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FUNCTIONAL MICROSCOPIC ANATOMY OF THE DIGESTIVE SYSTEM OF
Tetranychus urticae (ACARI, TETRANYCHIDAE)

BY Ursula MOThES • AND K. A. SEITZ

ABSTRACT: The digestive system of Tetranychus urticae is described using light and electron microscopy. It is divided into pharynx, esophagus, midgut and hindgut with anus. The midgut consists of the ventriculus, three cranial and two caudal caeca. The pharynx which is surrounded by specialised structures for food ingestion, encloses the pharyngeal sucker and opens at the top of the gnathosoma. These structures serve to form a partial vacuum, by means of which plant cell components flow into the ventriculus without permanent sucking process. Passing through the esophagus the food reaches the ventriculus and on to the caeca, where intracellular digestion starts. The midgut epithelial cells show different functions. The ventricular and cranial caecal cells are in stage of synthesis. In the caudal caeca some cells enter the stage of resorption and storage, leave the epithelium and become free cells of the midgut lumen (= phagocytes). After passing through the midgut in direction of the hindgut sphincter they change into excretory cells. The phagocytes take over specialised functions in digestion, whereas at the same time they serve as a system of distribution for storage and nutritive products and replace the missing hemolymph system.

RESUME: L'appareil digestif de Tetranychus urticae est décrit en microscopie classique et électronique. Il se divise en un pharynx, un oesophage, un intestin moyen et un intestin postérieur avec un anus. L'intestin moyen consiste en un ventricule, trois coccyms craniaux et deux coccyms caudaux. Le pharynx, qui est entouré par des structures spécialisées dans l'ingestion des aliments, renferme une ventouse pharyngienne et s'ouvre à l'extrémité du gnathosoma. Ces structures servent à former un vide partiel au moyen duquel les composants des cellules des plantes s'écoulent dans le ventricule sans un processus d'aspiration permanent. Passant à travers l'œsophage, les aliments atteignent le ventricule et continuent jusqu'aux coccyms ou débute la digestion intracellulaire. Les cellules épithéliales de l'intestin moyen montrent différentes fonctions. Les cellules du ventricule et des coccyms craniaux sont à un stade de synthèse. Dans les coccyms caudaux quelques cellules entrent dans un stade de resorption et de stockage, quittent l'épipithélium et deviennent des cellules libres de la lumière de l'intestin moyen (= phagocytes). Après avoir traversé l'intestin moyen en direction du sphincter de l'intestin postérieur, elles se transforment en cellules excrétrices. Les phagocytes remplissent des fonctions spécialisées de la digestion, tandis qu'en même temps ils servent de système de distribution des produits du stockage et des produits de la nutrition et remplacent le système de l'hémolymphe absent.

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INTRODUCTION

Light microscopic investigations on the morphology of the digestive tract of Tetranychidae were made by Blauvelt (1945), Anwarullah (1963) and Gasser (1951). The few descriptions of the alimentary canal of other acari are usually discussed from a more specialised point of view (Chinery, 1964; Hughes, 1950; Kuo et al., 1970; Moss, 1962; Prasse, 1967; Rohde, 1967; Wright, 1964). The above mentioned publications deal with non-phytophagous animals which have other nutritive requirements than the phytophagous Tetranychidae.

In addition to the morphology of the digestive system of Tetranychus, physiological and functional aspects have been described (Akimov et al., 1977; Kötter, 1978; Mehrotra, 1961; McEnroe, 1961 a, b, 1963; Wiesmann, 1968). Especially detailed are the descriptions and suggestions of the digestive processes of Tetranychus urticae by Wiesmann (1968) and Akimov et al. (1977). Because of the small size of Tetranychus urticae light microscopically investigations could not solve all problems concerning digestions. Although digestive processes at the molecular level could, of course, not be observed with the electron microscope, some observations on cytological structures may help for the understanding of digestion in phytophagous mites. In our present investigation on Tetranychus urticae we describe the pathway of food as well as the participating organs in food distribution and digestion.

METHODS AND MATERIALS

Rearing of the animals has been described elsewhere (Mothes et al., 1980). For scanning electron microscopy mites were fixed gradually in 1.4 % buffered glutaraldehyd for 2 h, 4 % buffered glutaraldehyd for 2-3 d and 2 % OsO₄ for 2 h. After dehydration in graded ethanol and ethanol/amylacetate the animals were critical point dried and coated with a 30-50 nm gold layer.

For light and transmission electron microscopy the mites were fixed whole in 4 % collidine-buffered glutaraldehyd for 2-3 d, followed by osmication for 15 min. After dehydration in graded acetone solutions the material was polymerized in Spurr's medium (Spurr, 1969). Semithin sections were cut with a LKB-pyramitome, stained with alcoholic methylene blue and interpreted with a Leitz Diavert interference contrast microscope. Ultra-thin sections were cut with a diamond knife on an LKB-ultratome III and stained with KMnO₄ and lead citrate (Reynolds, 1963) modified after Soloff (1973). Sections were observed with an Hitachi HU 12A electron microscope.

OBSERVATIONS

Mouth Region

The mouth organs of Tetranychus have been described by several authors (Becker, 1935; Blauvelt, 1945; Hislop 1976). Although only one publication exists, in which the author examined the gnathosoma with the scanning electron microscope (Akimov et al., 1977), we will not describe them in detail in this paper. The mouth organs are composed of the fused chelicerae (= mandible plate), the apex of which is changed into long stylets. The gnathosoma is accompanied by the pedipalps which contain the spinning apparatus (Fig. 1a). The mouth opening is located on top of the gnathosoma. The podocephalic canal runs as a cuticular depression along the dorsal side of the gnathosoma and carries the salivary gland secretions to the mouth opening (Fig. 1b). At the time of food uptake the animals are immobile. If they are fixed at this moment, the cuticular structures surrounding the apex of the gnathosoma are expanded. These structures consist of four outer cuticular lobes on the ventral part of the gnathosoma and four inner lobes surrounding the mouth opening on its ventral side (Fig. 1a, b). While not feeding the outer
Fig. 1a. — Gnathosoma fixed during active feeding. Circumoral lobes (CS) unfolded, mouth opening (MO) visible. Pedipalpus (PE), seta (SE), gnathosoma (GN).

Fig. 1b. — As fig. 1a. Higher magnification of the gnathosoma. Outer circumoral lobes (OL) unfolded, inner lobes (IL) surrounding the mouth opening (MO). Stylets (ST) withdrawn. Podocephalic canal (PC) in the dorsal midline of the gnathosoma. Pedipalpes (PE).

Fig. 2. — Gnathosoma in resting position. Circumoral lobes (CS) adhered, mouth opening closed, stylet opening (STO, arrow).
cuticular lobes are held tightly against the gnathosoma: the mouth opening and the podocephalic canal are closed (Fig. 2). In fixed animals the stylets are always drawn back.

**Pharynx and Esophagus**

The digestive tract of *Tetranychus urticae* possesses more or less morphologically distinct regions: pharynx, esophagus, ventriculus with caeca (= midgut), and hindgut with anus. The mouth opening is followed by a sclerotized pharynx (Fig. 3), including the pharyngeal sucker. Next is a less sclerotized region, the esophagus, which passes through the gnathosoma. It pierces the nervous system and runs ventrally into the ventriculus, the unpaired vesicular part of the midgut (Fig. 4). A cross-section through the anterior gnathosoma shows the position of the wide pharynx, including the sucker (Fig. 10a). Dorsally the stylets and the podocephalic canal are visible. The pharynx lumen is lined with a thick cuticle. The stylets are situated in a channel dorsal to the pharynx, enclosing nerve fibres (Fig. 10b). They cover the podocephalic canal which is a cuticular depression. The canal shifts downwards in the region where the stylets penetrate the mandibular plate and divides in the latitude of coxa I into its different ducts. The pharynx is followed by the esophagus which is surrounded anteriorly by the silk gland and caudally by the nervous system (Fig. 11). The esophagus is composed of only a few cells and lined by a thin cuticular innermost layer. This cuticle is very loose but covered with an electron dense layer. Aside from the differently shaped mitochondria the organelles are similar to that of the hypodermis: nuclei, few rER cisternae and storage products (Fig. 11). Where the esophagus joins the ventriculus a valve is formed (Fig. 12). Starch and thylakoid granules are sometimes found in the esophageal lumen.

![Fig. 3. Cross section of pharynx (PHA) inside the gnathosoma. Sucker (S), stylets (ST). Pedipalpes (PE) with silk glands (SG). Terminal silk gland bag (TSG).](image)

![Fig. 4. Diagram of the digestive tract showing the position of the light microscopical cross sections and summarizing the pathway of food through the alimentary canal as observed in serial sections. The esophagus runs ventrally into the ventriculus, where three cranial and two caudal caeca terminate (stippled). Between the two caudal caeca the hindgut (not stippled). The anus is formed as a ventral slit. Numbers and arrows indicate the stage of food transport and digestion.](image)

1. passage of food material into the ventriculus
2. dispersion of food into the caeca and uptake by phagocytes
3. return of metabolised material inside the phagocytes into the ventriculus
4. passage of excretory material into the hindgut
5. exit of excreta through the hindgut by formation of excretory balls.
FIG. 5. — Cross section of cranial caeca. Epithelium without protrusions. Phagocytes (PH) in different developmental stages \((x - x_3)\) lie close to the epithelium (arrow).

FIG. 6. — Cross section of the ventriculus. Ventral epithelium vacuolated (arrow). Phagocytes (PH), esophageal valve (double arrow), silk gland (SG), nervous system (NS), ovary (Ov).

FIG. 7. — Cross section of the ventriculus at the level of the caudal caeca. Ventral epithelium vacuolated (arrow), lateral epithelium with small protrusions (double arrow), epithelium adjacent the hindgut (HG) with excreted, refractive substances ( ), ovary (Ov).

FIG. 8. — Cross section of the anterior caudal caeca. Epithelial cells with protrusions (arrow). Epithelium adjacent the hindgut (HG) with few excreted cristals (double arrow), ovary (Ov), previtellogenic region.

FIG. 9. — Cross section of the posterior caudal caeca. Lumen (LU) filled with phagocytes (PH). Cells adjacent the hindgut (HG) with excreted material (arrow). Anus blister (AB, Analblase).
Fig. 10. — a. Stylets (ST) in their channel (SC). Underneath the looped podocephalic canal (PC) which is therefore cut twice. Pharynx lumen (PLU) with sucker (S) surrounded by a thick cuticle (CU) with a vacuolated hypodermis (HY).

b. High magnification of a cross section of the stylets with central nerve fibers (NF).

Fig. 11. — Cross section of the esophagus. Lumen (LU) with nutritive material (starch). Loose chitinisation with an electron dense layer lining the lumen (arrow). Mitochondria (MI).

Fig. 12. — Cross section of the esophageal valve. Lumen (LU) with partly digested chloroplasts (Ch). Surrounding epithelium (MGE) highly vacuolated. Midgut lumen (MGLU), Nucleus (N).
Fig. 13. — Ventricular epithelial cell. Nucleus (N) surrounded by mitochondria (MI) and ER cisternae (arrow).

Fig. 14. — Cranial caecal cell. Long ER cisternae (ER), mitochondria (MI) and vesicles (arrow). Cell borders (CB) formed of junctional complexes.

Fig. 15. — Anterior caudal caecal epithelium. Rough ER cisternae (ER) densely packed. Mitochondria (MI) surrounding the nucleus (N), vacuoles (V).
FIG. 16. — Early intracellular digestion. Amylaceous phagocyte (St) with inclusions (arrow). Nucleus (N) with a large nucleolus (NU) and condensed chromatine. Mitochondria (MI), ER cisternae (ER) and lipid droplets (L).

FIG. 17. — Amylaceous phagocyte in high magnification. Central vacuole (V) filled with starch granules in different stages of digestion (St 1-3). Cytoplasmic margin (CPM) enclosing mitochondria (MI) and ER.

FIG. 18. — Phagocyte with uptaken thylakoids. Vacuoles (V) with thylakoid granules (T) and electron dense inclusions (IN). Lipid droplets (L), Mitochondria (MI).

FIG. 19. — Phagocyte with uptaken thylakoids. Vacuoles (V) with condensed thylakoids (T) surrounded by cisternae of the rough ER.

FIG. 20. — Phagocyte with uptaken thylakoids. Central vacuole filled with partly digested thylakoids (T). Cytoplasm (CP) enclosing mitochondria (MI) and vesicles (arrow).
Ventriculus and Caeca

The ventriculus is the unpaired part of the midgut. Five caeca, two paired and one unpaired, terminate in the ventriculus: three run cranially and two caudally (Fig. 4). The lobed posterior caecum, which tightly encircles the oocytes, has two lobes, which may indicate that the posterior caecum was originally double. In the midline between the caudal caeca, the hindgut runs caudally, curving down in the posterior opisthosoma and emptying at the ventrally situated anus (Fig. 4).

Histological differences exist between the ventricular epithelium and its five caeca and the midgut epithelium adjacent the hindgut. The ventral ventricular epithelium encircling vitellogenic oocytes is highly vacuolated, whereas that of the lateral and dorsal walls is very dense (Fig. 6). Cytoplasmic protrusions as observed in the caecal epithelial cells are absent in the ventriculus and also in the cranial caeca (Fig. 5). The epithelium as shown under the electron microscope is formed of columnar cells in which dense cytoplasm, mitochondria and ER are located (Fig. 13). The nucleus is surrounded by mitochondria. Lysosomes are absent. The condensed nucleolus, a large number of free and ER-bound ribosomes and ER- and Golgi- vesicles indicate a synthetic function of these cells. The vacuolation of the ventral ventricular epithelium is due to high content of lipid droplets and other storage vesicles. The epithelium of the caudal caeca show ventral columnar and granular-vesicular cells (Fig. 8), although they do not differ essentially in their fine structure from those observed in the ventriculus. Nevertheless there are widespread ER-cisternae (Fig. 14) and a variable number of different vacuoles containing storage products (Fig. 15). In the blind closed caudal part, the lateral and laterodorsal cells of these caeca form protrusions into the lumen. Cells lying in the midgut lumen (Fig. 8, 9) differ from the other epithelial cells in their organell contents and inclusions (Fig. 16). Aside from a nucleus and few small mitochondria, lipid droplets, starch and vacuoles containing thylakoids can be observed.

Under the light microscope a developmental sequence of phagocytes released from the midgut epithelium can be established examining serial sections to their different staining behaviour. First a dark blue colouring of the whole cell can be observed while the phagocytes are lying in the caudal caeca (Fig. 9). Cranially the cells enlarge continuously and become light blue due to the development of a great central vacuole which is surrounded by a small cytoplasmic margin (Fig. 6, 7). These dark blue phagocytes, which are found in the blind end of the caudal caeca, do not differ essentially in their fine structure from the epithelial cells described above. They exhibit a more electron transparent cytoplasm and more vesicles than the epithelial cells. In the middle of the caudal caeca two types of phagocytes can be observed: one type phagocytizes starch to a great extent, so that only a thin cytoplasmic margin surrounds the central vacuole (Fig. 17). Cisternae of rough ER and vacuoles with different contents are packed loosely in the cytoplasm. The other type is characterised by a great number of thylakoid granules, which are condensed in vacuoles (Fig. 18, 19). Different stages of thylakoid digestion can be observed in the caecal lumen, although the fine structural way is not yet clear. The vacuoles filled with thylakoid granules are first surrounded by lipid droplets (Fig. 18). Condensation then begins, so that the contents are not easily discernible. A network of rough ER fills the spaces between the vacuoles (Fig. 19). The nearer the phagocytes are to the ventriculus the greater are the cytoplasmic reductions including a break down of its organelles. Residues of undigested thylakoid granules are concentrated in a central vacuole (Fig. 20). Phagocytes which are found near the hindgut show a cytoplasm reduced to a small margin, which surrounds the central vacuole. This vacuole contains fine granular, digested material and excretory products of different appearance (Fig. 21). Differences between the two types of phagocytes cannot be
observed in this stage of digestion. Before passing through the hindgut the cytoplasmic margin may break and the central vacuole empties its contents into the midgut lumen. Fig. 4 is summarizing the steps of food distribution and digestion observed thus far. The diagram is based on results of serial sections of many feeding and not feeding animals. The histological observations indicate a continuous process of digestion which enables us to sum up in the presented scheme.

Epithelial cells of the midgut close to the hindgut have another appearance. They are flat and contain numerous vacuoles filled with refractive material when examined under the light microscope. As stated earlier (Mothes et al., 1980) these cells are able to store excretory products. For that purpose the cells produce branches into the midgut lumen (Fig. 22). Despite the long branches no endocytotic activities are found. Descriptions of the fine structure of these cells, the way in which excrets are formed, and the fine structure and function of the hindgut are found elsewhere (Mothes et al., 1980).

**DISCUSSION**

When they start feeding all tetranychids pierce their host plant with their stylets which originate in the apex of the chelicerae. The location of a suitable place is possibly determined by nerve fibres which suggest chemo- or mechanoreceptors at the tips of the stylets.
The gnathosoma is pressed onto the wound and a partial vacuum is formed by withdrawing the pharyngeal sucker described by Blauvelt (1945). This mechanism enables the animal to feed on plant cell components without any sucking process. The differentiation of the gnathosomal apex must be an adaptation for this sucking event. The circumoral lobes (Akimov et al., 1977) ensure a good seal between the leaf and the gnathosoma, whereas at the same time the strong cuticle prevents a collapse during the partial vacuum.

On the one side the pharyngeal sucker closes the pharynx when not feeding, while on the other side it produces the partial vacuum by withdrawing, which enables the animal to feed continuously. Before food passes through the midgut, enzymes of the salivary glands must have destroyed the outer chloroplasts membrane, because inside the esophagus and ventriculus only thylakoid granules can be found. The components of the salivary secretions have not been demonstrated thus far and could, of course, not be demonstrated with the electron microscope.

According to Wiesmann (1968) the food of Tetranychus urticae consists of the following constituents beside water: chlorophyll, proteins, lipoids, carbohydrates and some inorganic acids. These in size relatively small food components surely require a specialised enzyme content. After passing through the pharynx and esophagus the ingredients reach the ventriculus and thereafter the posterior part of the caudal caeca, where enzyme activities can be found (Akimov et al., 1977). Our histological observations on the fine structure of the midgut epithelium indicate that protein synthesis occurs. If these proteins are enzymes and if they are secreted into the midgut lumen could not be demonstrated.

The way in which the cranial caeca participate in the processes of digestion could not be determined, since enzymatic activities are not found (Akimov et al., 1977) and our electron microscopical investigation do not permit conclusions. Excretory material is not formed and cellular protrusions, which become free phagocytes are not developed. The organellar contents may indicate a stage of protein synthesis (rough ER, Golgi-apparatus) although the nature of these proteins was not clear. Perhaps these caeca have the function of food distribution and supply to the prosomal organs.

Our results show that the content of ER is similar in the ventricular epithelium and the caeca, and depends on the physiological condition of the animal. According to Hughes (1950) the caeca are hepatopancreatic digestive glands with vesicular cells enclosing digestive enzymes. This is in contrary to Ehara (1960) who described a proximal reticular and a distal vesicular appearance of the caecal epithelium. Fine structural investigations however show that such a distinct difference in cell types should not be stated.

Depending on the type of available food a deposition of lipids may occur in all midgut cells. Even an elimination with hindgut excreta sometimes happens (McEnroe, 1961b; Mothes, unpubl.). Glycogen was not detected electron microscopically or histochemically in the digestive tract. Protein and glycogen stores are found only in four special cells, two of which are situated lateral to the dorsal hindgut epithelium and two lateroventral to the ovary of the female and the middle caudal caeca of the male (Mothes, unpubl.). The above mentioned observations support the results of Kötter (1978) who determined the nature of storage products of Tetranychus urticae biochemically. Akimov et al. (1977) localised proteases with an optimum of pH 5.0 in the midgut epithelium and suggested a special adaptation of the amylases for the specific host plant. Our investigations let us suppose that the activity of amylases may be bound on the free phagocytes originating in epithelial cells, as are parts of the enzyme system for the degradation of chlorophyll and cell membranes because of the site of intracellular digestion.

We agree with the opinion of Akimov et al. (1977), Prasse (1968), Wiesmann (1968) and Wright et al. (1964, in Anystis) that there are extreme functional changes in the midgut epi-
thelium which show two cell types, although few more cell organelles than absolutely necessary are present. Some of the epithelial cells protrude in the middle part of the caudal caeca, but the main part are found in the blind ends. This, and the digestive stages in phagocytes in the different parts of the midgut observed in serial sections of many animals, lead us to the conclusion, that the midgut cells go through a functional sequence. These stages can be shown electron microscopically. First the midgut cells contain a dense network or rough ER, which becomes vesicular at the beginning of protrusion (stage of protein synthesis). Whilst still in the epithelium some cells may absorb fatty acids, amino acids and carbohydrates, which could, of course not be examined in the electron microscope, and transform them into storage products. These stores can be observed in electron microscopical pictures (stage of resorption and storage). This is in contrary to McEnroe (1961b) who demonstrated the elimination of soluble low molecular weight material by a direct route from the esophagus to the hindgut. Because of the food components, which *Tetranychus urticae* ingests (see above), such a pathway may not be possible without starvation of the animal. Since we do not know what food components are the bases of the metabolism we are not able to determine their utilization and transformation into storage products or incorporation in species specific body material.

After protrusion these cells or cell parts leave the epithelium and become free phagocytes of the midgut where they phagocytize thylakoid granules and starch. After degradation of these food components, low molecular weight material may be released from phagocytes, which is used not only by metabolically active organs as oocytes but also by other cells for the formation of storage material as proteins and glycogen, which can be observed to a high amount soon after feeding in the specialized cells. Digestion of the chloroplast stroma, which was described by Bekker (1956) was not observed by us. On the contrary, the animals are able to digest whole chloroplasts, because no membrane residues were found in the excrements. If the phagocytes derive from whole epithelial cells (holocrine secretion; Blauvelt, 1946) or if they are only apical cell parts (apocrine secretion) could not be determined satisfactory. Although the demonstration of nuclei in phagocytes may indicate that they derive from holocrine secretion. Sites, where these cells are regenerated could not be observed thus far. Phagocytes seem to be specialized on the digestions of one food component (thylakoids or starch). If this implies that only one degradation enzyme system is enclosed in the special phagocytes could not be demonstrated.

In this system of digestion the alimentary canal has a distributory function, because it is in direct contact with all other organs and may serve to replace the deficient hemolymph system. Previtellogenic and early vitellogenic oocytes are in direct contact with the midgut lumen (Mothes et al., 1981). The anterior caeca provide the silk gland and prosomal glands, whereas the testis is in contact with the epithelium of the posterior caeca. In these regions of contact the midgut epithelial cells show some differentiation. These manifest, for example, in the highly vacuolated cells of the ventral posterior caeca which lie in close contact to vitellogenic oocytes.

At the end of their life span the phagocytes become excretory cells by passing through the hindgut laden with excretory materials (stage of excretion). The midgut food balls passing through the hindgut, which were described by Blauvelt (1945) in living animals represent phagocytes which seem to be refractive when examined under the light microscope presumably having a high content of excreted materials. This material is condensed inside the hindgut to excretory balls and eliminated by the anus (histology of the hindgut and the anus is described elsewhere, Mothes et al., 1980).

Subsequent investigations must clarify which enzyme systems are present, where they are located in the alimentary canal and which
metabolic pathways are essentially for this mite. In doing so we must consider, that *Tetranychus urticae* has no peritrophic membrane and so no protection of the midgut cells against enzymes seems to be necessary. Perhaps new knowledge about digestive processes and the break down of the thylakoid granules may be expected, which should also be of interest for botanical investigations.

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