buffer in 1 M sucrose and post-fixed for one hour in 1% osmium tetroxide held at pH 7.3 with 3.6×10^{-2} M veronal buffer containing invertebrate salt solution. A 15 minute rinse in veronal buffer was followed by dehydration in ice-cold graded ethanols, impregnation with propylene oxide at room temperature and embedding in Shell Epikote resin (epon 812). Silver to grey sections were cut with glass knives on a Cambridge (Huxley) ultramicrotome and mounted on formvar-coated or uncoated grids. These sections were double-stained with uranyl acetate and lead citrate and examined with an AEI EM6B electron microscope. Sections cut at 0.5 μ were mounted on glass slides, stained in Azur II in borax (Jeon, 1965) and examined with the light microscope.

The presence in some gastrodermal cells of large quantities of hematin often made the cutting of satisfactory thin sections difficult. The picric alcohol test described by Halton *et al.* (1968) was employed to identify the hematin.

Observations

The structure of the gastrodermis

The intestinal system of *Protopolystoma xenopi* is composed of two lateral ceca arising immediately behind the pharynx; these extend to the posterior of the worm and bear parallel diverticula on both medial and lateral surfaces. The majority of diverticula are blind-ending pouches but up to six of the medial branches extend across the mid-line and join the right and left ceca.

Light microscope examination revealed that the intestinal system is bordered by discontinuously arranged cells which have an irregular shape, possess basal nuclei and contain varying amounts of hematin enclosed in spheroidal vacuoles. The intervening cecal walls are apparently devoid of cells (Fig. 2).

With the electron microscope the cecal epithelium was found to consist of two components, the larger "hematin cells" referred to above, and a thin cytoplasmic layer composed of "connecting cells" (Halton *et al.*, 1968) covering the basement membrane between adjacent hematin cells. The structure and arrangement of the two components was most clearly observed in juvenile parasites and a relatively constant pattern was recorded (Fig. 1). The hematin cell protrudes from the cecal wall into the gut lumen and a portion of its lateral border is overlapped by an extension of the connecting cell system. The exposed apical plasma membrane bears numerous cytoplasmic processes usually up to 2 μ but occasionally 4 μ in length, and circular in cross section (diameter about 0.05 μ) (Figs. 4 and 5). The processes have an uneven distribution; in some areas they are regularly arranged, about 0.06 μ apart, whilst in others they are relatively scattered at intervals of 0.3–1.0 μ. The hematin cell contains a large basal nucleus with a prominent nucleolus, and lateral to this, in a region overlapped by connecting cell, is an endoplasmic reticulum and associated golgi complex (Figs. 5, 7 and 8). The reticulum forms an arc of up to eleven concentric cisternae which are interconnected laterally and studded with numerous ribosomes. Two golgi bodies are often present, one situated at each end of the endoplasmic reticulum. Small vesicles are associated with each complex and the contents of these and of the golgi cisternae are moderately electron dense. Small mitochondria are scattered throughout the cell whilst larger more numerous mitochondria are aggregated beneath the basement membrane

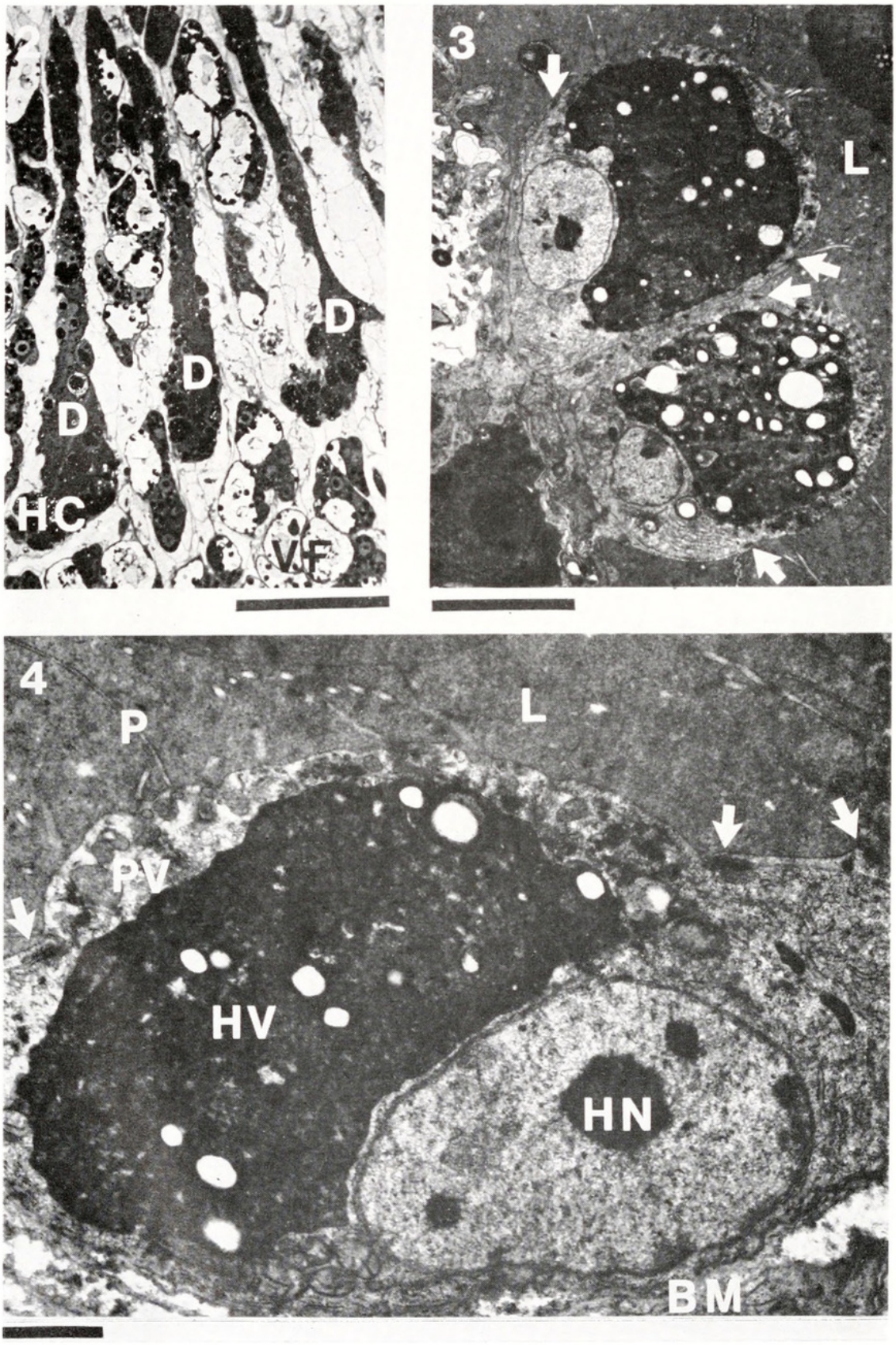


FIGURE 2. *P. xenopi*; light micrograph showing transverse section through cecal diverticula (D). Discontinuously-arranged hematin cells (HC) are interspersed with areas apparently devoid of cells; vitelline follicles (VF) are distributed in the inter-cecal parenchyma; scale bar, 50 μ.

FIGURE 3. *P. xenopi*; part of the gastrodermis showing two hematin cells protruding into the gut lumen (L). The very thin connecting syncytium covers the adjacent cecal wall and

of the gastrodermis (Fig. 8). One or more large membrane-bound vacuoles occur in a distal position in the cell, these usually measure about 12 μ in diameter but may reach 20 μ. They contain varying amounts of dense granular pigment, identified by the picric alcohol solubility test (Llewellyn, 1954; Halton *et al.*, 1968) as hematin, together with homogeneous lipid-like droplets. The hematin is often composed of splinter-like fragments which may also be observed scattered in the intestinal lumen (Fig. 13). Pinocytotic vesicles containing material almost indistinguishable from that in the gut lumen often occur in the distal cytoplasm between the free plasma membrane and the hematin vacuole. Fine tubules, approximately 0.06 μ in diameter, may also ramify through this region.

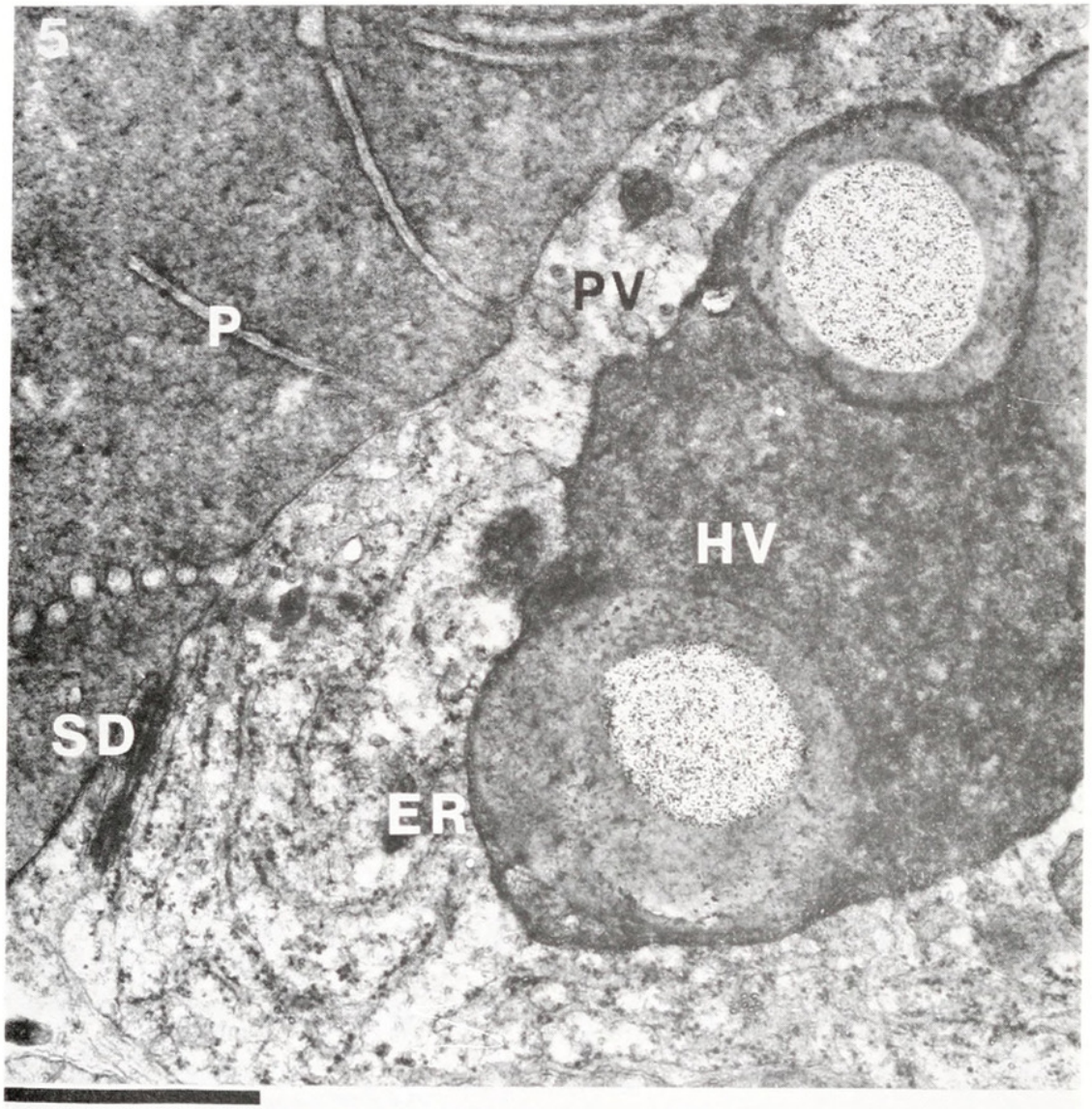
The connecting cell system is very thin, usually measuring up to 0.3 μ in section. It invariably intervenes between adjacent hematin cells and even where the latter are in close proximity they are separated by a thin cytoplasmic layer (Fig. 7). Where the hematin cells are well separated the connecting system forms a flat sheet overlying the basement membrane. Extensions of this system overlap a variable portion of the lateral border of each hematin cell and a septate desmosome is present at the point of maximum overlap (Figs. 5 and 6). Extensions also pass a short distance beneath the margin of the cell. The free plasma membrane of the connecting system does not form lamellae or other cytoplasmic processes and shows no evidence of pinocytotic activity. The cytoplasm is not as dense as that of the hematin cell and contains relatively scattered organelles. The connecting system intervening between hematin cells may contain small mitochondria, rough endoplasmic reticulum and golgi apparatus, but the extensions overlapping the hematin cells are generally very thin and devoid of inclusions. Pigment-containing vacuoles similar to those characteristic of the hematin cells do not occur in the connecting system. The nuclei are accommodated within swellings of the sheet-like cytoplasm, up to 3 μ in thickness, but they have been observed infrequently in the large number of sections examined. No cell junctions have been recorded, and the cytoplasm of the connecting system is apparently continuous.

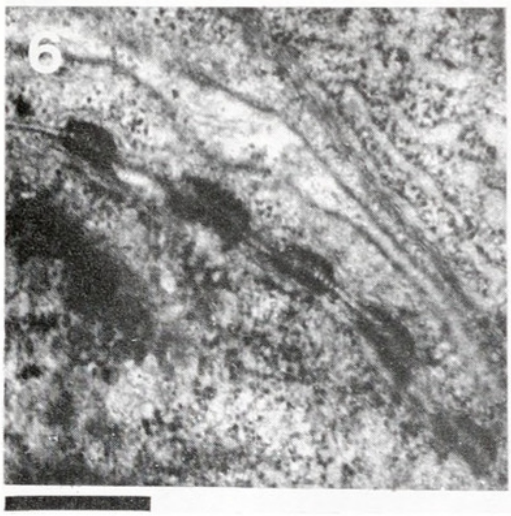
Structural changes accompanying digestion

Few intact erythrocytes have been observed in worms fixed during feeding and it is probable that hemolysis occurs immediately after ingestion. The erythrocyte nuclei, however, persist unchanged for several hours. In a recently-fed *P. xenopi* many hematin cells contain vacuoles of homogeneous, moderately electron-dense material almost indistinguishable from that in the gut lumen (Fig. 11). This appears to enter the cells principally by pinocytosis. Numerous pinocytotic vesicles occur at the surface of the hematin cell and these may be observed to pass through the distal cytoplasm and fuse with the large central vacuoles (Figs. 10 and 11). In

surrounds the lower half of each hematin cell; septate desmosomes (arrowed) mark the extent of the overlap. The hematin cell nuclei are basal and the distal region of each cell is occupied by a large vacuole whose contents are in the course of digestive breakdown; scale bar, 5 μ.

FIGURE 4. *P. xenopi*; the organization of the hematin cell. The nucleus (HN) lies close to the basement membrane (BM); cytoplasmic processes (P) project from the free distal border and numerous pinocytotic vesicles (PV) occur containing material indistinguishable from that in the gut lumen (L). The hematin vacuole (HV) contains fragments of hematin and lipid-like droplets. The lateral regions of the hematin cell are overlapped by the connecting syncytium, with septate desmosomes arrowed; scale bar, 1 μ.





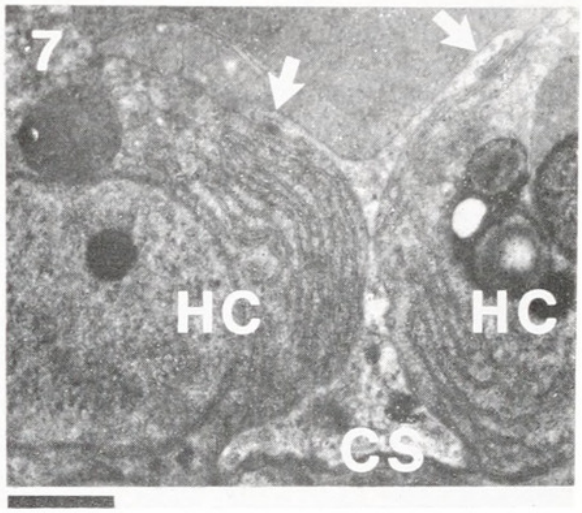


FIGURE 5. *P. xenopi*; hematin cell with vacuole (HV) in the initial phase of digestion, contents slightly denser than those of gut lumen with appearance of ferretin-like granules. Note rough endoplasmic reticulum with interconnected cisternae (ER), cecal cytoplasmic processes (P), probable pinocytotic vesicles (PV), portion of connecting syncytium with septate desmosome (SD); scale bar, 1 μ.

FIGURE 6. *P. xenopi*; detail of septate desmosomes between hematin and connecting cells; scale bar, 0.5 μ.

cells apparently taking part in the process of uptake for the first time a large volume of material may be absorbed very rapidly. A single vacuole forms within the cell which may become so swollen that only an extremely thin layer of cytoplasm (sometimes as little as 0.2 μ deep) encloses the vacuole distally. This condition may be achieved before any changes occur distinguishing the contents from those in the gut lumen. An additional means of hemoglobin uptake may be provided by the numerous fine tubules which are often present in the apical cytoplasm of the hematin cell. These apparently communicate between the free plasma membrane and the vacuole and may be observed to contain material similar to that in the gut lumen (Fig. 9).

During the course of digestion the contents of the vacuole become more electron-dense, presumably as water is withdrawn, and lipid-like droplets and fragments of hematin form initially around the periphery of the vacuole (Figs. 3 and 5). Twenty-four hours after feeding the contents of the majority of hematin cells are in an advanced stage of digestion. One or more vacuoles occupy the distal region of each cell; the vacuoles are packed with highly electron-dense fragments of hematin together with lipid-like droplets and stacks of myeloid fibrils. The high lipid content of the vacuole may be derived from the breakdown of the phospholipid envelopes of the erythrocytes. Hemoglobin uptake can apparently continue for a considerable period as cells heavily laden with hematin may show signs of active pinocytotic absorption.

The enzymes of intracellular digestion are probably derived from the cisternae of the endoplasmic reticulum. Small lysosome-like vesicles are produced by the extensive network of cisternae and these have been observed to fuse with the membrane of the adjacent hematin vacuole.

Hematin accumulates within the cells over a relatively long period and in living adult worms the major part of the intestinal system is an intense black-brown. Hematin discharge occurs continuously, but even in worms starved for four days a considerable amount of intracellular pigment remains. The membrane-bound hematin vacuoles are discharged intact and have been observed lying free in the gut lumen. In living worms the pigment spheres circulate with the gut contents, they eventually disintegrate and fine fragments of hematin become scattered throughout the gut. The mode of discharge of the hematin vacuole has proved difficult to interpret; the attachment of protruding hematin cells to the cecal wall is frequently very tenuous both in young cells in the initial stages of absorption (Fig. 3) and in older hematin-laden cells (Fig. 12). Hematin vacuoles surrounded by a thin layer of cytoplasm have been observed apparently in the process of detachment from the gastrodermis (Fig. 13); however, in many cases it is probable that the cell was sectioned apically and the vacuole was, in life, attached to the cecal wall at a higher or lower plane. At the ultrastructural level no areas of discontinuity or disruption in the cecal epithelium caused by the possible shedding or disintegration of the hematin cells have been observed, and no detached cecal cells have been found in the gut lumen.

FIGURE 7. *P. xenopi*; view of adjacent hematin cells (HC) showing position of intervening connecting syncytium (CS). Hematin cells with prominent collateral cisternae of endoplasmic reticulum, part of digestive vacuole visible in the cell on the right and the nucleus in the cell on the left. The cytoplasm of the connecting syncytium is less dense, septate desmosomes arrowed; scale bar, 1 μ.

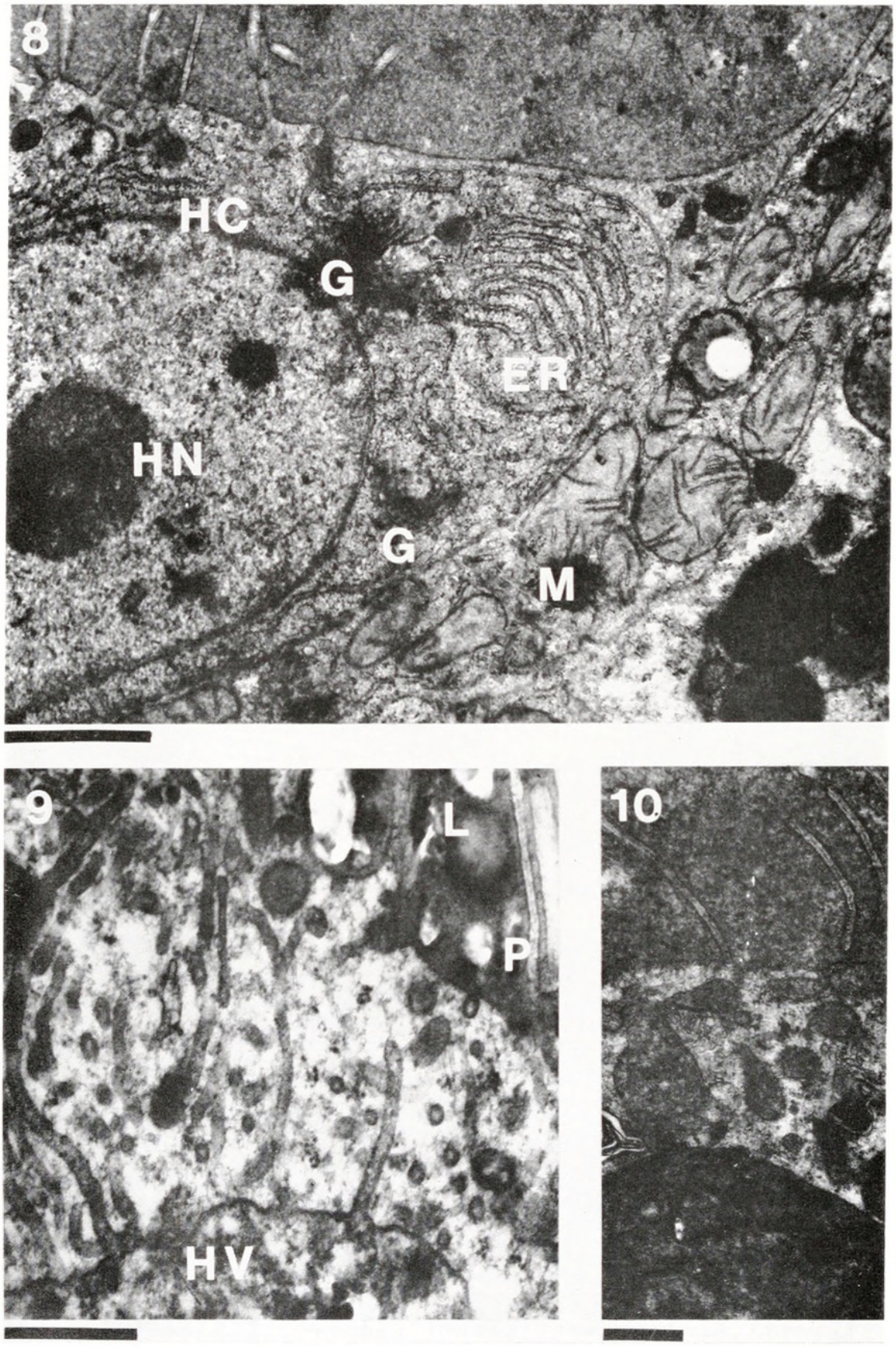


FIGURE 8. *P. xenopi*; lateral region of a hematin cell (HC) overlapped by the thin sheet-like connecting syncytium without cecal processes. Lateral to the hematin cell nucleus (HN) is a well-developed endoplasmic reticulum (ER) with two golgi bodies (G). Large mitochondria (M) are aggregated beneath the basement membrane; scale bar, 1 μ.

FIGURE 9. *P. xenopi*; distal cytoplasm of hematin cell showing intracellular tubules between hematin vacuole (HV) and free distal membrane, the latter bears cytoplasmic processes (P) extending into the gut lumen (L); scale bar, 0.5 μ.

In most pigment-laden cells the hematin vacuole is situated in the distal region and the nucleus and other organelles are confined basally. Discharge of the vacuole may be achieved simply by its extrusion through the free plasma membrane without affecting the rest of the cell. On the other hand, portions of cells distended with hematin which protrude into the gut lumen as in Fig. 12 may become detached more or less accidently due to body movements. Such detachment during the violent contractions accompanying fixation may account for previous observations (Jennings, 1959; Halton and Jennings, 1965) that some hematin-laden cells may break down or be shed intact from the cecal wall. Certain other products of digestion, including isolated lipid-like droplets and membrane-bound myelin figures may be extruded separately through the free plasma membrane of the hematin cell.

Development

The arrangement of alternate hematin and connecting cells observed in adult parasites was found to be established in the youngest larvae of *P. xenopi* examined, those fixed two weeks after experimental infection of the host. The growth and development of the parasite is accompanied by certain changes in the morphology of the gastrodermal components. In juvenile parasites, fixed two months after infection, the hematin cells are scattered over the cecal wall, they usually contain a single hematin vacuole and conform to the relatively constant pattern described above (Fig. 2). In an adult *P. xenopi*, fixed over four months after infection, the hematin cells are numerous and closely packed, each occupies a relatively larger area of the cecal wall and contains several spheroidal hematin vacuoles. There is also variation in the appearance of the connecting system during the course of development. In juvenile parasites, the syncytium is thin and sheet-like, with extensions which partially overlap the well-separated hematin cells (Fig. 14A). The latter may sometimes be more or less circular in section, attached to the basal tissues by a relatively narrow neck. In these circumstances the connecting system encloses the lower half of the cell, supporting it in a cup-like sheath (Figs. 3 and 14B). In older parasites where the more numerous hematin cells are usually closely-packed and columnar the connecting system forms narrow strips sandwiched between adjacent cells. In section the syncytium is relatively deep, extending from the basement membrane to the cecal border of the hematin cells (Fig. 14C).

In view of the gradual increase in the number of hematin cells during the course of the parasite's development, sections have been examined for the occurrence of hematin cell primordia in or below the cecal epithelium. Discrete cells have been observed beneath the syncytium; in section these are largely occupied by the nucleus, surrounded by a thin layer of dense cytoplasm containing ribosomes and mitochondria. These may represent initials which give rise to emergent hematin cells but the process of development has not been recorded.

Discussion

There is a close similarity in the cellular arrangement of the gastrodermis of *Protopolystoma xenopi*, revealed by the present study, and that of *Diclidophora*

Figure 10. *P. xenopi*; distal cytoplasm of hematin cell showing pinocytotic entry of material from the gut lemen to the hematin vacuole; scale bar, 0.5 μ.

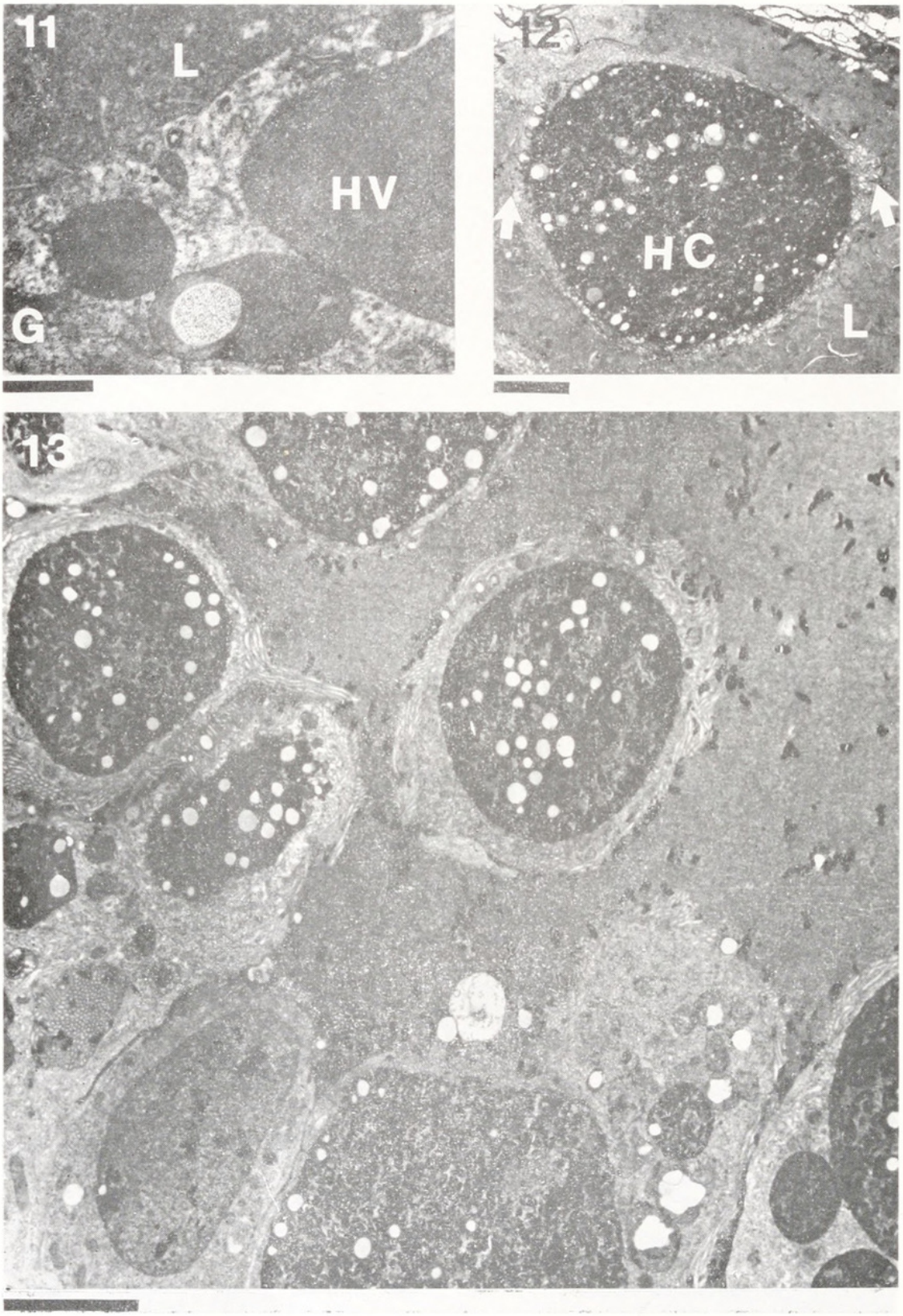


FIGURE 11. *P. xenopi*; hematin cell showing passage of food material from the gut lumen (L) to the digestive vacuole (HV). Breakdown is already initiated in one of the incoming vesicles; note the adjacent golgi complex (G); scale bar, 1 μ.

FIGURE 12. *P. xenopi*; part of hematin-laden cell (HC) protruding into gut lumen (L) and attached to the cecal wall by a narrow neck. The connecting syncytium extends around the lower half of the cell (maximum overlap arrowed); scale bar, 4 μ.

FIGURE 13. *P. xenopi*; part of cecal epithelium showing apparent detachment of hematin-laden vacuole, scattered fragments of hematin occur in the gut lemen. The disposition of the

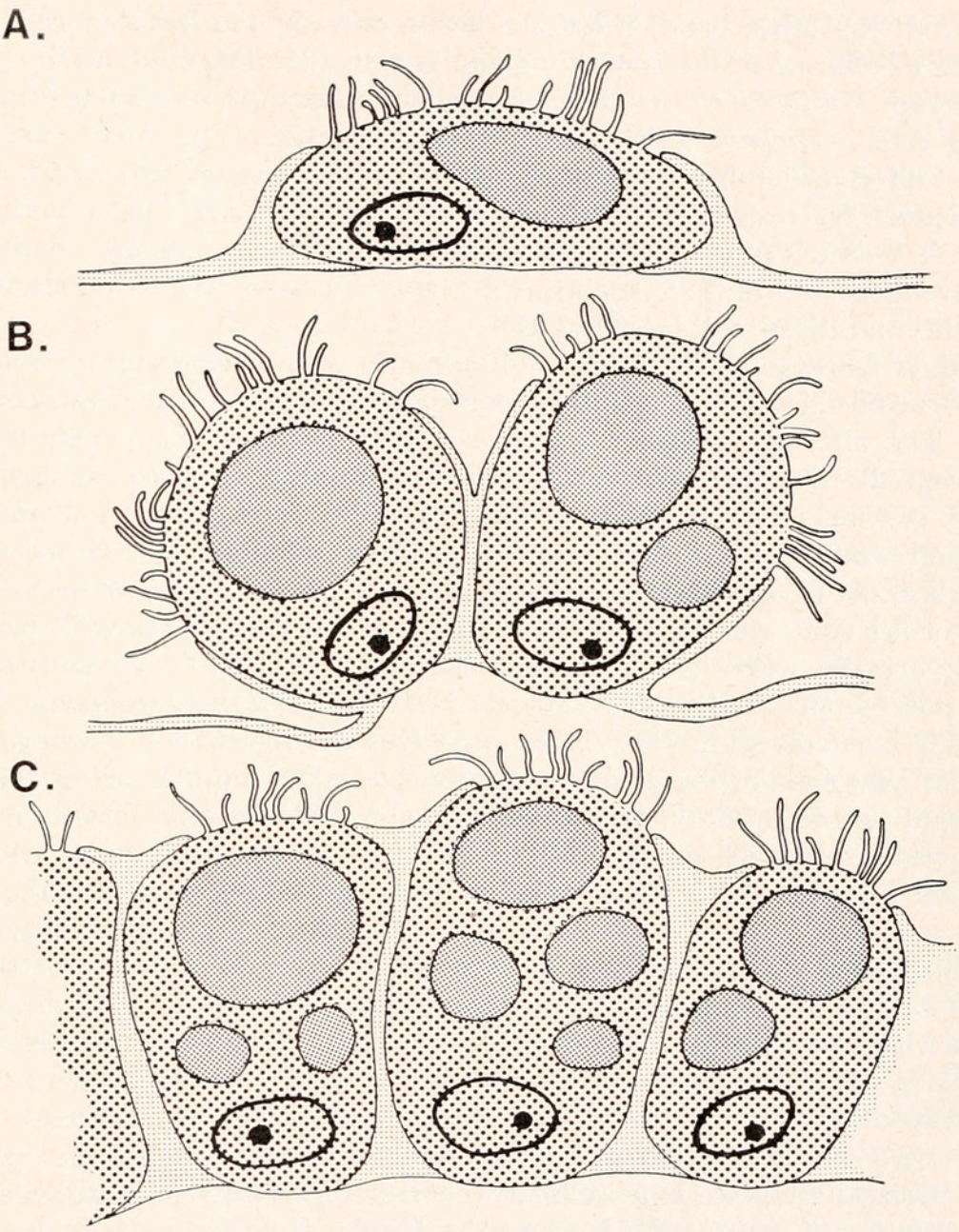


FIGURE 14. *P. xenopi*; variation in the arrangement of the components of the cecal epithelium. Hematin cells with hematin vacuoles and basal nuclei, densely stippled; connecting syncytium, lightly stippled. For explanation see text.

merlangi reported by Halton *et al.* (1968). In both monogeneans the cecal epithelium is composed of two distinct cell types; hematin cells alternate with a previously unrecognized connecting cell system which covers all areas of the cecal wall between adajacent hematin cells. No inter-cellular junctions have been observed within the flat, sheet-like connecting system, and the view of Halton *et al.* (1968) that this exists as a syncytium is supported.

There are certain differences in the ultrastructure of the gastrodermal components in the two species. Halton *et al.* (1968) recorded that in *D. merlangi* protoplasmic projections occur on the free surface of both types of cecal cell. In

epithelium suggests, however, that this plane of sectioning does not represent the actual process of detachment; scale bar, 4 μ.

P. xenopi, on the other hand, these are borne only by the hematin cells and the free plasma membrane of the connecting cell is smooth. The cytoplasmic processes of *D. merlangi* are in the form of lamella which differ in size on the hematin and connecting cells. However, the hematin cell processes of *P. xenopi* are circular in section and considerably longer than the equivalent structures of *D. merlangi* (2.0–4.0 μ and 0.6 μ respectively). The appearance of the cells loaded with hematin differs in *D. merlangi* and *P. xenopi*. In the former, numerous small pigment vacuoles are dispersed in the cytoplasm; in the latter, a few relatively large spheres occur in the mid-distal region of the cell.

A gradual increase in the number of hematin cells occurs during the growth of *P. xenopi* and this may, perhaps, be correlated with the increasing needs of the parasite. The alternate arrangement of the two epithelial components could be derived from the development of hematin cells from initials arising beneath the connecting system. The eruption of these through the syncytium to expose the apical region would result in the observed cellular relationship. However whilst possible primordia have been recorded, the process of eruption has not been observed.

Much of the course of digestion in *Protopolystoma xenopi* revealed by electron microscopy accords with that determined by Jennings (1959) from histochemical and light microscope studies of the closely related *Polystoma integerrimum*. The hematin cell is involved in the visible processes of digestion. The products of extracellular hemolysis of ingested erythrocytes are taken into the cell by pinocytosis and digestion proceeds within large membrane-bound vacuoles. There are apparently no previous records of intracellular microtubules communicating between the distal border and the digestive vacuole. These commonly occur in the actively absorbing cells of *P. xenopi* and it seems probable that they assist in the entry of hemoglobin. Their occurrence may be linked with the observation that the initial absorption of the blood meal is very rapid. The distribution of the connecting syncytium which partially overlaps the distal margins of the hematin cells involves a reduction in the absorptive surface area; it is possible that the system of microtubules compensates for this limitation. The cecal cytoplasmic processes may be concerned with the absorption of low molecular weight compounds. However, they may perhaps facilitate extracellular "contact digestion" as postulated for the similar structures of other animal groups by Ugolev (1960) and Jennings (1968, 1969). This purely catalytic function might explain their occurrence on only one cell type, the digestive cell, in *P. xenopi* but on both cell types in *D. merlangi*. The much greater length of the processes in the former species might compensate for their restricted distribution.

The degradation of hemoglobin leads to the accumulation of an insoluble pigment, probably largely hematin, within the vacuoles and these are shed intact from the cell, apparently by simple extrusion. As suggested by Jennings (1959, 1968), the eventual breakdown of the spent hematin vacuoles could result in the release of intracellular digestive enzymes and these may initiate partial extracellular breakdown of the next blood meal.

Ultrastructural studies indicate the need to revise earlier interpretations of both the form and function of the polyopisthocotylean gastrodermis. The formation of insoluble residues of hemoglobin breakdown within the digestive cells creates problems unique to this parasite group. Previous light microscope studies suggested

that elimination is achieved by the partial breakdown or shedding of the hematin-laden cell. This interpretation, involving the cyclical loss and replacement of the digestive cells, gained support from the apparently discontinuous nature of the gastrodermis. However, electron microscope observations show that a second cell system is interposed between all adjacent hematin cells, and the gastrodermis remains an organized and continuous structure throughout life. Hematin elimination is achieved by the extrusion of intact vacuoles; there is no evidence from ultrastructural studies for the breakdown of the entire cell, and previous light microscope observations may have been influenced by the effects of fixation. The view that the digestive process involves considerable wastage of cellular materials and represents an incomplete adaptation to the blood-feeding habit is considered to be no longer tenable.

The function of the connecting system is obscure. The syncytium apparently plays no obvious role in the digestive processes. There is no evidence of pinocytotic uptake nor of secretory activity; the relatively scattered organelles and the infrequent occurrence of nuclei suggest that an active physiological role is unlikely. Other characteristics indicate the possibility of a physical role. The cecal epithelium is regularly subjected to vigorous deformation by the contractions of the body muscles. The hematin cells protrude from this epithelium and contain relatively dense structures, the hematin vacuoles, in their distal regions. In surface view, the connecting syncytium forms a flat sheet of cytoplasm overlying the whole of the cecal wall and perforated by a system of pores—the tips of the hematin cells. This organization suggests that the syncytium may perform a skeletal function, providing both support and protection for the hematin-laden digestive cells and for the relatively delicate underlying tissues.

The ultrastructural differences between *D. merlangi* and *P. xenopi* concerning the form and occurrence of the cecal cytoplasmic processes may reflect the systematic separation of the two monogeneans. The organization of the two cell type gastrodermis, on the other hand, may be a common feature of all Polyopisthocotylea. Jennings (1968) has noted the constant association of the blood-feeding habit, the intracellular production of hematin and the apparently discontinuous gastrodermis in all the polyopisthocotyleans so far examined. Alternative digestive pathways have been determined in other blood-feeding flatworms. In certain digenean species hemoglobin degradation involves the splitting of the heme group extracellularly and hematin production is confined to the gut lumen, whilst in others digestion results in the breakdown of hemoglobin to completely soluble compounds (Halton, 1967). In these forms the problems associated with the accumulation and elimination of intracellular hematin do not arise. Whilst the digestive pathways of the Polyopisthocotylea probably do not involve the cyclical degeneration and wastage of cellular materials suggested by previous writers, other important functional considerations emerge. The gut of acoelomate animals is highly susceptible to the stresses of body movement and the effects are potentially most harmful where digestive cells contain protruding masses of dense iron-containing pigment. The support and protection of these tissues may have been an important factor in the early development of the blood-feeding habit amongst monogeneans. In accordance with views of monogenean evolution expressed recently by Llewellyn (1963) and Halton and Jennings (1965), the Monopisthocotylea probably occupy the ancestral

habitat and retain the primitive feeding methods. The Polyopisthocotylea, on the other hand, have apparently invaded secondary sites of infection and have become blood-feeders. The present studies throw further light on the form and function of the gastrodermis and suggest that the evolution of the skeletal connecting syncytium was a necessary concomitant of the specific digestive pathways developed by the Polyopisthocotylea.

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Summary

1. Ultrastructural studies reveal that the cecal epithelium of the monogenean *Protopolystoma xenopi* is composed of two cell types. Hematin-containing cells are discontinuously arranged and alternate with a thin cytoplasmic layer, the connecting syncytium.

2. The connecting syncytium forms a flat sheet overlying the cecal wall, it surrounds the individual hematin cells and is perforated only by their distal tips. The ultrastructure of the syncytium suggests that an active physiological role is unlikely.

3. The hematin cells are involved in the visible processes of digestion. After initial extracellular hemolysis the blood meal is absorbed by pinocytosis; intracellular breakdown continues within large membrane-bound vacuoles and leads to the accumulation of hematin; this insoluble product is eventually eliminated by the discharge of intact vacuoles, apparently by simple extrusion.

4. There is no evidence for the detachment or partial disintegration of the hematin-laden cells, and the cecal epithelium remains at all times a continuous structure.

5. Since the hematin cells are partially overlapped by the connecting syncytium, active absorption is limited to a relatively small area of the hematin cell surface. A system of microtubules communicating between the free cell border and the hematin vacuole may participate in hemoglobin uptake and compensate for the reduced absorptive area. The exposed hematin cell border bears numerous cytoplasmic processes and these may facilitate contact digestion.

6. The structural and physiological organization of the polyopisthocotylean gastrodermis is characterised by the formation of dense iron-containing pigment within the relatively vulnerable digestive cells. It is considered that the connecting syncytium performs a skeletal role, giving support and protection to the hematin cells and the underlying tissues.

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