Zeitschrift: Acta Tropica
Herausgeber: Schweizerisches Tropeninstitut (Basel)
Band: 32 (1975)
Heft: 2

Artikel: The ultrastructure of the midgut of hematophagous insects
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DOI: https://doi.org/10.5169/seals-312077

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The Ultrastructure of the Midgut of Hematophagous Insects

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As with other organ systems, the insect gut shows great diversity from one group of insects to another. But there are also basic similarities. In all insects, in fact in all arthropods, there is a gross differentiation into foregut, midgut and hindgut based on the embryological origin of these three regions (see House 1974, or any textbook of entomology). The fore- and hindguts are ectodermal in origin and are lined with a cuticle which is continuous with that on the outside of the animal. The cuticle of the foregut is relatively impermeable; that of the hindgut is relatively permeable, at least in certain areas. The midgut, whose embryological origin seems somewhat diverse, has no cuticle; however, the midgut epithelium is usually not directly exposed to the food bolus because there is usually present an acellular secreted membrane appropriately called a peritrophic membrane. The delineation between the three parts of the gut is abrupt – it occurs at one particular cell boundary (see Fig. 5 in Richards & Richards 1971). For digestion and pathogen transmission we are mostly concerned with the midgut, and the remainder of this paper will deal exclusively with the midgut.

Staying within the context of this symposium, there are three aspects to be considered: the production and secretion of enzymes, the absorption of digestive products and of substances not needing digestion, and the survival of pathogens with or without penetration of the midgut epithelium. The last of these involves consideration of the gut lumen as a specialized microhabitat. I will consider only the structural aspects leaving chemical, physiological control, and ecological aspects to the later speakers.

An important aspect is barriers, which in biological systems most commonly means membranes. There are usually five membranes between food and the hemocoel of the insect. These are (Fig. 1): 1. the peritrophic membrane, 2. the outer plasma membrane of the midgut epithelium, 3. the inner plasma membrane of this epithelium, 4. the basement membrane (= basal lamina), and 5. what we have called the 'organ investment layer'. It is conceivable that all of these are chemical barriers, but they all have supportive functions too, and it is commonly suggested that the peritrophic membrane protects the epithelial cells from abrasion by food particles. Rigorous proofs remain for the future.

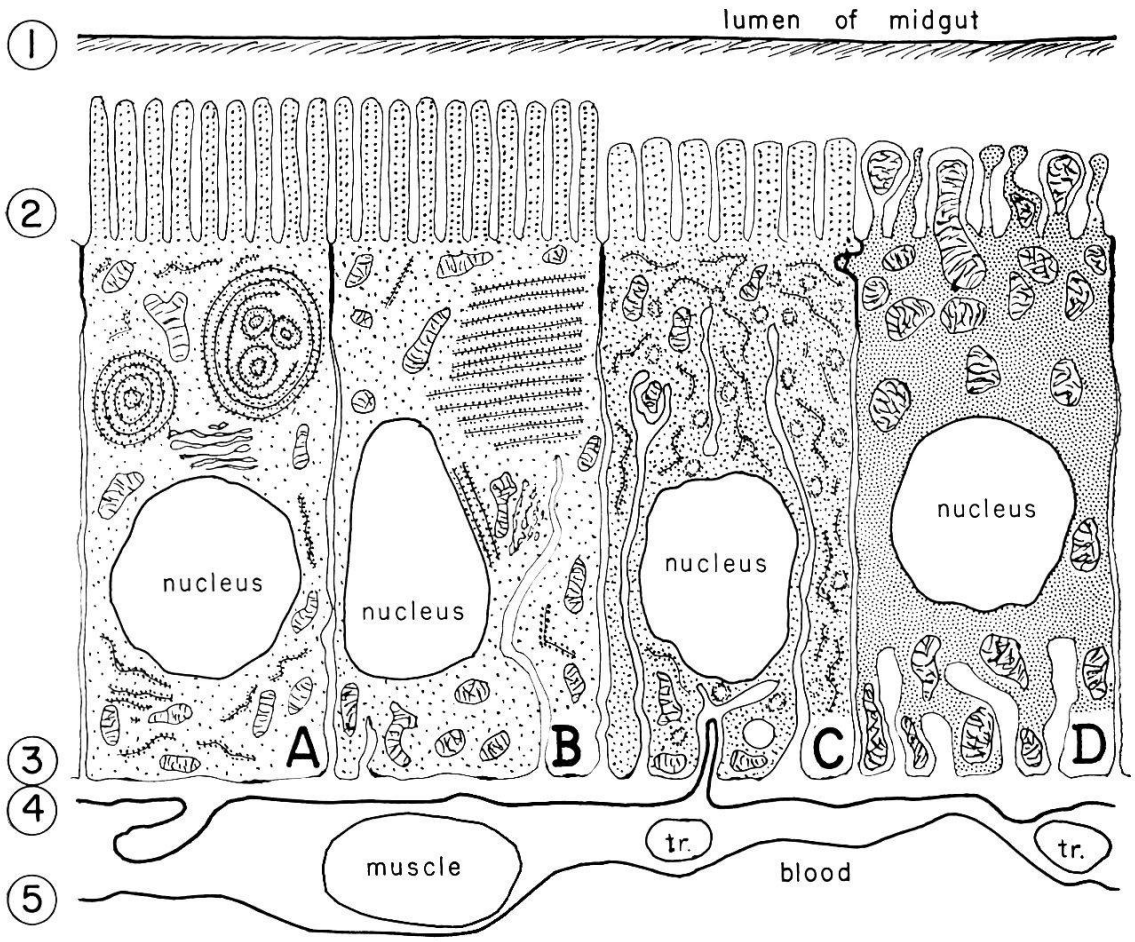

Fig. 1. Diagrammatic sketch of some cell types found in insect midguts with identification (1–5) of the membranes that occur between food and blood. Cell *A* based on unfed adult female mosquito (see BERTRAM & BIRD); cell *B* based on adult flea; cell *C* based on larval mosquito in full secretory activity; and cell *D* based on specialized (ion transport?) cell in gastric caecum of mosquito larva. Membranes: 1 = peritrophic membrane, 2–3 = outer and inner plasma membranes of midgut cells, 4 = basement membrane (= basal lamina), and 5 = organ investment layer.

1. The peritrophic membrane

It is commonly said that there are two kinds of peritrophic membranes (PM). The difference is whether the PM is secreted by all the midgut cells or only by a ring of cells at the anterior end of the midgut; this difference is probably trivial. Of at least potentially greater interest is whether the PM is secreted continuously (as in larval Diptera and some adults) or only as a result of the presence of food in the gut lumen (as in the adult female mosquito). In the latter case it is at least conceivable that pathogens could go to the gut cells *before* production of a PM (and hence not have to penetrate such). In some insects (including fleas) a PM appears to be absent.

In thickness, the PM, in different species, ranges from a fraction of 1 μm to some 10–12 μm. In thin sections viewed in an electron micro-

scope it may appear as a granular simple sheet (adult female mosquito). Or it may be more complicated with such a simple granular-appearing sheet being underlain by several microfibrous layers connected by very fine microfibers (Fig. 2). The microfibers may be arranged in random, hexagonal or orthogonal array as elaborately and comprehensively surveyed by PETERS (1969). The microfibers contain chitin but this polysaccharide may be in a different crystallographic form from that found in the cuticle. The number of fibrous layers is somewhat variable. In general there are fewer fibrous layers in younger instars than in older ones. In 4th instar larvae of *Aedes aegypti* there are usually 3–5 fibrous layers, and a survey of larvae of about a dozen genera of mosquitoes shows this to be the usual range. However, in some specimens of some species *(Culex restuans* and *Anopheles albimanus)* we have found areas where there were 12, 15 or even 20 superimposed fibrous layers (Fig. 3). The most complicated PM I have seen occurs in larvae of *Simulium* where there are microfibrous layers (orthogonal array) of three different magnitudes (Fig. 4). The center-to-center spacings approximate 15, 35 and 120 nm; this is a ratio of 1:2:8 (only the largest spacing comes close to approximating the center-to-center spacing of microvilli).

The development of microfibers involves extracellular aggregation of molecules into microfibers. For some cases, certain authors (e.g. PETERS 1969) have suggested that the gross orientation of the microfibers is templated on a corresponding surface of microvillar tips. In other cases, the orientation is demonstrable after separation from the midgut cells (RICHARDS & RICHARDS 1971) or, as in the case of *Simulium* larvae, of an entirely different magnitude.

2. *Cellular debris*

One commonly finds cellular debris trapped between the PM and the midgut epithelium (Fig. 8). This is to be expected in those insects where there is a regular degeneration and replacement of the gut cells, but it is also not uncommonly found in cases such as mosquito larvae where there is no cell replacement and presumably no degeneration of whole cells. One commonly finds in midgut cells bodies that appear to be degenerating organelles. These have been termed cytolysomes. Presumably these can be discharged to the gut lumen without disintegration of the entire cell.

3. *The outer plasma membrane and microvilli*

The outer plasma membrane appears uniform and with the thickness typical of unit membranes, i.e. 8–10 nm. Usually the surface area of this

membrane is increased by regular projections called microvilli (Figs. 5 to 6). The microvilli (MV) are tightly packed and commonly 4–8 times as long as broad. As such they increase this surface area 20–50 times. Sometimes the MV are up to 25 times as long as broad; the surface area then increasing about 100 times. Occasionally MV are even longer with correspondingly greater increase in surface area. But on some midgut cells (or at some times such as during ecdysis) MV may be rudimentary or even absent (Fig. 7). MV on a particular cell, and most commonly over many adjacent cells, are extremely regular and have internal fibers which extend as 'roots' into the body of the cells (NOIROT & NOIROT-TIMOTHÉE 1972).

The MV are near the limit of resolution of a light microscope and give rise to the appearance that has been called a 'striated border'.

4. Cell types

The midgut may be grossly differentiated into anterior midgut, posterior midgut, etc. Correlated with this the cells may appear to be different, or they may appear the same, or different cell types may be interspersed either randomly or in some regular manner. In the adult female mosquito BERTRAM & BIRD (1961) reported that the cells are all similar. In larvae of the same species adjacent cells may vary considerably in density of the cytoplasm and concentration of ribosomes (Figs. 5, 13). In blowfly larvae there are several distinct types (cuprophilic and lipophilic) for which there is correlated functional information based on histochemistry (WATERHOUSE & WRIGHT 1960).

In certain cases one finds cells with projections that do not have the fine structure of MV (though some authors have termed these MV). The 'goblet cells' of moth larvae are such (ANDERSON & HARVEY 1966). Sim-

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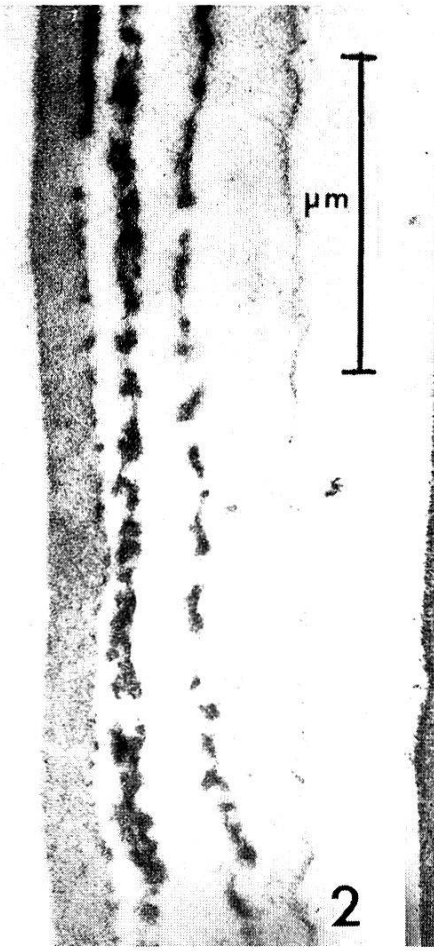
Fig. 2. Peritrophic membrane of a 4th instar mosquito larva *(Aedes aegypti)*. A seemingly granular layer towards the food (left of picture) is underlain by several microfibrous layers which are held together by very fine randomly arranged microfibers not visible in this picture.

Fig. 3. Peritrophic membrane of a different 4th instar mosquito larva *(Anopheles albimanus)* with 15 fibrous layers in the bottom part of the picture but 20–21 in the top part at this area. Gut lumen on left of picture. Other specimens of this species showed only the 2–4 fibrous layers usual in mosquito larvae.

Fig. 4. Peritrophic membrane of a black fly larva *(Simulium,* subg. *Simulium,* probably *S. venustum)*. Gut lumen at top of picture. Although this oblique section is heavily contaminated with stain it nonetheless shows three superimposed sets of orthogonally arranged microfibers with center-to-center spacings of about 15, 35 and 120 nm respectively.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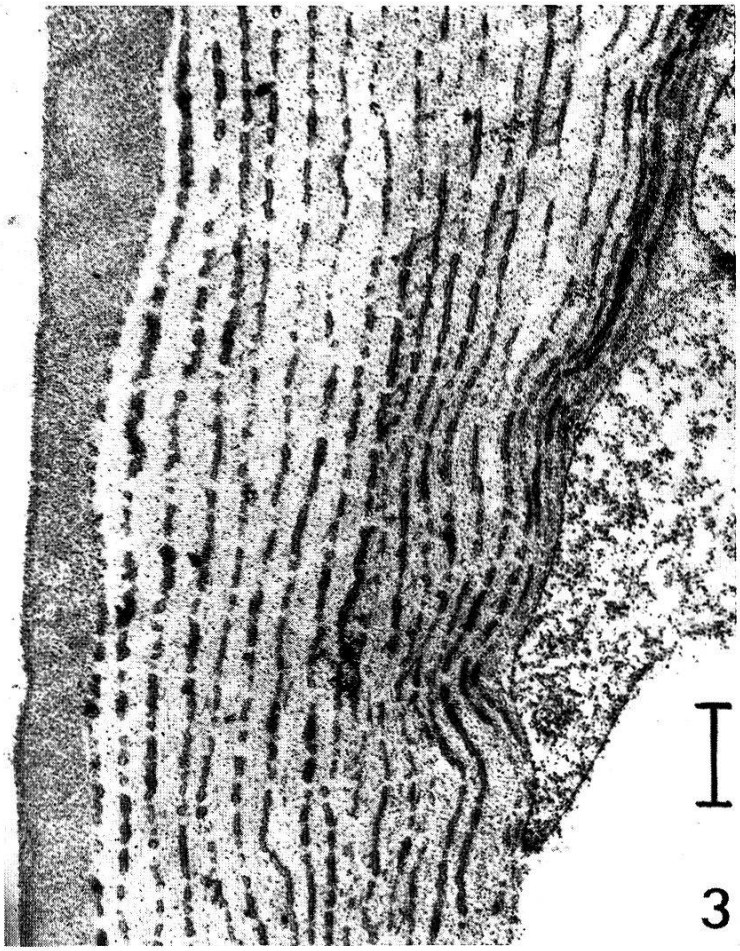
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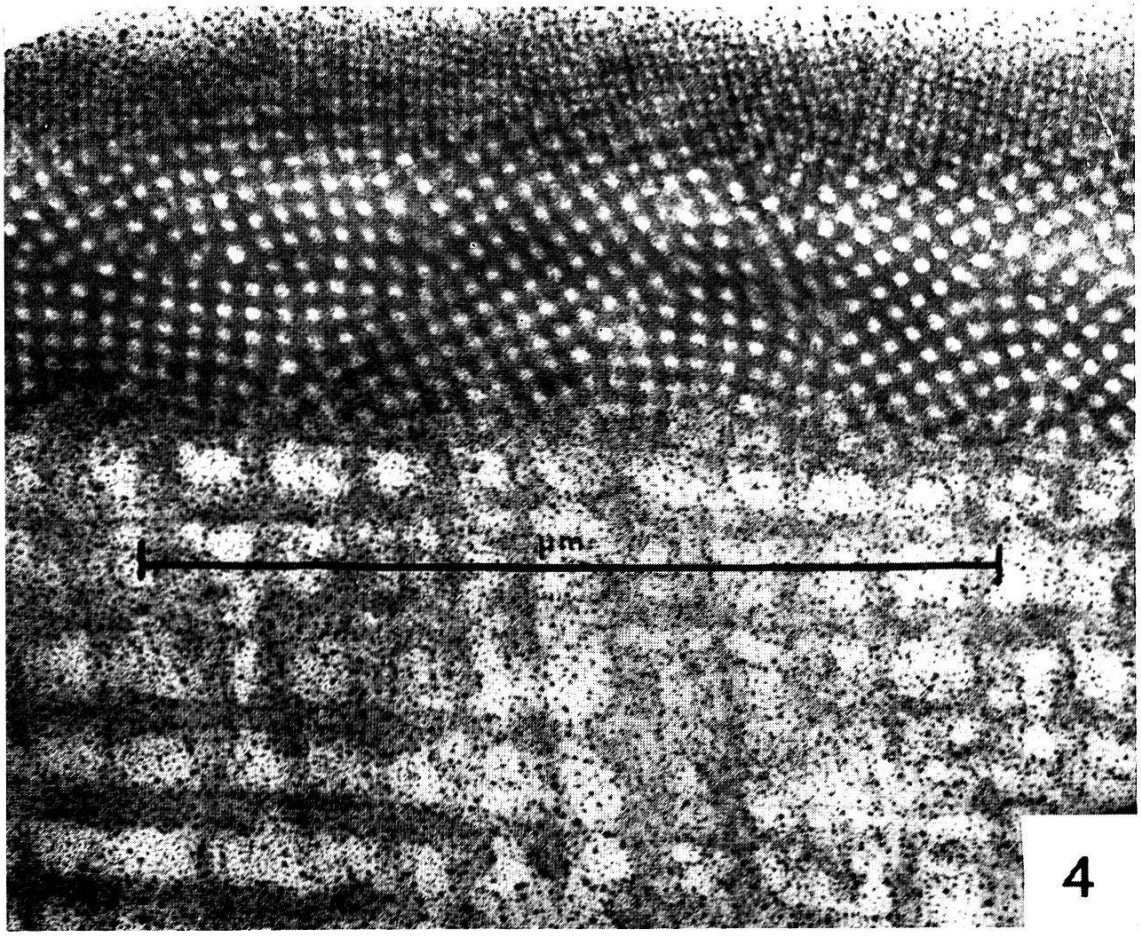
μm
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ilar cells are found among the cells in the gastric caeca of mosquito larvae. Such occasional cells have projections that are less regular than MV, do not have internal fibers extending as 'roots' into the cell, and contain a large mitochondrion or free ribosomes or both (Fig. 13). In *Cecropia* larvae, ANDERSON and HARVEY suggest that these odd cells are specialized as ion pumps (K^+). In mosquito larvae they are found only in the caeca, and it is only the caeca that are reported by RAMSAY (1950) to perform appreciable osmotic work; it will be interesting to find out if these cells function as metabolic pumps.

5. *Cell organelles*

Cytoplasmic organelles are the usual ones but there is a great development of granular or rough endoplasmic reticulum (ER). Ribosomes are generally thought to be responsible for protein synthesis. And it has been suggested that ribosomes synthesizing digestive enzymes must be attached to ER to keep the enzymes segregated to prevent digestion of the cells producing the enzymes. Whether this suggestion is correct or not, midgut cells have much rough ER.

In inactive gut cells (unfed insects) the ribosomes may be localized on balls of ER which appear in sections as tight whorls (Fig. 1A) or in stacks of sheets (Figs. 1B, 9). When the insect is fed, the ER disperses through the cytoplasm (Figs. 1C, 5), and recently quantitative or morphometric analyses have been begun on changes occurring as inactive midgut cells become active and then return to an inactive state (HECKER et al. 1974). Ribosomes may also be found on ER vesicles in active cells (Fig. 6). In the odd cells treated above, that have projections that are not typical MV, the ribosomes are free and pack the cytoplasm (Fig. 13).

Mitochondria are numerous in gut cells (Figs. 8, 9, 12, 13) but seem to show no special features in either structure or distribution.

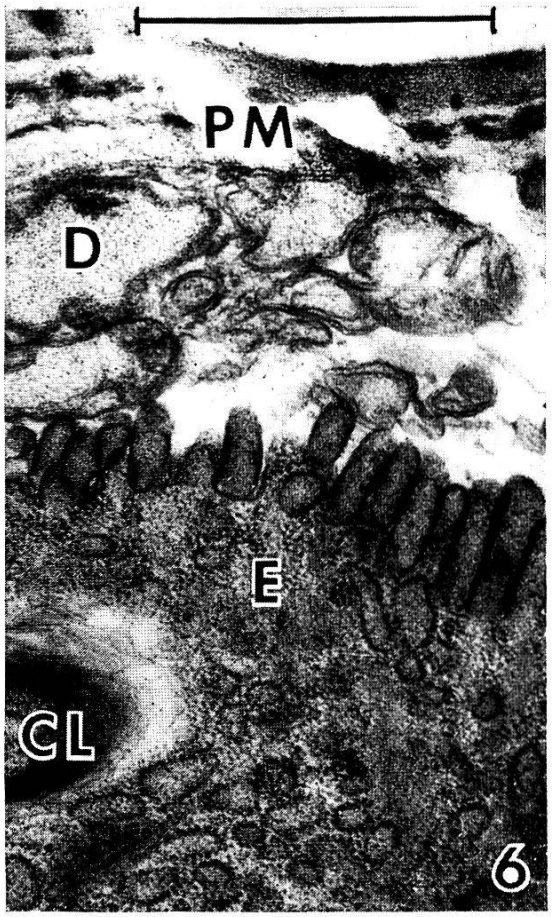
Fig. 5. Parts of two adjacent active cells in midgut of a 4th instar mosquito larva *(Aedes aegypti).*

Fig. 6. Cell debris *(D)* trapped between midgut epithelium *(E)* and peritrophic membrane *(PM)* of a 4th instar mosquito larva *(Aedes aegypti).* Part of a cytolysome (CL) is also present.

Fig. 7. Low power view of midgut epithelium of a 1st instar mosquito larva *(Aedes aegypti)* at a place where microvilli were rudimentary (perhaps due to approaching moult). Gut lumen and microvilli on left, hemocoel on right.

Fig. 8. Higher magnification picture within preceding (rotated 90°).

μm
5


PM
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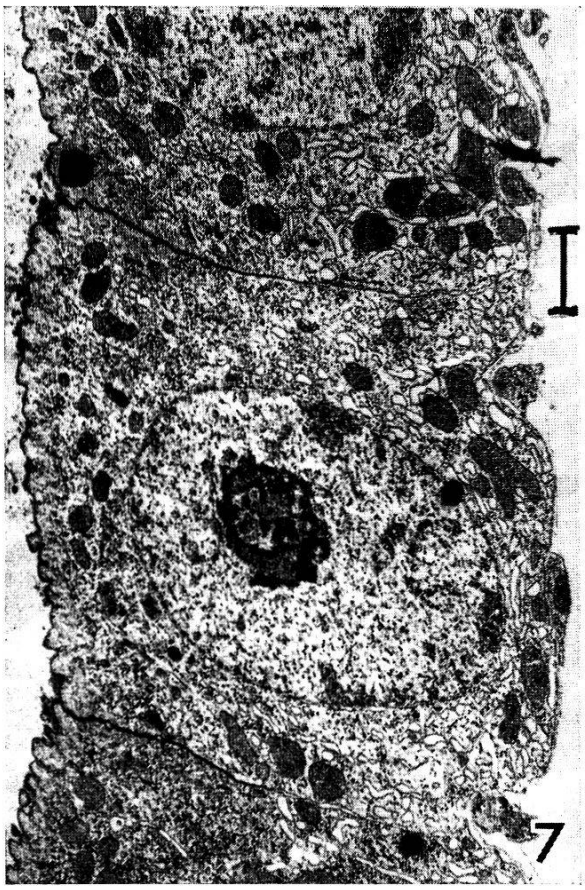
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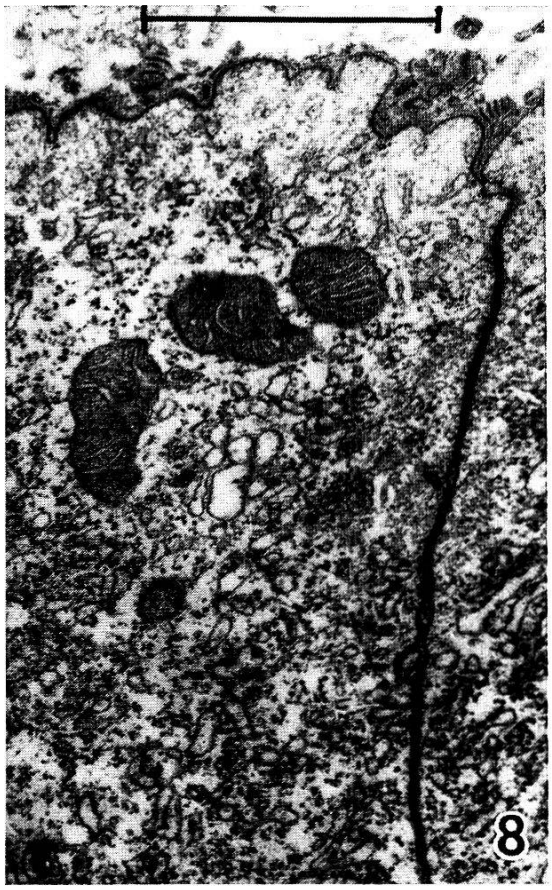
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For mammalian cells that secrete digestive enzymes, PALADE (1961) and others have developed a picture of enzyme liberation by ribosomes, its accumulation in vesicles associated with the Golgi apparatus, and finally its ejection as secretory vacuoles. This interpretation is based particularly on acinar cells of the pancreas. Insect midgut cells do not show this secretion sequence. Insect midgut cells do have a high concentration of ribosomes on ER but the Golgi apparatus, although usually present, seems poorly developed. Typically, the Golgi apparatus of midgut cells of insects is unimpressive; in some cases it has been reported to be absent (WATERHOUSE & WRIGHT 1960). And neither I nor others (BERTRAM & BIRD 1961, NOIROT & NOIROT-TIMOTHÉE 1972, etc.) have seen indication of vacuoles discharging into the lumen of the insect gut. This statement is true both for secretion of precursors for formation of the PM and for secretion of digestive enzymes.

Intercellular junctions between midgut cells are the usual gap junctions, septate junctions and desmosomes (REINHARDT & HECKER 1973). In the midgut of a moth tight junctions have also been recorded (SMITH 1968).

6. *The inner plasma membrane and basal labyrinth*

The plasma membrane at the inner or hemocoel side of the midgut epithelium commonly has its area increased by indentations. These indentations are mostly infoldings of the plasma membrane; they do not have either the columnar structure or the regularity of MV. They range from a few which may even be limited to intercellular boundaries to so many that the area of the inner plasma membrane is tremendously increased (Figs. 10, 12). There is considerable variation, sometimes even within a short distance in a particular midgut epithelium. The variation is not only in the number of infoldings but also in the depth to which they penetrate, their diameter, and the amount of branching.

The space formed by these infoldings and indentations is really intercellular space. It is bounded on one side by the midgut cells and on the other side by the basement membrane. It is commonly termed the basal labyrinth.

The plasma membrane at the inner side of the midgut epithelium resembles that at the outer side in having the structure of a unit membrane, but it differs in having local differentiation giving a visible

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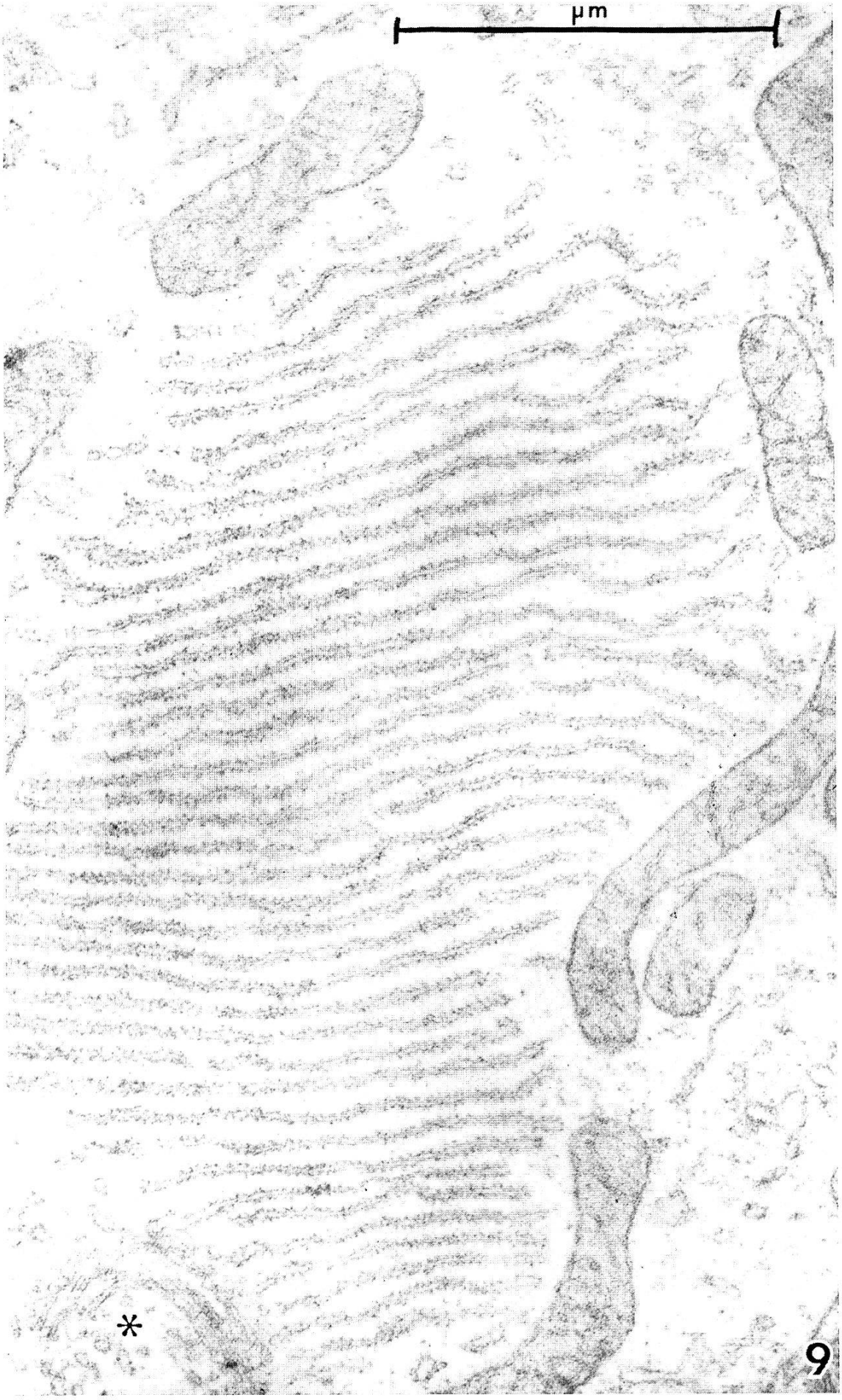
Fig. 9. Portion of a midgut cell in an adult of a flea (*Ctenophthalmus* sp.) showing stacked rough endoplasmic reticulum, mitochondria and the indistinct Golgi complex (asterisk).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9

mosaicism. There are thickenings, sometimes called 'hemidesmosomes' (Fig. 11); in some places there seems to be attachment into the basement membrane; and there may be a different appearance to the membrane at the base of the cells in contrast to that lining the infoldings (Fig. 12). Mammalian workers are now finding functional significance to such differentiation; presumably such will be found for insect epithelia too (see BERRIDGE & OSCHMAN 1972).

7. *Basal membranes*

Between the inner plasma membrane and the hemolymph there is always at least one membrane; commonly there are two. The one of these that is always present is the basement membrane that is found at the base of all epithelia and around all organs. It is commonly termed the 'basal lamina' when around an internal organ. The basement membrane is much thicker than a unit membrane, commonly 50–100 nm thick. It may show no internal differentiation in thin sections viewed with an electron microscope, or contain collagen microfibrils, or show an elaborate and regular internal differentiation (RICHARDS & RICHARDS 1968, REINHARDT & HECKER 1973).

The basement membrane is always closely associated with that part of the inner plasma membrane that is at the base of the epithelial layer, although at occasional spots it may extend a short distance into an infolding of the basal labyrinth or form a small outpocketing (Fig. 1 and RICHARDS & RICHARDS 1968). In some electron microscope pictures there is a suggestion that there is some ultramicrofibrous connection

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Fig. 10. Low power view of midgut epithelium of a 4th instar mosquito larva *(Anopheles freeborni)* in an area where the basal labyrinth is maximally developed. The very heavy staining of this section obscures cellular details but gives the infoldings and indentations maximal contrast. Microvilli and a small piece of peritrophic membrane in upper left corner.

Fig. 11. Inner plasma membrane and closely applied basement membrane (basal lamina) of two midgut cells of an adult flea (*Ctenophthalmus* sp.). Shows mosaicism of membrane with hemidesmosomes and intercellular space (asterisk).

Fig. 12. Higher magnification of a small portion of a midgut cell of a 4th instar mosquito larva *(Aedes aegypti)* showing the basal labyrinth and its relation to the basement membrane (bm).

Fig. 13. Section showing parts of two adjacent cells in a gastric caecum of a first instar mosquito larva *(Aedes aegypti)*. The cell on the right has dense cytoplasm and typical long microvilli. The cell on the left has long projections that do not have the structure of microvilli and that contain large mitochondria or free ribosomes or both.

10

*
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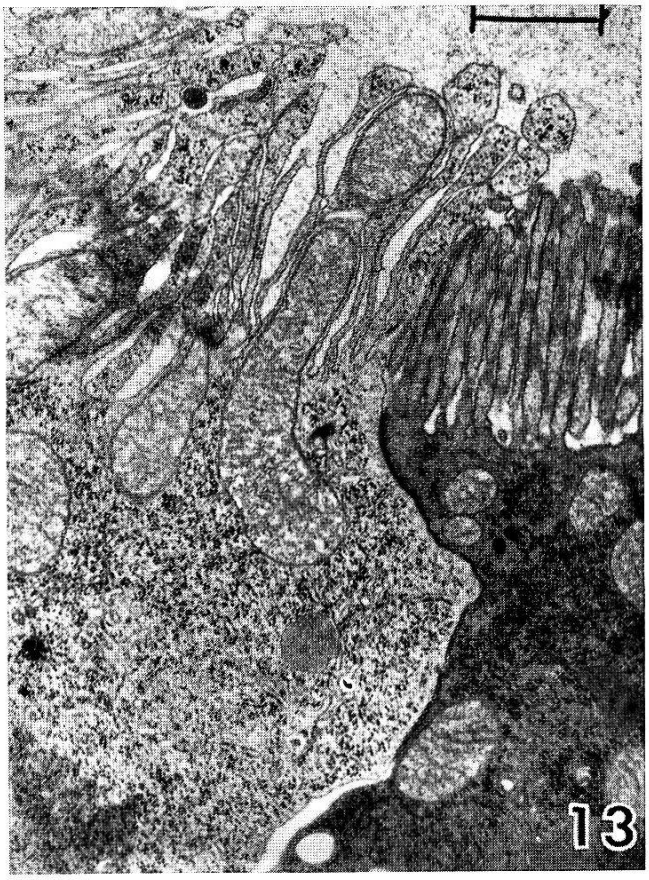
bm
12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between the inner plasma membrane and the basement membrane.

In at least some insects there is a distinct fifth membrane of uncertain origin which we have referred to as the 'organ investment layer' (RICHARDS & RICHARDS 1968). It resembles a simple basement membrane and appears as a single 'granular' layer to which collagenous (?) microfibers attach. Perhaps this layer is not a chemical barrier but only a supporting envelope helping hold muscles and tracheae to the gut. To judge from pictures in the literature it is not universally present (e.g. BERTRAM and BIRD show no such for adult mosquitoes although we find it in larval mosquitoes).

In considering penetration of the barriers of the gut wall, one commonly considers only digestive enzymes getting into the gut lumen and digestion products being absorbed and passed on to the hemolymph. But some one or more of the basal membranes (numbers 3–5 of Fig. 1) is a barrier to certain compounds in the hemolymph [perhaps analogous to the well-known blood-brain barrier of mammals]. For instance, some very potent drugs (e.g. ouabain, concanavalin, oligomycin or actinomycin D) can be injected into the hemolymph of at least certain insects with little or no apparent effect. Considering the known action of these drugs, and their effects in tissue culture, we have to conclude that they simply do not get from the hemolymph into the tissue cells. Despite statements in some elementary textbooks of entomology, the hemolymph does not bathe individual cells; it is separated by at least a basement membrane. And the basement membrane or one of the other membranes internal to the midgut epithelium is a penetration barrier for compounds in the hemolymph.

Conclusions

The ultrastructure of the midgut of a number of insects has been reported, and it seems there is now enough information for planning definitive studies. We do not yet know for hematophagous (or other) insects which membranes are barriers to what; whether midgut cells in general secrete and absorb simultaneously; and various other points. We do know that in certain insects there are several different kinds of cells in the midgut (especially from work of WATERHOUSE and WRIGHT, 1960); and that gross differences between groups occur, such as the absorption of hemoglobin by hematophagous bugs but not by biting flies or fleas (WIGGLESWORTH 1943).

It seems to me clear that we must be careful in applying the interpretations of mammalian data to insects. In mammals, digestive enzymes are primarily secreted by glandular diverticula the cells of which have rough ER and pour their secretion from vesicles into the gut whereas the absorbing cells of the gut wall have smooth ER. In insects,

the normal gut epithelium both secretes and absorbs (HOUSE 1974); how then can one compare it with the situation in mammals? And, as already mentioned, several workers on insect midguts have not found the secretion picture described from mammalian cells. However, the mammalian workers have pioneered in developing techniques that we can apply to insects. With material to be examined by electron microscopy we can now visualize the localization of certain enzymes, determine the penetration and distribution of marker molecules of various sizes, utilize autoradiography, determine the effects of specific inhibitors, and numerous other things. Hopefully, such studies will be vigorously pursued in the coming decade.

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