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FINE STRUCTURE OF THE 'HINDGUT' OF THE TWO-SPOTTED SPIDER MITE, *TETRANYCHUS URTICAE*, WITH SPECIAL REFERENCE TO ORIGIN AND FUNCTION

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ABSTRACT

Mothes-Wagner, U., 1985. Fine structure of the 'hindgut' of the two-spotted spider mite, *Tetranychus urticae*, with special reference to origin and function. *Exp. Appl. Acarol.*, 1: 253—272.

The ultrahistology of the 'hindgut' of the spider mite *Tetranychus urticae* is described, a new terminology of the histological portions, based on the presence and absence of cuticle, is presented, and functional characteristics are discussed.

The alimentary canal of the spider mite consists of the cuticle-lined foregut (pharynx, esophagus, esophageal valve), a cuticle-free midgut, and a cuticle-lined hindgut with anal slit. The portions of the midgut are the ventriculus with three cranial and two caudal caeca, and the posterior midgut with two distinct cell types. Both portions are separated by a sphincter. The anterior lateral walls of the ∇-shaped posterior midgut which terminates in the dorsal region of the ventriculus show histological variability. Cells are either asymmetrical with long apical projections (=typical transporting epithelium) or show resorptive characteristics and storage products (=resorptive epithelium). The dorsal and posterior lateral epithelium consists of flat glandular cells containing large granular secretion grana. It is suggested that these cells synthesize mucoid substances for the facilitation of excretion transport.

The differentiation and function of the posterior midgut epithelium are discussed with respect to the formation of different elimination products.

INTRODUCTION

The post-oral digestive system of the Acari generally consists of a pharynx and an esophagus which passes through the nervous system (= ectodermal foregut) and leads to the ventriculus. Two or more caeca terminate in the ventriculus and provide an additional surface area for digestive processes (=entodermal midgut). Digestion itself is intracellular, with caecal cells protruding into the lumen, leaving the epithelium and becoming free floating phagocytes (Ehara, 1960; Anwarullah, 1963; Mothes and Seitz, 1981; Mothes-Wagner, 1982). Undigested material localized in faecal phagocytes

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passes to the 'hindgut', which leads to a rectum opening externally at the anus (=ectodermal hindgut) (Krantz, 1978). Although some authors believe that many of the higher trombidiformes lack a complete gut (Ehara, 1960), and that the 'hindgut' functions as an excretory tube (Hughes, 1950, 1952, 1959; Baker and Wharton, 1952; Evans et al., 1961), other authors suggest that the digestive system is continuous and that the transition from midgut to hindgut is formed by special structures (sphincter or valve) (Ehara, 1960; Anwarullah, 1963; McEnroe, 1963; Prasse, 1967; Vistorin, 1969; Alberti, 1973).

The 'hindgut' or dorsal excretory organ of the Acari is divided into more or less well defined regions. However, the terminology and origin of these regions is confused: colon (intestine, hindgut, posterior midgut; ectodermal–entodermal), hindgut (post-colon, rectum; entodermal–ectodermal) and anus (Brody et al., 1972). Ultrastructure and possible function of the dorsal excretory organ of the phytophagous spider mite *Tetranychus urticae* (Acari, Tetranychidae) have been described in a previous paper (Mothes and Seitz, 1980). In the present paper the focus has been on the question whether histologically different portions can be observed, and whether these portions can be the basis for interpreting origin and specialized function. Preliminary results indicate that the appearance and histology of the organ vary (Mothes-Wagner, 1982); this is thought to depend upon feeding and food characteristics between the developmental stages and the adult, resulting from the kind of plant cells pierced and sucked out (Mothes and Seitz, 1981) as well as upon the physiological characteristics of the host plant.

The present paper describes the ultrahistology of the 'hindgut' of *T. urticae* by means of standardized culture and serial sections, divides the organ into its histological and functional portions, and discusses the origin (entodermal–ectodermal) and function of these portions with respect to previously published information on other acarine species.

MATERIALS AND METHODS

Mites were reared following the method described earlier (Mothes and Seitz, 1980). Specimen preparation for electron microscopy was carried out according to the method described by Mothes-Wagner et al. (1984). The photographs presented in the figures are all taken from serial sections.

RESULTS

Based on structural characteristics as well as on the presence (ectodermal) and absence (entodermal) of cuticle (see discussion), the alimentary canal of *T. urticae* can be divided into an ectodermal cuticle-lined foregut (pharynx, esophagus, esophageal valve), an entodermal midgut (ventriculus, caeca, posterior midgut) and an ectodermal, cuticle-lined hindgut (rectum with anal slit) (Mothes and Seitz, 1980, 1981) (see Diagram). In contrast to other mite

species (Prasse, 1967; Brody et al., 1972) and results in a previous publication on *T. urticae* (Humiczewska and Mielnicka, 1983), a peritrophic membrane was not observed in any midgut portion, due to the intracellular digestion (Figs. 2, 3, 7—10, 15, 16). Until now, no general histological differences could be detected between the developmental stages, males and females. The malpighian complex, only present in adult females, joins the gut between two portions of the posterior midgut (Mothes and Seitz, 1980; Mothes-Wagner, 1982) and places it between two entodermal sections (Fig. 16). The structure of the ventriculus and caeca as well as the digestive processes inside the lumen and phagocytes have already been described (Mothes and Seitz, 1981).

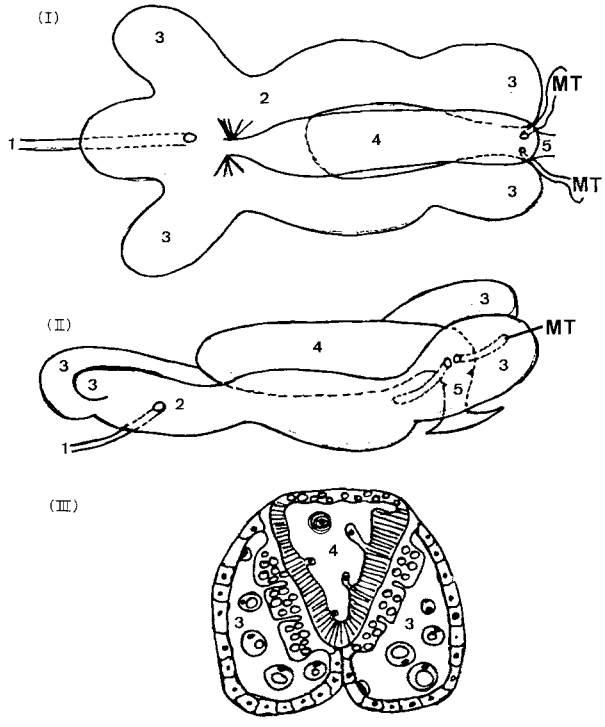


Diagram A. Representation of the alimentary canal of *T. urticae*. I, Frontal view. II, longitudinal view. III, cross section. (1) Esophagus (= ectodermal); (2) ventriculus; (3) cranial and caudal caeca, and (4) posterior midgut with Malpighian tubules (= entodermal); (5) rectum and anal slit (= ectodermal). (MT), Malpighian tubules.

Posterior midgut

The posterior midgut of the two-spotted spider mite terminates in the dorsal region of the ventriculus by a sphincter (Fig. 2). Two cell types are observed in the epithelium situated in the anterior lateral walls of the ∇-

shaped organ and in the dorsal and posterior lateral walls respectively (see Diagram).

Anterior lateral epithelium

The entrance aperture of the posterior midgut is a slit generally compressed by fine muscles (= sphincter) (Figs. 1, 2). The epithelial cells of this most anterior portion form small microvillous protrusions and contain glycogen granules (Fig. 1). Posteriorly, the lateral walls are composed of cells, mostly three to five per cross section, which generally exhibit long projections into the lumen, resulting in an enlarged cell surface (Figs. 2, 3). Mitochondria of varying appearance (roundish, Fig. 2; elongate, Fig. 3; sometimes circular, Fig. 3) can be found in these projections. Nuclei and a few vacuoles are situated basally (Fig. 3).

In the presence of crystalline material inside the lumen, the length and degree of extension of the epithelial projections may be reduced, and electron-dense bodies and vacuoles occur (Figs. 5—10). Similar electron-dense inclusions are also observed in swollen projections (Fig. 5), where they are surrounded and interspersed with small globules (Figs. 5, 6a,b) (Mothes and Seitz, 1980). These globules are observed to be strung on tubular or platelike structures only half their diameter (Fig. 6b). The electron-dense inclusions of amorphous material with the accompanying globules are constricted and thus participate in the formation of the faecal pellet (Fig. 22). The epithelial cells may contain numerous glycogen granules, fatty droplets, cisternae of rough ER, and large mitochondria exhibiting an extremely dense matrix (Figs. 8, 9, 10). Because of the accumulation of storage material, projections can be either attached to one another (Fig. 10) or be swollen (Fig. 9), resulting in an apparently compact epithelium. Small electron-dense particles situated in the periphery of the epithelial cells are delivered and accumulate at the periphery of the crystalline concretion (Fig. 9a,b).

Faecal phagocytes

Faecal phagocytes, which enter the posterior midgut from the ventricules at intervals, are closely attached to the epithelial cells (Figs. 12, 13) during their passage through the lumen. They exhibit a small cytoplasmic margin surrounding a large central vacuole with undigested or partly digested material including small lipid droplets, residues of starch grana, different vesicles, amorphous substances, disrupted plant mitochondria, and sometimes thylakoid fragments (Figs. 11, 12, 13). The cytoplasmic margin itself encloses numerous smaller vacuoles with electron-dense or membranous contents, vesicles, mitochondria, fatty droplets, and bacteria (Fig. 11). During passage through the posterior midgut a decrease in thickness and increase in electron density of the cytoplasmic margin, the disappearance of cytoplasmic inclusions and excretory vacuoles, and the final bursting of the cell can be observed (Figs. 12—14). The undigested and not reabsorbed material is concentrated in the faecal pellet (Fig. 22).

Fig. 1. Entrance aperture of the posterior midgut located in the dorsal ventriculus. Epithelial cells (EC) (flat, containing glycogen granules: arrow), mitochondria (M), vesicles (double arrow) and few cisternae of rough ER. The apical plasma membrane forms short microvillous projections (arrow head). Hypodermis (HY), basement membrane (BM). Cell contacts formed as tight junctions (asterisk). × 17 000.

Fig. 2. Posterior midgut just behind the entrance aperture. Epithelial cells form long apical projections which nearly close the lumen (LU). Dorsal wall (arrow) formed of electron-dense cells exhibiting large granular vacuoles (V). The posterior midgut epithelium and the adjacent caecal epithelium (CE) are separated by a basement membrane in which muscles are embedded (MU), forming a sphincter. × 3000.

Fig. 3. Lateral wall of the projecting posterior midgut. Epithelial cells form long apical projections (arrow), resulting in a large surface area. Mitochondria (double arrow) are closely associated with the projections. (CE), caecal epithelium; (V), vacuoles. × 4500.

Fig. 4. Dorsal wall of the posterior midgut. Epithelial cells contain large vacuoles with granular contents (V), mitochondria (M), cisternae of rough ER (arrow), and glycogen granules (double arrow). The apical membrane forms only small microvillous projections. × 17 000.

Fig. 5. Swollen projections of the lateral posterior midgut epithelium contain an electron-dense inclusion (I) surrounded and interspersed with small globules (arrow). Mitochondria (M) located peripherally. (B), bacteria; (G), Golgi apparatus. × 9600.

Fig. 6a, b. Higher magnification of the globules surrounding the electron-dense inclusion (I). Globules formed of an electron-dense envelope enclosing an electron-lucent centre and sometimes an electron-dense central body. Globules can be stringed on tubules or plates (arrow) half the diameter of the globules. × 36 000.

Fig. 7. Lateral wall of the projecting posterior midgut showing only short apical projections (AP) but numerous vacuoles (V). Mitochondria (M) are small. Electron dense inclusions (I) are surrounded by globules (arrow). × 11 000.

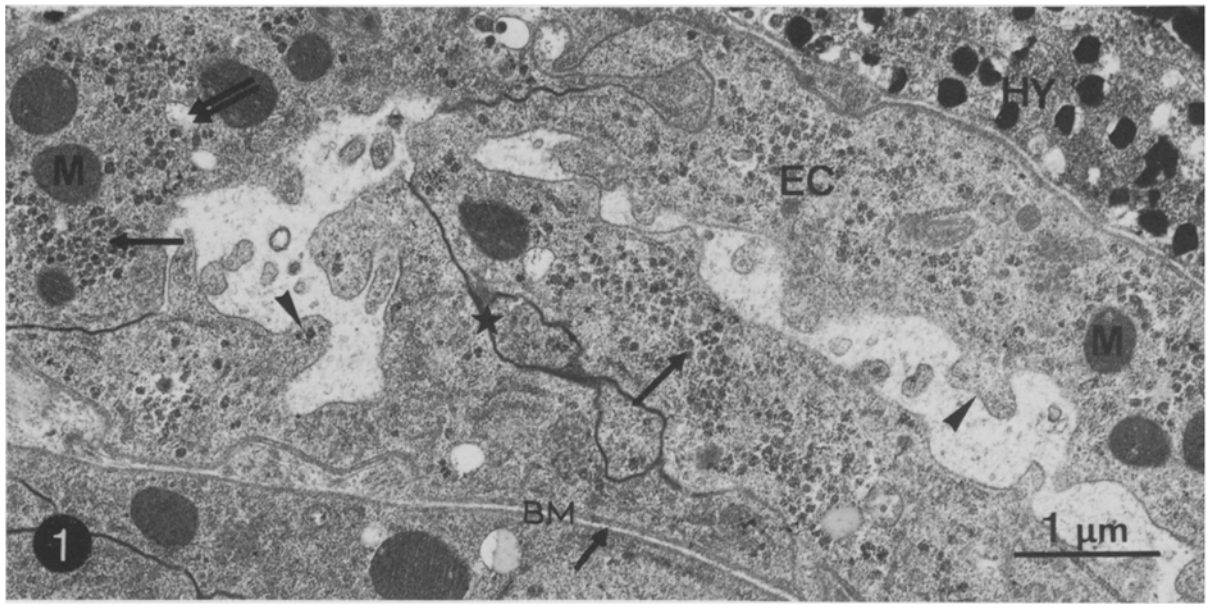
Fig. 8. Lateral wall of the projecting posterior midgut. Cells exhibit swollen apical projections (arrow), large mitochondria (M), glycogen granules (double arrow), numerous small vesicles (asterisk), and a nucleus (N). × 6000.

Fig. 9. Lateral wall showing numerous glycogen granules (arrow), fatty droplets (F) and extremely dense mitochondria (M) located apically. The crystalline concretion (CY) located in the posterior midgut lumen seems to formed of material excluded from the epithelial cells (inset; arrow). × 12 000; inset: × 25 000.

Fig. 10. Projections of the lateral wall closely attached, resulting in a compact epithelium. Cells exhibit numerous fatty droplets (F) and large mitochondria (arrow). Residues of faecal phagocytes (FP) with fragmented plant mitochondria (double arrow) are closely attached to the epithelial cells. (— — —) Border of epithelium. × 6000.

Fig. 11. Faecal phagocytes passing to the posterior midgut. The central vacuole (CV) contains partly digested or undigested granular material. It is surrounded by a cytoplasmic margin enclosing numerous large vacuoles with excretory material (V), small vesicles (arrow), mitochondria (M), and bacteria (B). × 10 000.

Fig. 12. Faecal phagocyte. Reduction of the cytoplasmic margin (CM) with its organelles and inclusions during passage through the posterior midgut. × 6000.



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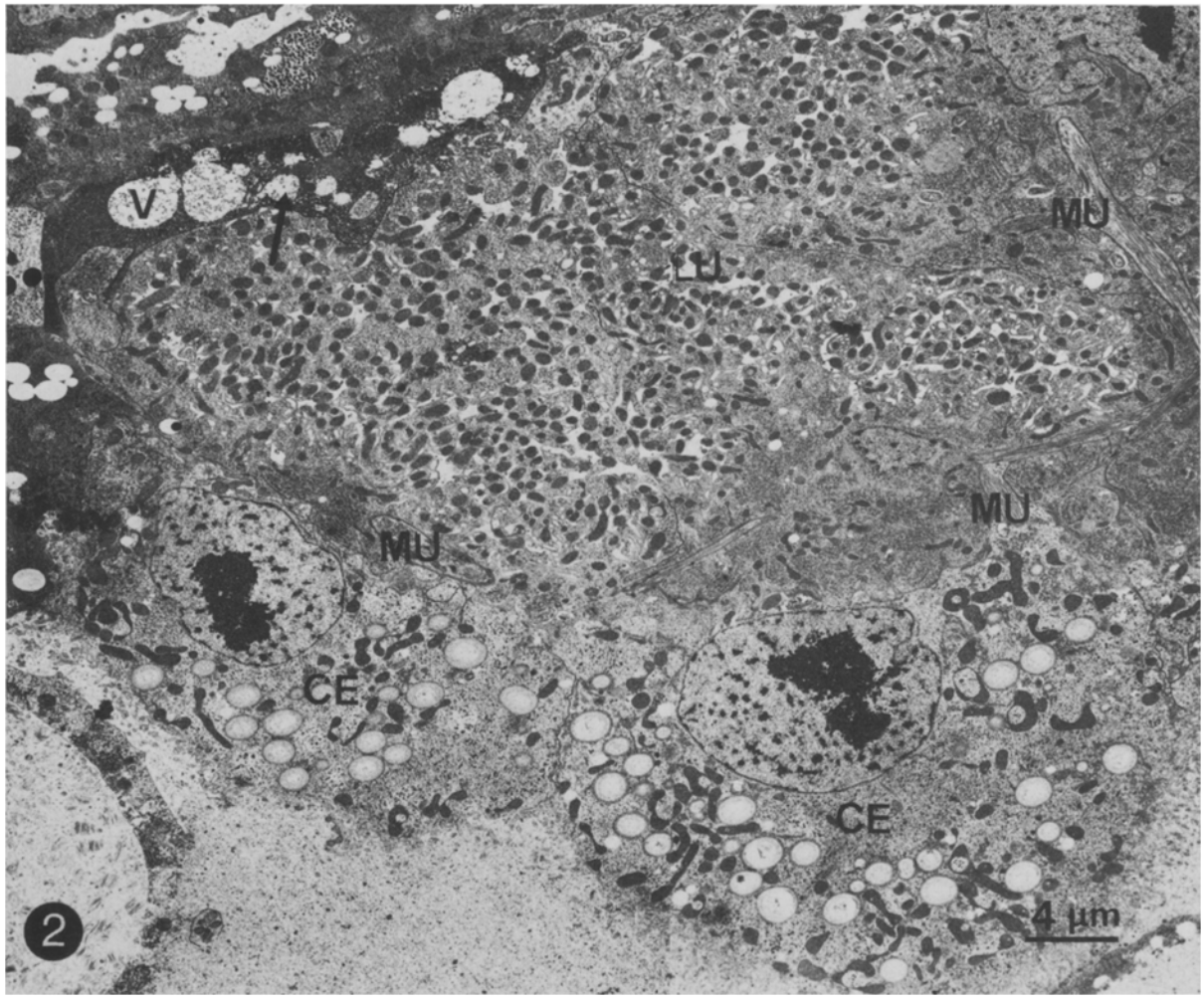

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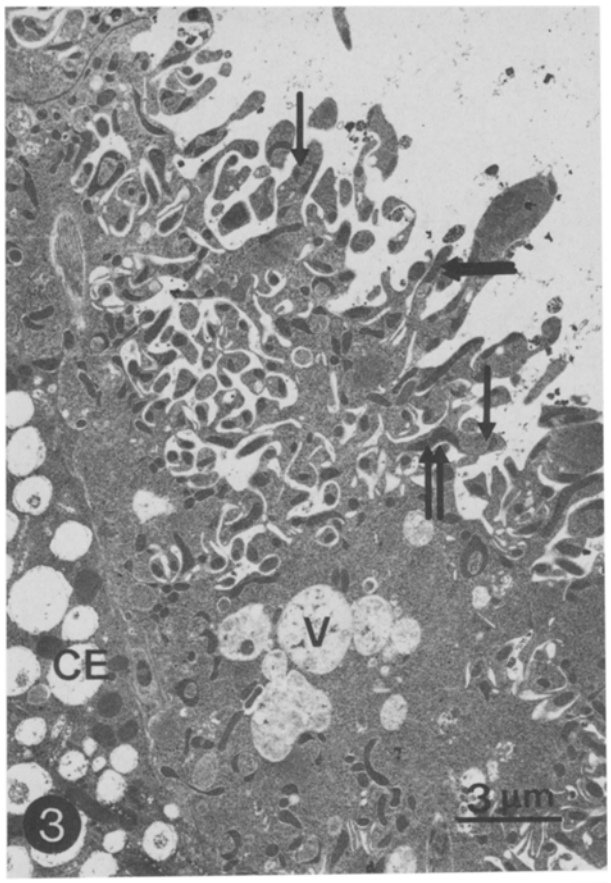
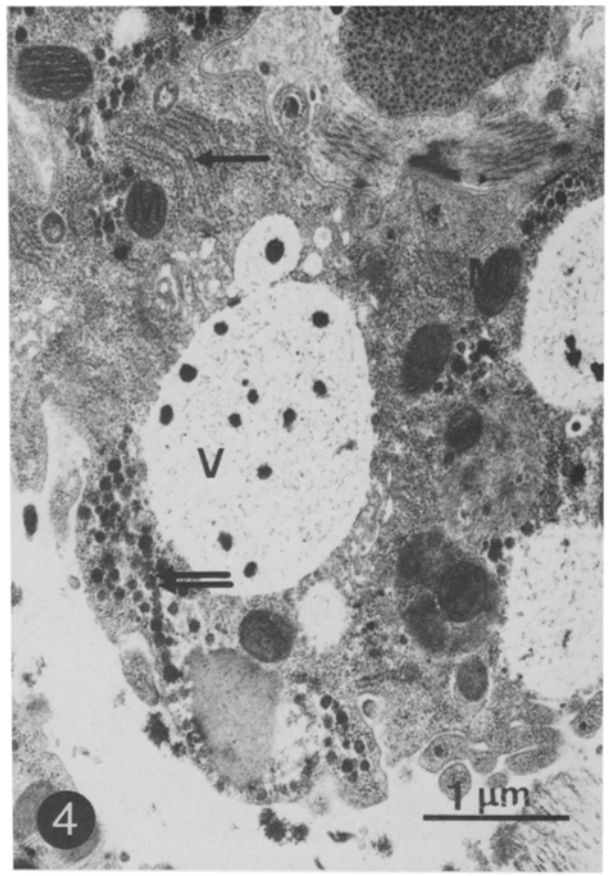

CE
V
3 µm
3


V
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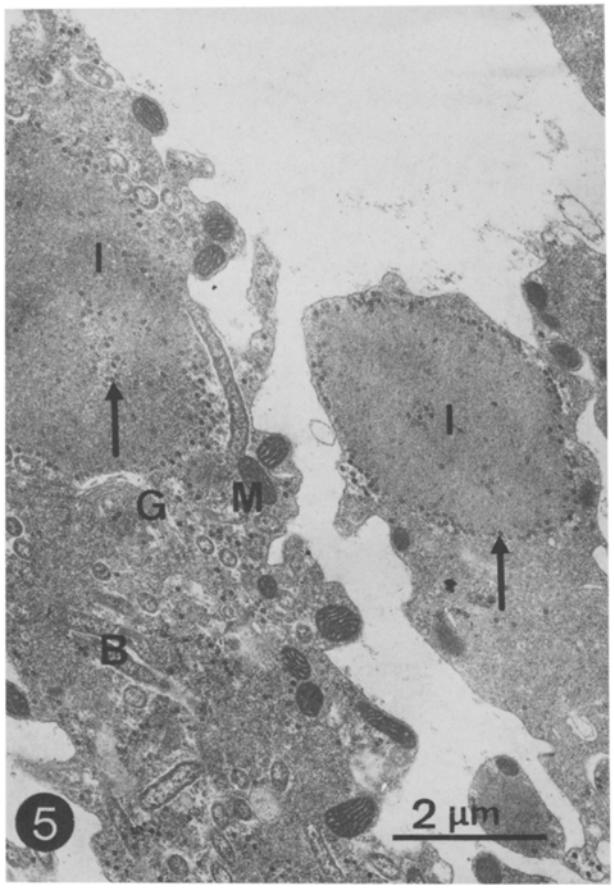
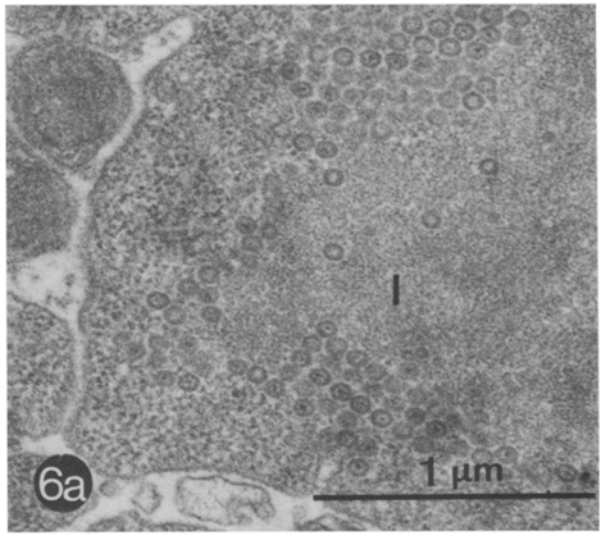
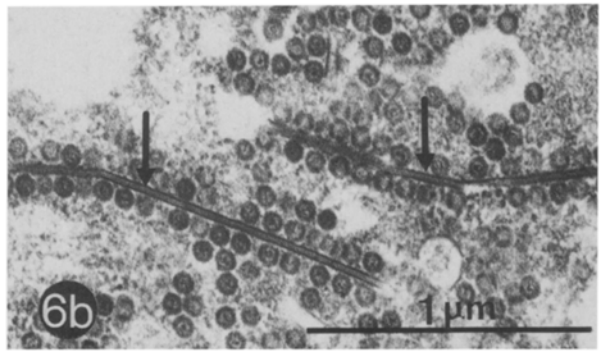
4


I
I
G
M
B
2 µm
5


I
1 µm
6a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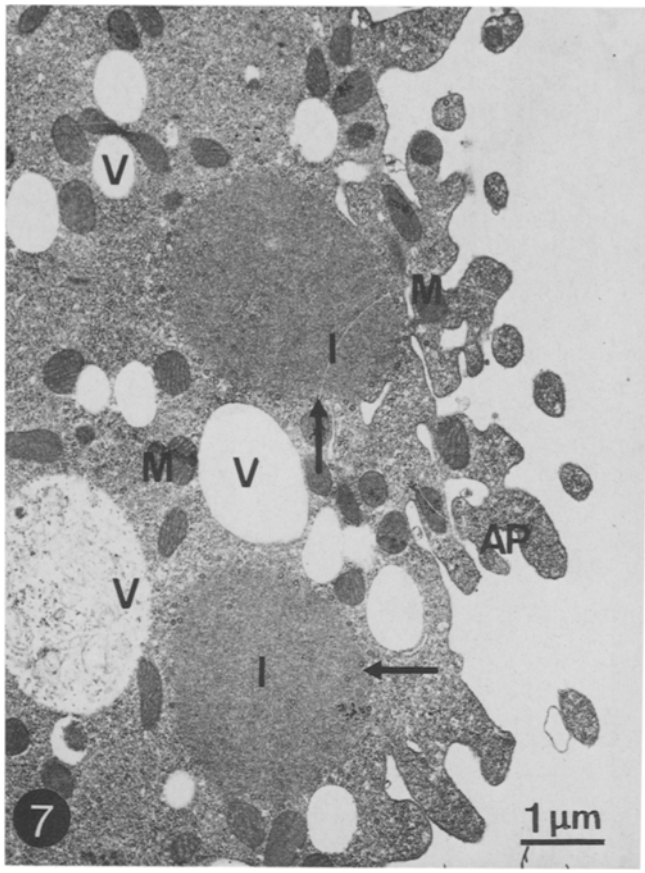
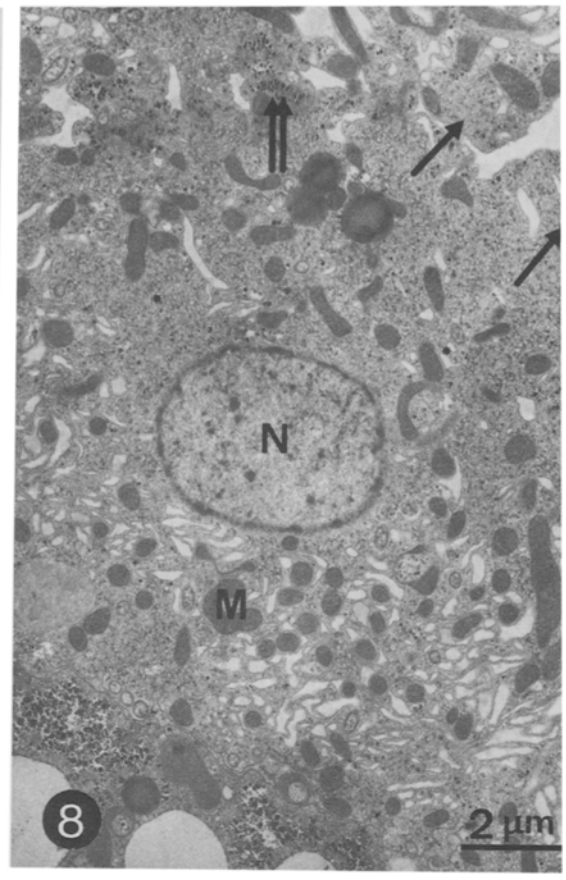
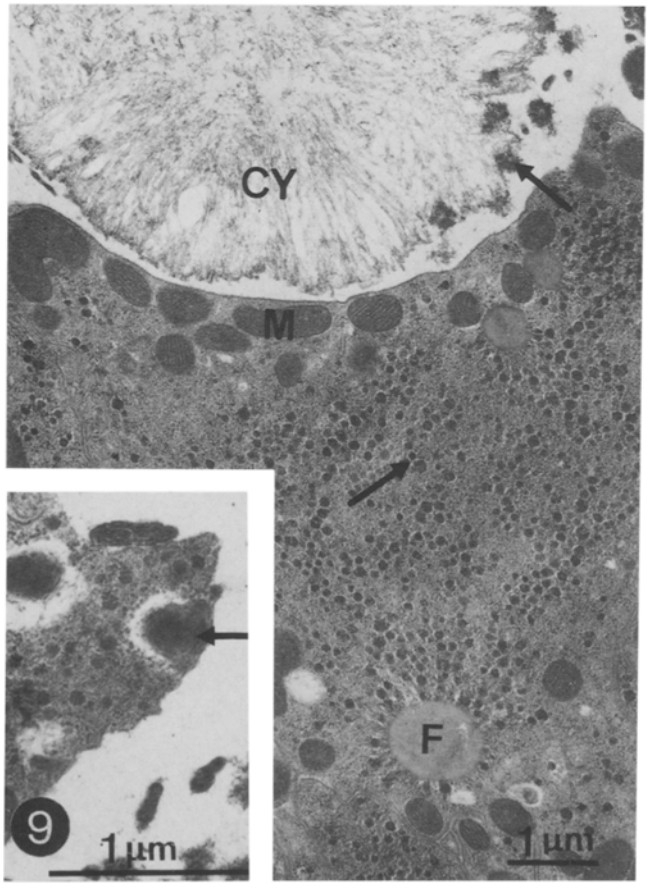
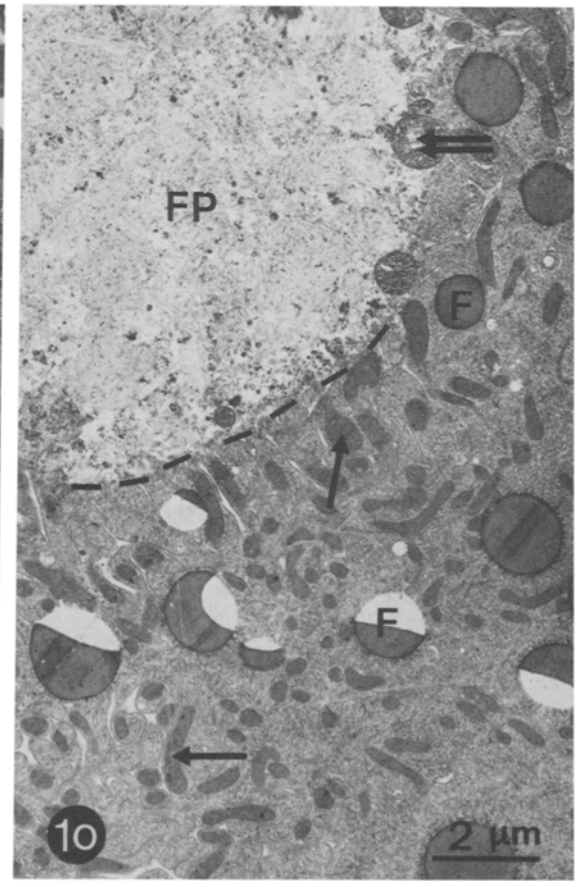
6b

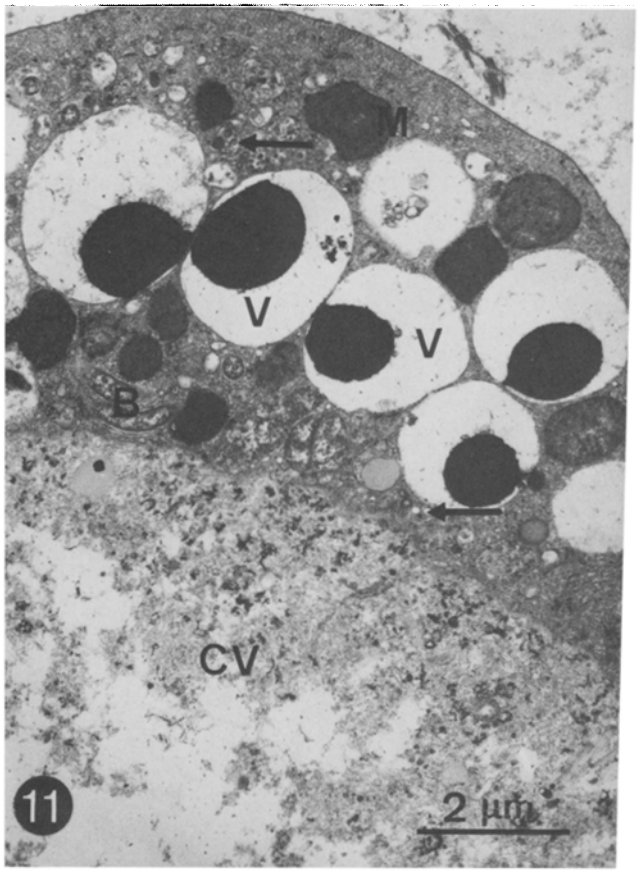

V
M
I
M
V
AP
V
I
1µm
7

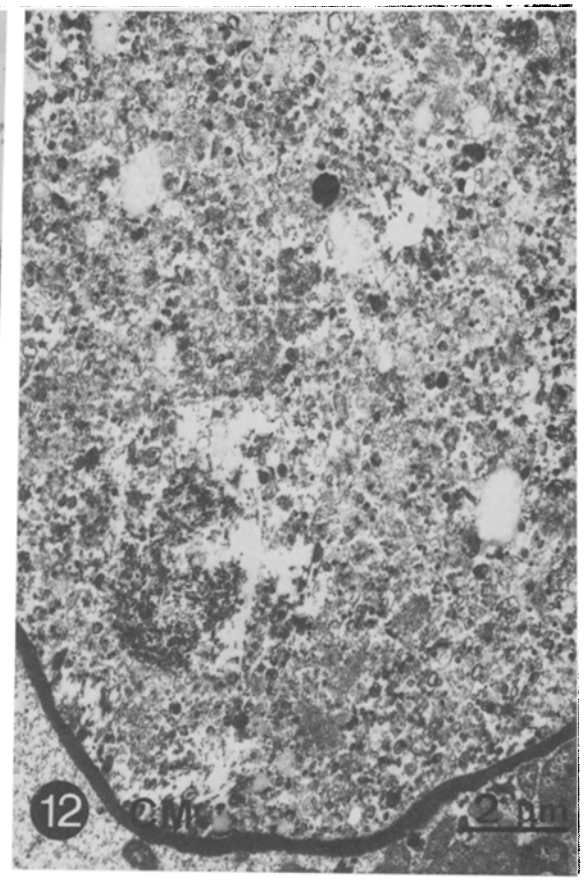

N
M
2µm
8


CY
M
F
1µm

1µm
9


FP
F
F
2 µm
10


M
V
V
B
CV
11
2 µm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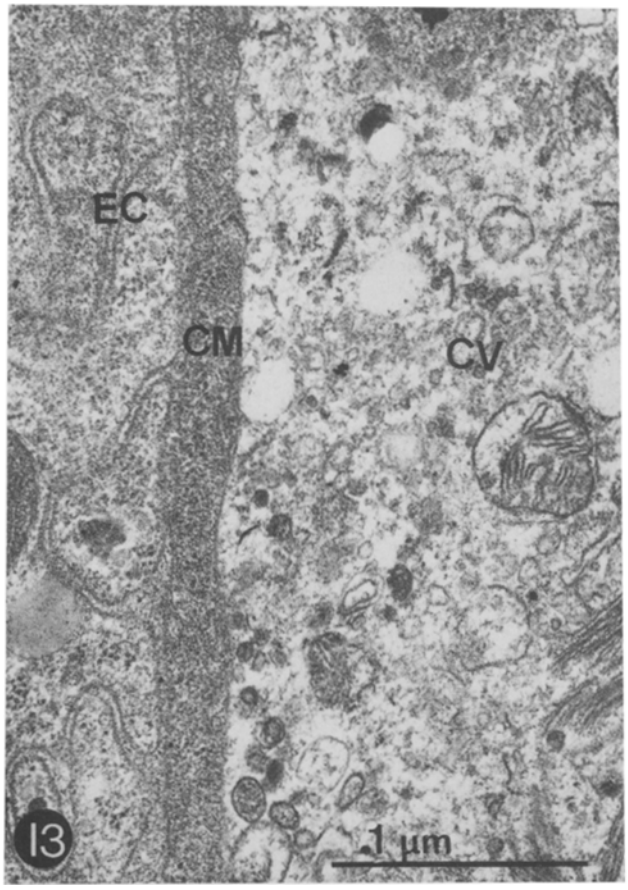
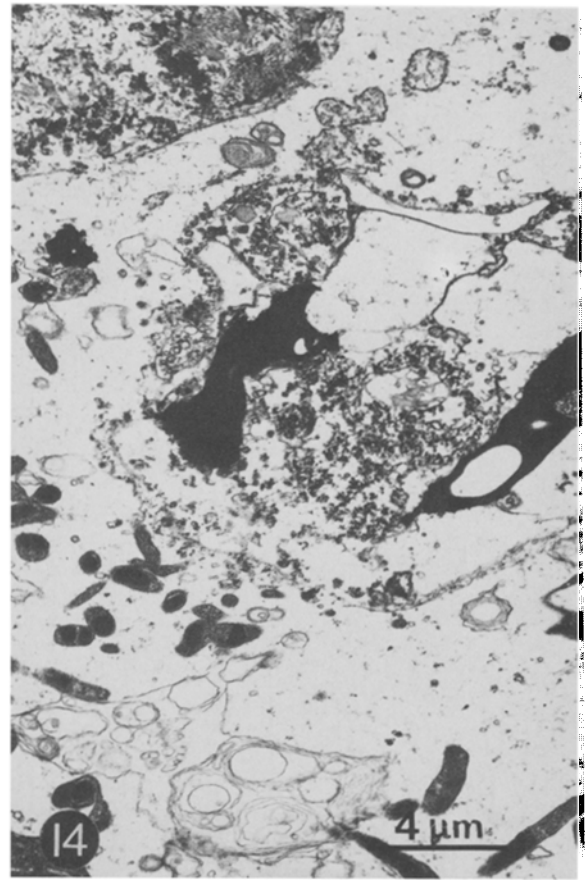
2 µm


EC
CM
CV
13
1 µm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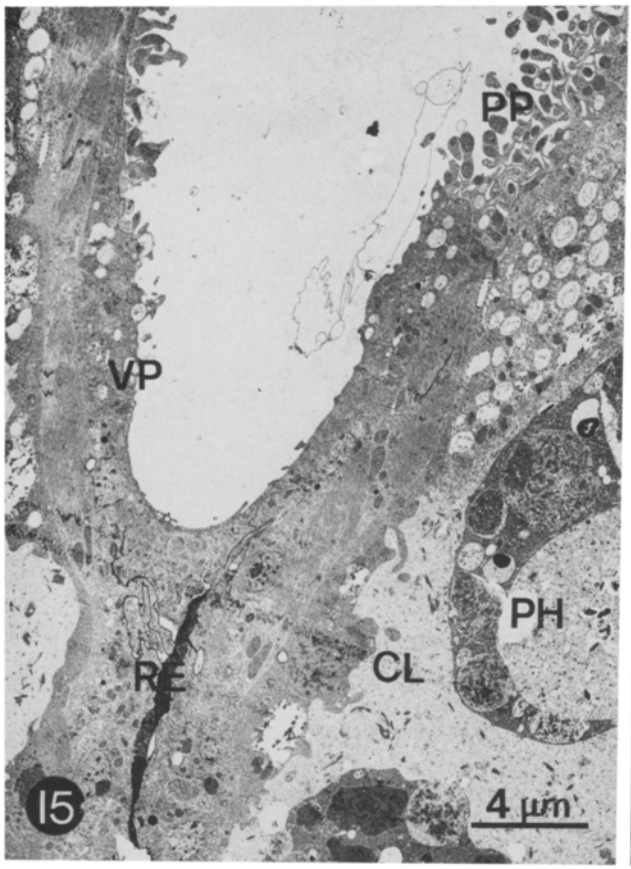
4 µm


PP
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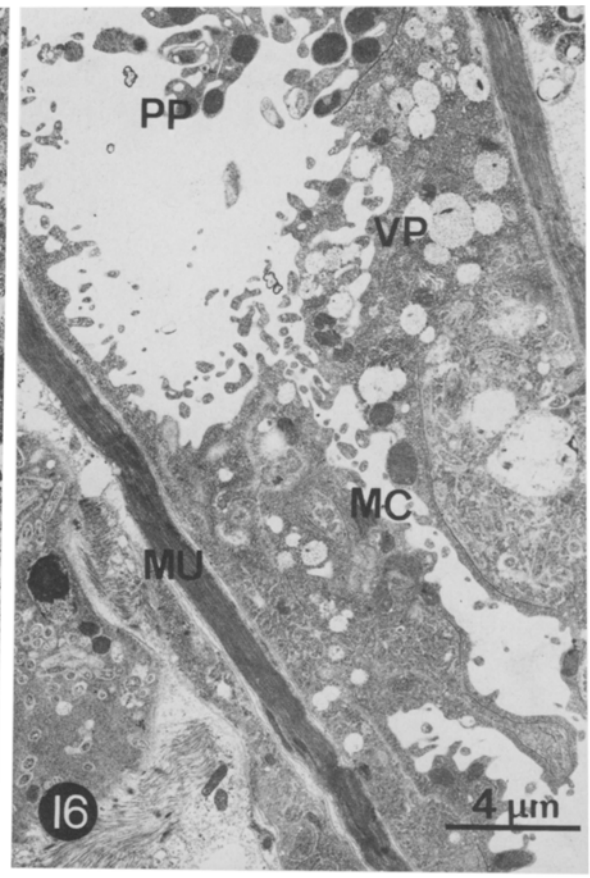
4 µm


PP
VP
MC
MU
16
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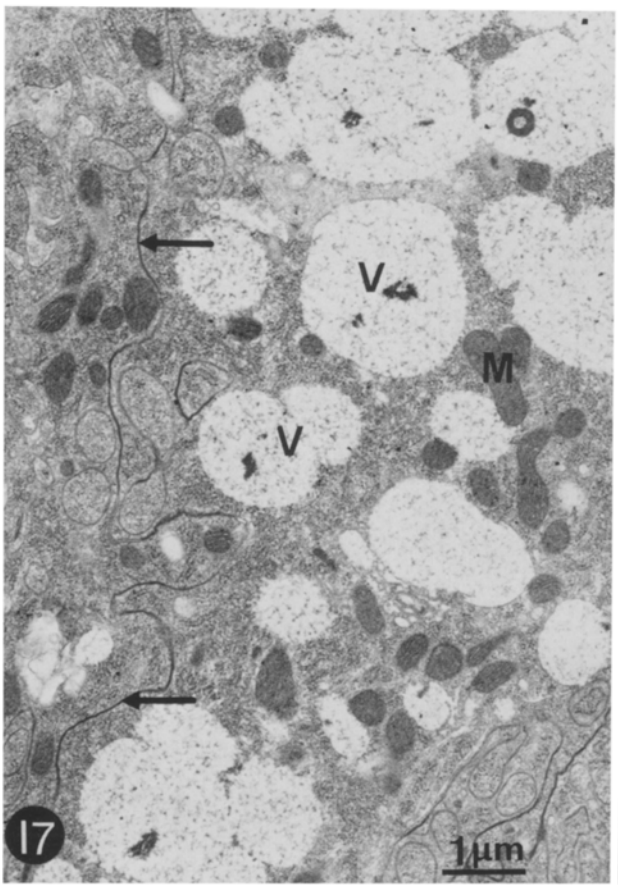
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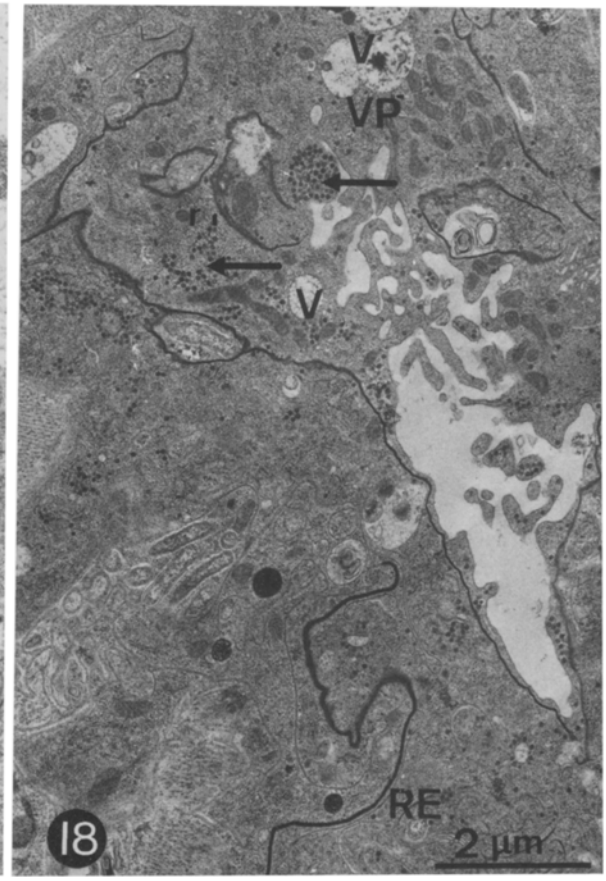
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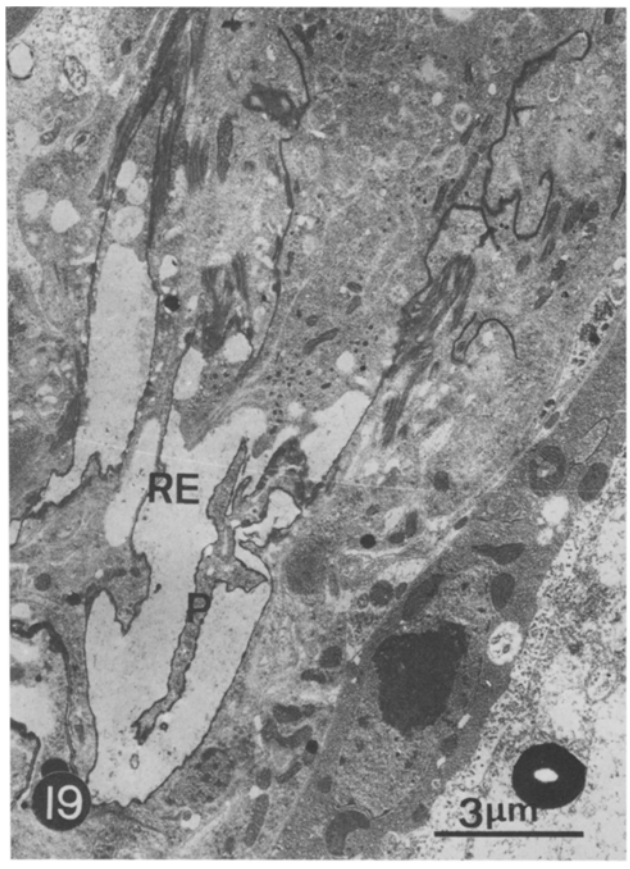
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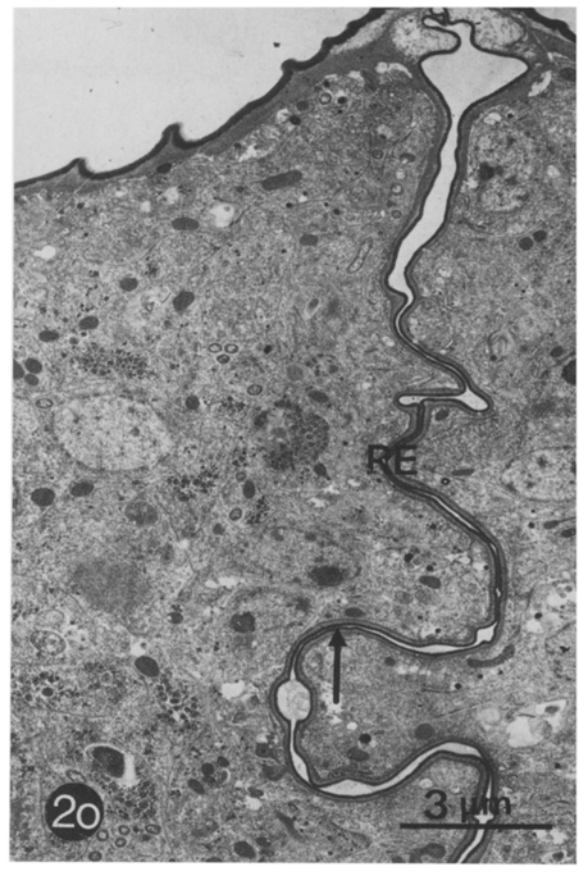
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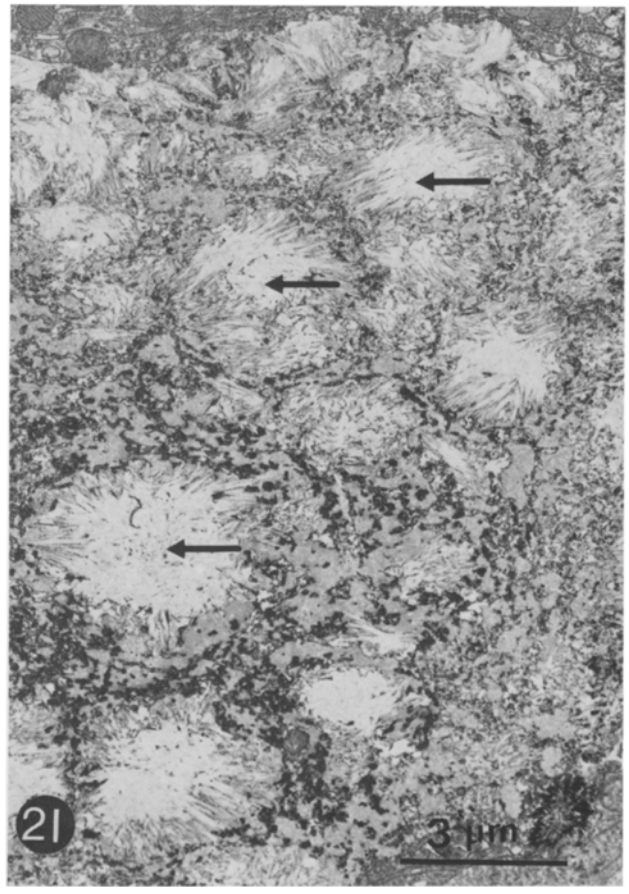
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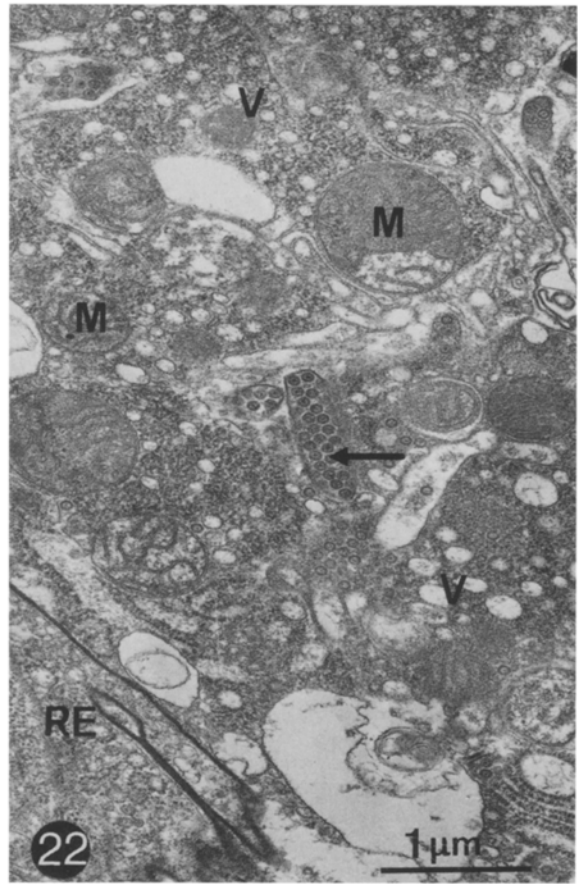
V
M
M
V
RE
22
1µm

Fig. 13. Faecal phagocyte, with a small cytoplasmic margin (CM) surrounding the central vacuole (CV) is closely attached to the epithelial cells (EC) of the posterior midgut. × 30 000.

Fig. 14. Residues of faecal phagocytes inside the posterior midgut lumen, showing degenerated excretory materials. × 4500.

Fig. 15. Transition from the projecting (PP) to the vacuolated posterior midgut (VP) of an adult female. Caecal lumen (CL) with phagocytes (PH). (RE), rectum. × 3600.

Fig. 16. Termination of the malpighian complex (MC) between the projecting (PP) and the vacuolated portion (VP) of the posterior midgut. (MU), muscles. × 4500.

Fig. 17. Epithelial cell of the vacuolated posterior midgut exhibiting numerous vacuoles with granular content (V), and small mitochondria (M). Cell contacts formed mostly of tight junctions (arrow). × 10 500.

Fig. 18. Transition from the vacuolated posterior midgut (VP) to the rectum (RE) in an adult female. Epithelial cells of the posterior midgut contain numerous accumulations of the small globules (arrow) and vacuoles (V). × 9600.

Fig. 19. Complex structure of the rectum (RE) of an adult female. Epithelial cells form long plugs covered with cuticle (P). × 6800.

Fig. 20. Rectum (RE) of an adult male lined with a strong cuticle (arrow). × 6600.

Fig. 21. Crystalline concretion as an elimination product, consisting of an amorphous material with several condensation centres (arrow). × 7200.

Fig. 22. Faecal pellet as elimination product consisting of degenerated mitochondria (M), numerous vesicles (V), accumulations of globules (arrow) and different inclusions embedded in a cytoplasmic matrix. (RE), rectal epithelium. × 17 500.

Dorsal and posterior lateral epithelium

The cells of the dorsal and posterior lateral epithelium of the posterior midgut are flat, form only few and very short microvillous projections, contain numerous vacuoles with fine granular contents, cisternae of rough ER, and small electron-dense mitochondria (Figs. 2, 4, 15—17). Sometimes glycogen granules are observed (Fig. 4). The transition from the projecting to the vacuolated portion of the lateral epithelium is very abrupt (Figs. 15—17) and corresponds with an alteration in caecal epithelial cells adjacent to the posterior midgut (Mothes and Seitz, 1980, 1981; Mothes-Wagner, 1982, 1985). In adult females, the Malpighian complex joins the gut at the transition of these two posterior midgut portions (Fig. 16).

Hindgut or rectum

Following the posterior midgut is the short, cuticle-lined rectum. In adult females, the transition is very complex, in that the rectal epithelium forms

long cuticle-covered plugs (Fig. 19). Portions of the posterior midgut seem to extend between the rectal wall, apparently forming a breech-plug. The rectum of the developmental stages and adult males is formed in a much more simple way, as the plugs are lacking (Fig. 20). The epithelial cells at the midgut/hindgut transition contain numerous accumulations of the small globules already observed in the anterior lateral walls (Fig. 18).

Faecal products

End products of the digestive process are, first, faecal pellets (Fig. 22) consisting of numerous vesicles, residues of mitochondria, globules, and cytoplasmic portions; second, crystalline concretions exhibiting several condensation centres (Fig. 21); and third, droplets of a yellowish fluid.

DISCUSSION

Terminology

Studies dealing with the structure and function of the hindgut of mites are carried out preferably on the sarcoptiform group, including primarily terrestrial mites which, with few exceptions, are non-predatory in habit (Krantz, 1978). As already pointed out for this group by Baker (1975), in tetranychids there is also a considerable variation in the nomenclature of the single gut portions and little attention has been paid to the function of these portions (Table 1).

The division of the gut into its three primary regions — foregut, midgut, and hindgut — should be made using the criterion of presence or absence of cuticle (Seifert, 1970; Brody et al., 1972; Czihak et al., 1976), because the entrance of the Malpighian tubules (if present) into the gut seems not to be a positive landmark to differentiate midgut and hindgut (Brody et al., 1972; Baker, 1975). Taking this definition as a basis, it can be stated that only the last, cuticle-lined portion of the gut of *T. urticae* is a true hindgut or rectum, and that all portions located anterior to this region should be attributed to the entodermal midgut.

Extremely little attention has been paid to the origin of the dorsal wall consisting of flat vacuolated cells (Blauvelt, 1945; Ehara, 1960; McEnroe, 1963; Wiesmann, 1968; Mothes and Seitz, 1980). Blauvelt (1945), Mothes and Seitz (1980), and Wiesmann (1968) described them as a part of the rectum which, according to the previous definition, attributes the organ's epithelium entodermal and ectodermal origins at the same time. The present study demonstrates that the dorsal wall of the posterior midgut is structurally continuous with the region preceding the cuticle-lined rectum and thus has an entodermal origin.

According to the structural characteristics resulting in functional properties (see next section), the alimentary canal of *T. urticae* can be divided into

TABLE 1

Nomenclature of single gut parts according to different authors

Reference	Nomenclature		
A. Sarcoptiformes			
Hughes and Hughes (1938)			rectum
Hughes (1959)	colon	post-colon	rectum
Prasse (1967)	colon	post-colon	rectum
Rohde and Oemick (1967)	colon		rectum
Kuo and Nesbitt (1970)	colon		rectum
Brody et al. (1972)	posterior midgut		hindgut
Baker (1975)	colon	post-colon	rectum
B. Trombidiformes			
Blauvelt (1945)	excretory organ		true hindgut
Ehara (1960)	hindgut		
McEnroe (1963)	hindgut		
Anwarullah (1963)	excretory organ		hindgut
Wiesmann (1968)	hindgut		rectum
Vistorin (1969)	colon	post-colon	rectum
Alberti (1973)	colon		rectum
Krantz (1978)	intestine	hindgut	rectum
Akimov and Barabanova (1978)	hindgut		
Paran (1979)	intestine		rectum
Mothes and Seitz (1980)	hindgut		rectum
Humiczewska and Mielnicka (1983)	hindgut		
Mothes-Wagner (1985)	posterior midgut		hindgut

an ectodermal, cuticle-lined foregut (pharynx, esophagus, esophageal valve), an entodermal midgut (ventriculus, caeca, and posterior midgut consisting of a transporting and a secreting epithelium), and an ectodermal, cuticle-lined hindgut (rectum with anal slit). Questions concerning the uptake and digestion of food material have been dealt with in a previous paper (Mothes and Seitz, 1981).

Function

It is generally supposed and accepted that the 'hindgut' of the trombidiform mites functions as an organ for both excretion and defaecation (Blauvelt, 1945; McEnroe, 1961; Anwarullah, 1963; Wiesmann, 1968; Mothes and Seitz, 1980; Mothes-Wagner, 1982), which includes resorption and secretion processes (McEnroe, 1963; Prasse, 1967; Brody et al., 1972; Baker, 1975; Mothes and Seitz, 1980; Humiczewska and Mielnicka, 1983). Such processes are closely related to transmembrane transport and find expression histologically in a specialized transporting epithelium. Additionally, it is known (Wiesmann, 1968) that tetranychids eliminate different excretory/defaeca-

tion products: a yellowish fluid, crystalline concretions, and black faecal pellets.

The following is a short summary of the investigated mite species, demonstrating the histological characteristics of the single 'hindgut' portions (Table 2).

According to the presented results it can be stated that the posterior midgut of *T. urticae* is formed of two distinct regions. The anterior lateral epithelium shows a variable histology. When no luminal material is found, the epithelium generally consists of asymmetric cells which form long apical projections, but no basal infoldings. These projections are comparable to the leaflet folding pattern of the transporting epithelia which do not seem to occur in vertebrate epithelial cells but are frequently found in arthropod epithelia (Cioffi, 1984). Cells which have long apical leaflets and short or absent basal channels are supposed either to reabsorb or to secrete ions (Marshall and Wright, 1974). Large mitochondria extending into the projections have a close association with the plasma membrane. Consequently, the anterior lateral walls of the posterior midgut represent a typical transporting epithelium ('nephritic organ' of Blauvelt, 1945) with the universal characteristic of a juxtaposition of mitochondria and plasma membranes, extremely dense mitochondria, apical membrane projections, and a strong alkaline phosphatase (McEnroe, 1963) and ATPase activity (Schlüter, 1980; Bradley, 1984). This corresponds with the observation of McEnroe (1963) that small molecules, large volumes of water, and ions in solution are passed rapidly to the 'hindgut' (esophageal—hindgut shunt), and that those substances required by the mite are directly absorbed in the 'hindgut'. It is supposed that the elimination product formed during the 'projecting state' of the anterior lateral epithelium represents the yellowish fluid observed by Blauvelt (1945) and Wiesmann (1968). This, of course, could not be demonstrated by electron microscopy.

If crystalline concretions or residues of faecal phagocytes are obvious in the posterior midgut lumen, the apical projections of the lateral epithelial cells are shortened or club-shaped swollen. Simultaneously, a large amount of storage products is accumulated inside the cells; these products are suggested to be reabsorbed from the attached faecal phagocytes. In this 'resorptive state' the epithelium can be compared to metabolically active tissues of the midgut caeca or glands of other arthropods. However, it is not clear whether this storage material is a reserve for the energy-requiring activities of the mite (for example moulting), whether it is a withdrawal of osmotically effective material in an inert form, or whether it is the basal energy supply for transport processes occurring at intervals.

It is suggested that the storage material plays an important role in the general metabolism of this mite species, for a fat body is lacking (Mothes-Wagner, 1982). Both the projecting anterior lateral epithelium and the adjacent caecal epithelial cells are proposed to be the equivalents of the fat body of insects (Mothes-Wagner, 1985), whereby the posterior midgut may take over an additional function in osmoregulation.

TABLE 2

Histological characteristics of the single 'hindgut' portions

Reference	Colon		Post-colon		Rectum	
A. Sarcoptiformes						
Hughes and Huges (1938)	Sphincter	Peritrophic membrane, comparable to midgut	Sphincter	Brush border	Sphincter	Columnar cells
Prasse (1967)		Small cells, ciliated				Cuticle lined
Rohde and Oemick (1967)		Conical, columnar projections			Narrowing	Flat to columnar, brush border
Kuo and Nesbitt (1970)		Posterior midgut (long microvilli)				Brush border, dorsal: squamous
Brody et al. (1972)		Columnar, pseudo-stratified				Cuticle lined
Baker (1975)				Brush border		Cuticle lined
B. Trombidiformes						
Blauvelt (1945)		Excretory organ (glandular, vesicular)				Thin layer, evenly distributed
Ehara (1960)	Valve	Hindgut (columnar, dorsally vacuolated)				
McEnroe (1963)	Compressed slit	Hindgut (dorsal: squamous; lateral: glandular, brush border				Without brush border
Anwarullah (1963)		Excretory organ (glandular, brush border)				
Wiesmann (1968)		Hindgut (glandular, vesiculated, brush border)				Without brush border
Alberti (1973)	Sphincter	Brush border				Lining
Vistorin (1969)	Sphincter	Prismatic, without microvilli	Sphincter	Brush border	Valve	Flat
Humiczewska and Mielnicka (1983)		Hindgut (fimbriated border)				
Mothes-Wagner (1985)	Sphincter	Posterior midgut (dorsal and posterior: squamous, lateral: long projections)				Cuticle lined

In this context, it should be mentioned that the supposition of Baker (1975) — the colon may act as a filtering mechanism separating off and dispensing undigested food materials — is contrary to that of Akimov (1973), who believed that luminal digestion occurs in the colon. The present study contributes to this controversy by demonstrating that faecal phagocytes are closely attached to the epithelial cells and change their appearance during passage through the posterior midgut, and that simultaneously storage material accumulates inside the epithelial cells. As a result it can be stated that digestion and distribution of food material, formation of special excretory products and a partial resorption of digested food occurs in the ventriculus and caeca (Mothes and Seitz, 1981). However, reabsorption of digested material and formation of the final excretory products as well as the faecal pellets takes place in the posterior midgut.

This leads to the problem of determining the nature of the excretory material which is characterized by electron microscopy as a crystalline concretion of amorphous material exhibiting several condensation centres. It has been reported (Kaufman and Sauer, 1982) that in ticks, as in other arachnids, the end-point of the nitrogen metabolism is guanine rather than uric acid (Blauvelt, 1945; McEnroe, 1961, 1963; Hartenstein, 1970; Krantz, 1978), although urates and uric acid are detected in the faecal pellets of *T. urticae* (Humiczewska and Mielnicka, 1983). Only a few histochemical tests have been carried out to elucidate the sites of guanine deposition. Is it the caecal epithelium adjacent to the posterior midgut, which exhibits concentric excretory depositions (Mothes and Seitz, 1980, 1981; Mothes-Wagner, 1982, 1985); is it the ventriculus, where faecal phagocytes containing excretion vacuoles accumulate before passing to the posterior midgut; or is it the crystalline concretion located inside the posterior midgut lumen? Histochemical tests will contribute to this question and clarify the distribution of digestive enzymes and metabolic activities of this mite.

The present study demonstrates that each of the previously observed excretory/defaecation products of *T. urticae* can be related to histological characteristics of the epithelial cells. Fluid excretory material is produced by the cells forming a typical transporting epithelium — which is supported by the apparent 'nothingness' inside the lumen. Faecal phagocytes, only passed into the posterior midgut lumen at intervals (Alberti, 1973; Mothes-Wagner, unpublished results), contribute to the formation of crystalline concretions and faecal pellets — which corresponds to the observation of Prasse (1967) and Wiesmann (1968) that both elimination products are mixed. However, it is not really clear in which way the crystalline concretions are formed.

In this context, the role of the electron-dense material surrounded and interspersed with small globules and the function of these globules themselves should be mentioned. It was believed (Mothes and Seitz, 1980) and it is still believed that the globules may have a function in the formation of the faecal pellet. On the other hand, Martoja and Ballan-Dufrancais (1982)

described similar structures as virus-like particles. However, no proposal for their occurrence inside the anterior lateral epithelium and the transition from midgut to hindgut, or for their actual function, can be presented.

The dorsal and posterior lateral epithelium of the posterior midgut is supposed to synthesize and secrete a mucous material (because of the intense staining for proteins inside the cytoplasm) which facilitates the transport of the crystalline concretions. Whether the cells contribute to the formation of the concretions could not be demonstrated satisfactorily, but it seems unlikely. The rectum of *T. urticae*, representing the true hindgut, does not function in the formation of the excretory products, as no further alterations of the elimination products are observed.

Conclusion

The presented ultrastructural study coordinates structure and function of the 'dorsal excretory and defaecation organ' of the two-spotted spider mite, *Tetranychus urticae*, and contributes to the elucidation of the confused terminology of previous investigations. However, a final statement concerning digestive processes and metabolic activities, as well as a final proposal concerning the functional characteristics of the posterior midgut, can be made only after subsequent histochemical tests.

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