

THE STRUCTURE AND FUNCTION OF THE ALIMENTARY CANAL
IN *HISTIOGASTER CARPIO* (KRAMER, 1881)
ACARI — SARCOPTIFORMES

BY

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INTRODUCTION

Previous descriptions of the anatomy of the alimentary canal of Sarcoptiform mites have included a number of species, more recently notably, *Glycyphagus domesticus* De Geer (HUGHES and HUGHES, 1938), *Tyroglyphus farinae* Linn. (HUGHES, 1950), *Histiostoma laboratorium* Hughes (PERRON, 1954), *Caloglyphus mycophagus* Megnin (ROHDE and OEMICK, 1967), *Caloglyphus berlesii* Michael and *Caloglyphus michaeli* Oud (PRASSÉ, 1967), *Acarus farris* (Oud) (BOCZEK, JURA and KRZYSZTOFOWICZ, 1969). There is a considerable variation in the nomenclature of the organs described and little attention has been paid to function. The reviews of MICHAEL (1901, 1903), VITZHUM (1943) and HUGHES (1959) have dealt with functional morphology and anatomy, and HUGHES (1950), has studied the physiology of the alimentary canal in *T. farinae*.

The present work describes the anatomy and histology of the gut of another acarid mite, *Histiogaster carpio* (Kramer), relating this to function as far as possible, and attempts to clarify some of the present confusion in the literature on the nomenclature of the gut in Sarcoptiform mites.

H. carpio has been described by WOODRING (1966) and recorded from sewage filter beds by SOLBÉ, WILLIAMS and ROBERTS (1967).

MATERIALS AND METHODS

Mites were collected regularly from the zoogloal film surrounding the surface stones on the filter beds at the Esholt (Bradford) Sewage Works. They were normally fixed within an hour or two of collection or kept alive and starved in cells previously described by BAKER (1970 a). Fixation for routine histology was in the Dubosq-Brazil modification of Bouins fluid, in formalin for sections to be subsequently stained by the Feulgen method, and in 10 % formalin buffered to pH 7.0 and held at 6°C for enzyme histochemistry. Mites were orientated prior to sectioning

using the method previously described (BAKER, 1970 *b*). For enzyme studies, individual mites or blocks were rapidly dehydrated through graded acetone solutions at 6°C, cleared in xylol at 20°C and impregnated and embedded in low melting point paraffin wax (45°C). Sections were normally cut at 10 μ . Heat inactivated controls were used in the histochemical work.

In addition to Delafield's haematoxylin and eosin, sections were stained in periodic acid Schiff and fast green, and Feulgen and fast green. The following histochemical methods were used : the indoxyl acetate method for non specific esterase (HOLT and WITHERS, 1952), the L-leucyl- β naphthylamide method for the leucine aminopeptidase reaction (BURSTONE and FOLK, 1956), the azo dye method for acid phosphatase (BURSTONE, 1958) and the calcium salt method for alkaline phosphatase (GOMORI, 1952).

OBSERVATIONS

The terminology of the gut in Sarcoptiform mites is confused and attempts by HUGHES (1950, 1959) to standardize this have met with only partial success. Table I is included to indicate the variable terminology which has been used. The present study lends support to the general nomenclature adopted by HUGHES (1950, 1959) and except where stated, follows this in the text.

TABLE I. — Comparison of the terminology used to describe certain parts of the alimentary canal in Sarcoptiform mites.

Akimov (1973)	ventriculus	colon	post colon	rectum
Boczek, Jura et al. (1969)	stomach	ileum	colon	rectum
Hughes (1959)	stomach	colon	post colon	rectum
Michael (1901)	midgut	colon	rectum	rectum
Rohde and Oemick (1967)	stomach	colon	rectum	
Vitzhum (1943)	midgut	"Dunndarm" small intestine	colon	rectum

Anatomy and histology of the alimentary canal

The pharynx, lying on the ventral side of the gnathosoma, is gently curved in longitudinal section with a thickly sclerotized wall. Inserted on to the roof of the pharynx are five sets of dilator muscles originating on the internal skeleton of the sub-cheliceral shelf.

The oesophagus runs almost horizontally backwards, through the brain, to open into the antero-ventral portion of the stomach. Paired oesophageal valves project into the lumen of the stomach, and prevent food being regurgitated. The oesophagus is approximately 130 μ m long and 25 μ m wide and has a thin cuticular lining. The lumen is often packed with food which gives a positive reaction to the P.A.S. test. A strong acid phosphatase reaction is seen in the

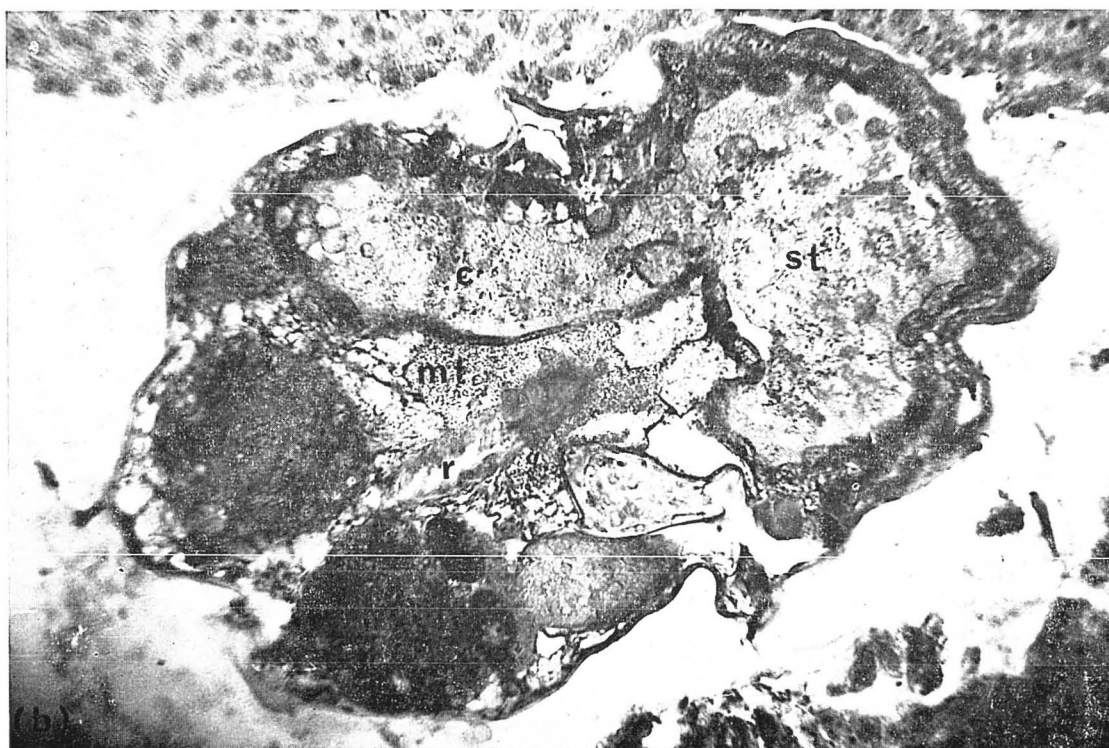
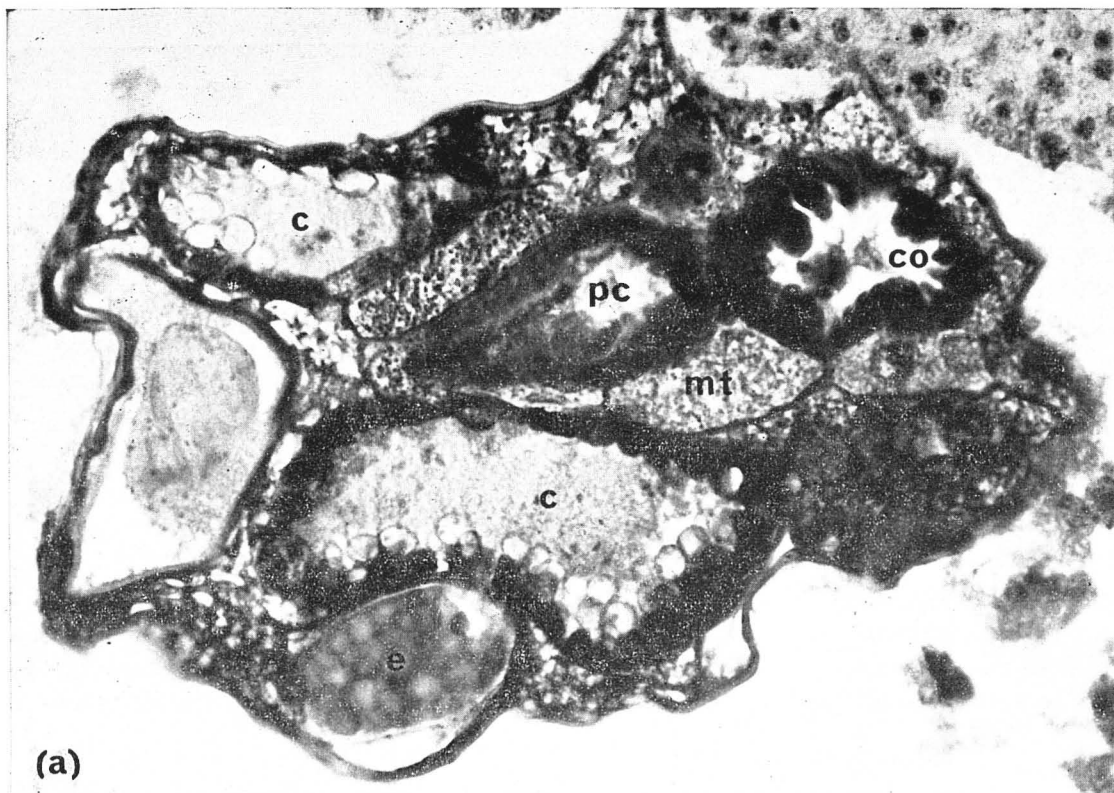


PLATE I :

- (a) Horizontal longitudinal section of the body of a female *Histiogaster carpio* to show the following parts of the alimentary canal. c., caecum ; co., colon ; e., egg ; p.c., post colon ; mt., malphigian tubule. Haematoxylin and eosin. $\times 245$.
- (b) Horizontal longitudinal section of the body of the same animal as (a) from a more ventral aspect. c., caecum ; mt., malphigian tubule ; r., rectum ; st., stomach. Haematoxylin and eosin. $\times 220$.

oesophagus both in whole mounts and in sections of mites starved for six days to empty the gut and then fed for one hour on boiled yeast (Plate II (a)).

The stomach and caeca (= midgut) are extensive organs lying mainly in the ventral region but the caeca are reflected backwards dorsally.

There is a marked variation in cell morphology in the midgut. The gastrodermis consists of a single layer of squamous, dome, or cuboid cells lying on a basement membrane. The cells, 4-20 μm high, are highly vacuolated and have a distinct nucleus which lies in the lower half of the cell. (Plate IV (a)). The luminal surface consists of a plasma membrane composed of microvilli which appear to form a continuous lining.

The lumen of the stomach is normally packed with bacteria, mainly coccoid and bacillus forms but also contains much larger bodies having a similar form to the epithelial cells. It is assumed that these have become detached from the midgut epithelium and play a role in the digestive process. The stomach epithelium extends into the midgut caeca and forms part of its inner and antero-lateral walls.

The posterior and outer halves of the caeca have a morphologically distinct structure. Interspersed between vacuolated, often pointed, columnar cells (20 to 30 μm in height) are some very large claviform cells (50 to 75 μm in height). The distal portions of these have an apical swelling or blister which projects deeply into the lumen of the caecum. The distal portions constrict, nipping off spheres into the lumen which are 12 to 20 μm in diameter. These spheres are without nuclei and lie, sometimes in very large numbers, almost filling the caecal cavities. Unlike the cells forming the wall of the stomach, the luminal surface of the caeca lacks microvilli. (Plate IV (b)).

The colon (ileum or small intestine of other workers — see Discussion) lies in a dorsal position above the stomach, roughly at the point where the caeca below it divide into two. It normally contains a bolus of food. The wall is composed of a lining of closely packed columnar cells, approximately 15 to 30 μm in height but with nuclei at different levels forming a pseudo-stratified epithelium, subject to stretching when a bolus is present. In such cases the wall has a more flattened appearance. The epithelial cells do not produce the characteristic blebs seen in the caecal epithelium. The bolus shows a strongly positive reaction to the tests for acid and alkaline phosphatase, non-specific esterase and P.A.S. but there was no reaction for these enzymes in the colon wall.

The post colon (HUGHES, 1950) lies between the colon and rectum. (Plate I (a)). The lining is composed of cells, 18 μm tall with an inner brush border approximately 9 μm high. The cells have a distinct centrally placed nucleus. The organ is partly surrounded by the granular portion of the Malpighian tubules. There is a strong alkaline phosphatase reaction in the area of the brush border, a positive P.A.S. reaction and traces of acid phosphatase are found in the lumen and wall, but no non specific esterase has been detected in this organ.

Faecal pellets in this region appear to have lost much of their earlier enzyme activity.

The posterior portion of the alimentary canal, the rectum, runs down from the post-colon to the anus, forming the rectum. This is a straight tube approximately 160 μm in length and 30 μm in diameter with a narrow lumen lined by an indistinct cellular structure, probably a syncytium, covered on the inner side by a thin cuticular lining (Plates I (a), I (b), II (b)). The anus has a pair of anal valves, the cuticle of which is continuous with the chitinous intima of the rectum.

The Malpighian tubules arise at the junction of the colon and post-colon and run backwards dorsally on either side of the gut as far as the rectum. They are approximately 200 μm long and 40 μm wide, and composed of two distinct parts, a proximal portion which has few granules and a larger distal portion containing numerous granules 1 to 3 μm in diameter.

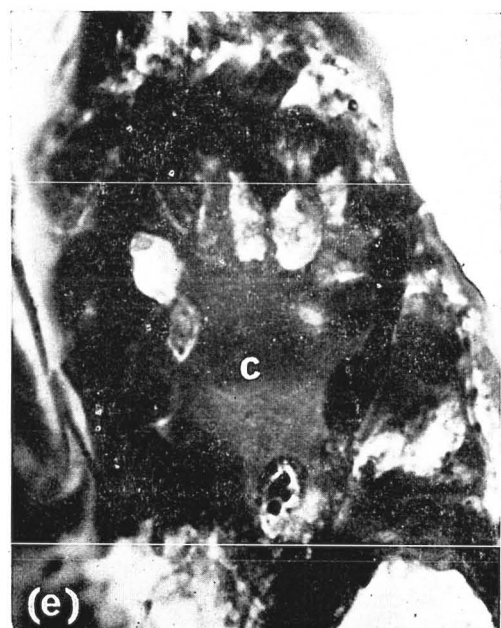
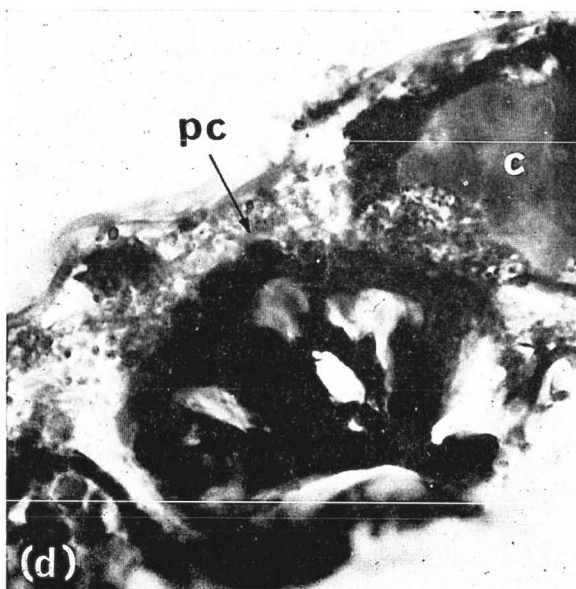
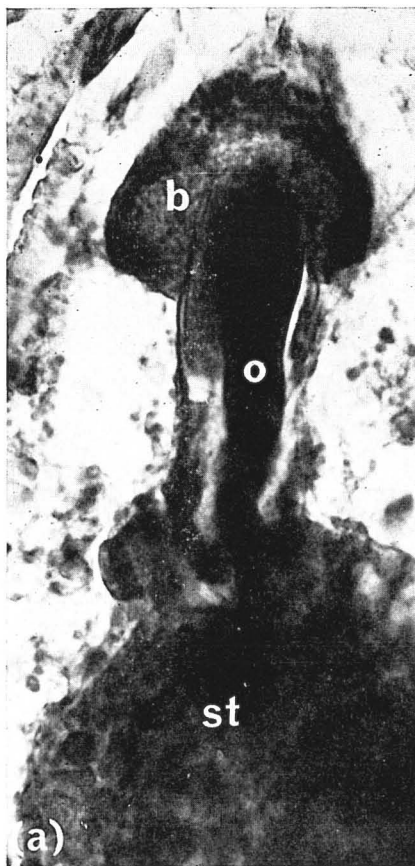


PLATE II :

- (a) Horizontal longitudinal section of the mite, starved for seven days and then fed on boiled yeast cells. The stomach is seen filled with yeast cells and a strong acid phosphatase reaction is present in the oesophagus and in the area of the stomach adjacent to the oesophagus. b., brain ; o., oesophagus ; st., stomach. $\times 645$.
- (b) High power horizontal longitudinal section of the rectum. r., lumen of the rectum. Alkaline phosphatase and nuclear fast red. $\times 595$.
- (c) Transverse section showing non specific esterase reaction in the claviform cells of the wall of the gut caecum. $\times 465$.
- (d) Transverse section showing alkaline phosphatase reaction in the post colon. $\times 500$.
- (e) Transverse section showing alkaline phosphatase reaction in the wall of the gut caecum. c., lumen of the caecum on one side. $\times 595$.

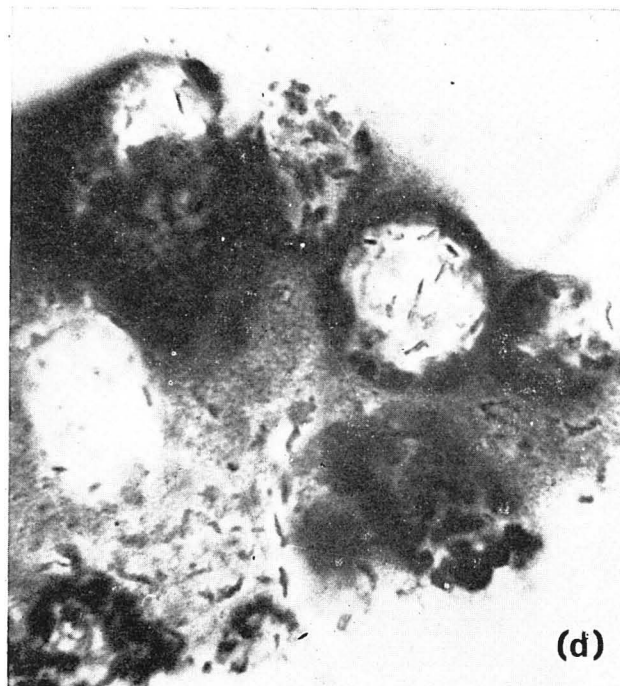
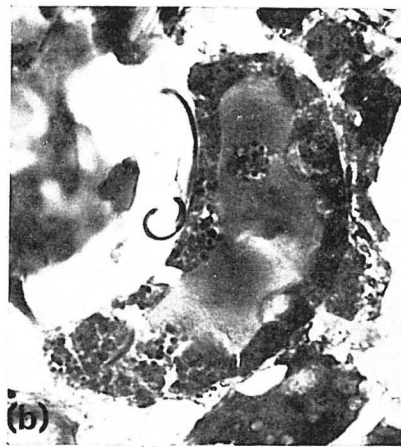
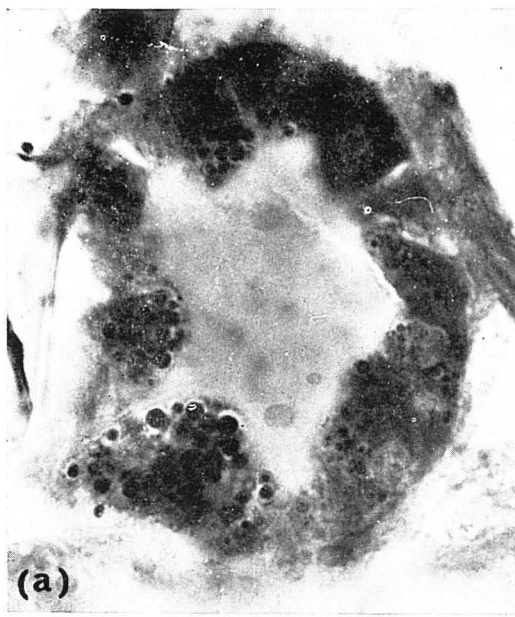


PLATE III :

- (a) Transverse section of the anterior end of the gut caecum of *Histiogaster carpio* showing intense alkaline phosphatase activity in the epithelial layer of the wall. Gomori's calcium salt method. $\times 1000$.
- (b) Transverse section of the gut caecum of the same animal taken more posteriorly showing intense alkaline phosphatase activity in certain of the cells of the epithelium, the growth of two ball shaped cells projecting into the lumen and an isolated sphere "cell" lying in the lumen. Gomori's calcium salt method. $\times 530$.
- (c) Transverse section of the same animal as (a) and (b) taken from the posterior end of the gut caecum. The outer wall shows a widespread proliferation of clavate vacuolated cells projecting deeply into the lumen, the distal ends of which lack alkaline phosphatase activity. Gomori's calcium salt method. $\times 460$.
- (d) Transverse section of part of the gut caecum of *Histiogaster carpio* showing non specific esterase activity around the periphery of isolated sphere "cells" and rod shaped bacteria in the lumen and also within the isolated spheres. Indoxyl acetate method for esterases. $\times 1200$.

Occurrence and distribution of certain enzymes in the midgut

The cells lining the walls of the caeca and stomach show considerable variations both in their form and in the distribution of various enzymes within them. It is clear that this variation of structure equally applies to the different regions of the midgut of the same animal.

Alkaline phosphatase

Plate III (a, b and c) shows a series of sections taken from the midgut of the same animal passing progressively from the anterior to the posterior end. At the anterior end, the tall claviform vacuolated cells are absent, the wall being composed of cells approximately 4 to 20 μm in height and 6 to 26 μm across, loaded with sites of alkaline phosphatase activity (Plate III (a)). On the posterior and outer walls of the caeca are large numbers of tall club shaped cells projecting deeply into the lumen of the caecum (Plate III (c)). Their height is very variable, roughly between 50 to 75 μm and they are approximately 6 to 14 μm across. The apical portions of these claviform cells lack alkaline phosphatase activity, which is confined to the cells of lower height as Plate III (b and c) illustrates.

Nonspecific esterase

The claviform cells of the midgut wall are loaded with sites of non specific esterase activity as Plate II (c) illustrates. Enzyme sites are also found around the periphery of the isolated spheres. Plate III (d) illustrates the distribution of non specific esterase in these isolated apical spheres. This enzyme is also found in large amounts, both in the lumen of animals fixed immediately after collection and in animals starved for up to seven days.

Acid phosphatase

A strong reaction occurs in the lumen in specimens fixed soon after collection and as a broad band below the outer membrane in the distal portions of the claviform cells forming the caecal wall. Some of the isolated apical spheres are entirely filled with acid phosphatase, others show a broad band of activity as described above, whilst others appear to lack this enzyme. Like non specific esterase, the reaction for acid phosphatase persists in the lumen of animals starved for up to a week.

'Leucine aminopeptidase'

No demonstrable reaction was found for this group of enzymes.

The nutrition of the mite

The sucking pump mechanism produced by the highly muscular pharynx draws in food which passes, probably mixed with salivary secretions, along the oesophagus to the stomach and caeca. Rod shaped bacteria, 2 to 4 μm in length and coccoid forms 1 μm in diameter revealed by the non specific esterase reaction, are present in large numbers in the lumen of the gut caeca.

Bacillus forms are also seen in the distal ends of the club shaped cells and in the isolated spheres of recently fed mites (Plate III (d)).

The bacteria in the lumen are presumed to form the main component of the diet of these animals. Mounts of living animals and squashed preparations indicated the presence also of unicellular algae, probably coccoid Chlorophyceae or Xanthophyceae but these were not positively observed in sections of the gut.

Although it proved difficult to keep mites alive and starve them sufficiently to completely

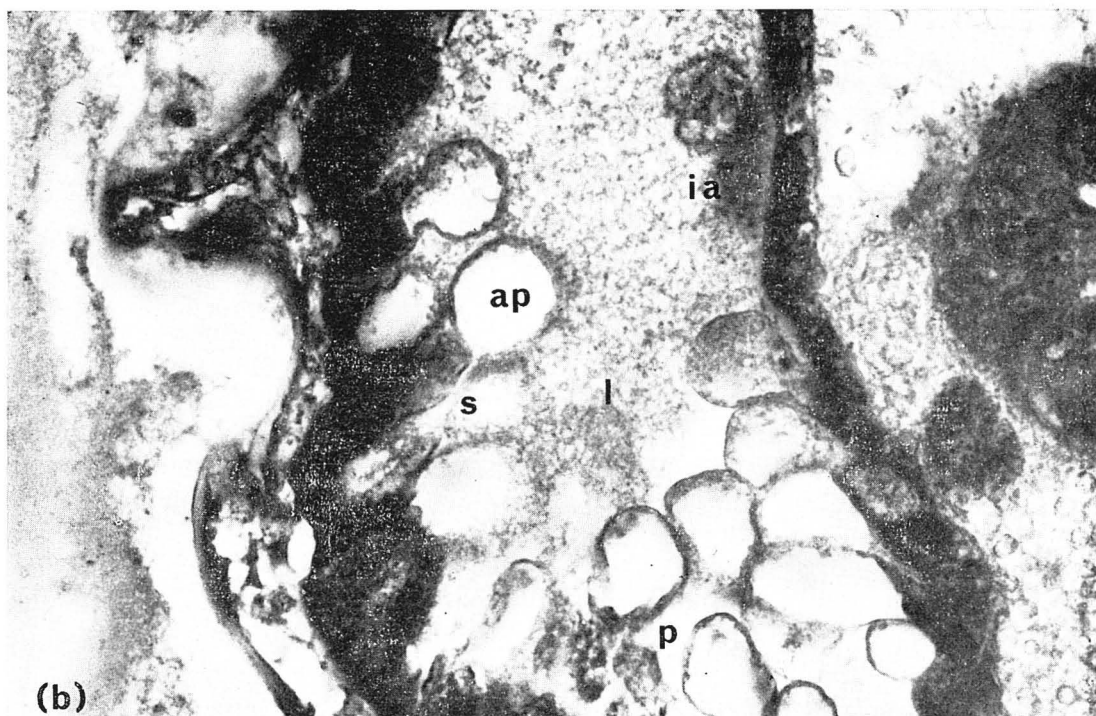
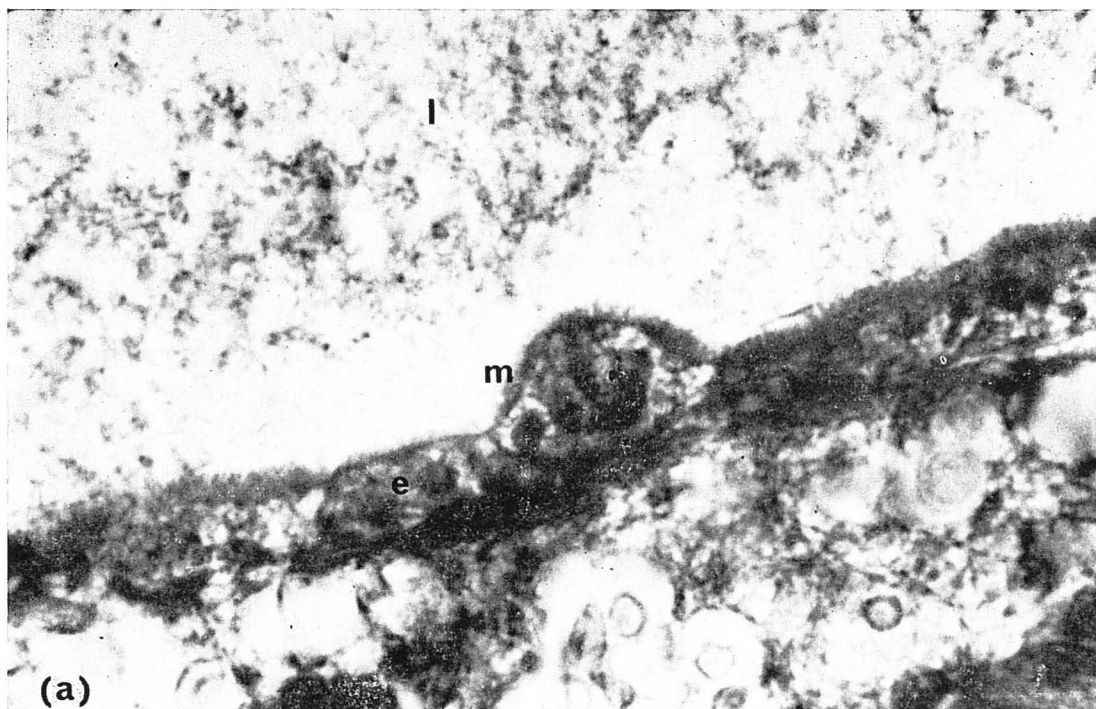


PLATE IV :

- (a) Light micrograph of a vertical longitudinal section of *H. carpio* showing the epithelium of the stomach, the luminal surface of which bears microvilli. A vacuolated dome shaped cell is centrally placed. The lumen is packed with food. e., epithelial cell of gastrodermis ; l., lumen of stomach ; m., microvilli, Haematoxylin and eosin. $\times 1400$.
- (b) Light micrograph of a vertical longitudinal section of the same animal as in IV(a) showing part of the gut caecum of one side. A large number of claviform cells are present, projecting deeply into the lumen. These cells are lacking in the inner anterior portion of the epithelial lining, the structure of which is similar to that of the stomach wall. a.p., apical blister ; i.a., inner anterior portion of the caecum ; l., lumen of the caecum ; p., posterior portion of the caecum ; s., thin narrow stalk attaching apical blister to rest of the claviform cell. Haematoxylin and eosin. $\times 700$.

empty the gut of food, some observations were made after isolating mites in cells for several days without food. During this time the midgut epithelium gradually assumes a more flattened appearance with increasingly fewer club shaped cells and isolated spheres. Patches of taller cells, however, persist, particularly in the dorsal wall of the midgut and the lumen continues to show acid phosphatase and non specific esterase activity during this time.

DISCUSSION

The main areas for the digestion and absorption of food are the stomach and caeca as VIRZHUM (1943), HUGHES (1950, 1959) and PRASSÉ (1967) believed for other Sarcoptiform mites. The strong acid phosphatase activity recorded in the oesophagus was, however, unexpected. RILEY (1972) has recently described esterase activity in the oesophagus of a pentastomid. It is possible that the salivary secretions produce the acid phosphatase reaction, which is still apparent at the oesophageal end of the stomach.

Authors including HUGHES (1950) and PERRON (1954) have assumed that the epithelium of the midgut of Sarcoptiform mites consists of one kind of cell undergoing morphologically distinct phases depending upon their developmental state and reflecting the sequence of digestion and absorption which occurs in this epithelium. PRASSÉ (1967), however, working on *Caloglyphus* spp. describes two kinds of cell in the epithelial layer of the midgut wall which he calls the digestive cell (Verdaumgszelle) and the gland cell (Drüsenzelle). The descriptions he gives appear to fit closely the morphology and distribution of the cell types described in this account. In the case of *H. carpio* it is not yet certain whether they are distinct kinds of cell or merely phases of one cell type but it is clear at least that their morphology suggests functionally distinct roles. PRASSÉ (1967) believed that the large vacuoles in the gland cells of the stomach wall contained digestive enzymes but was not certain whether these cells were absorptive in function. The microvilli and the strong alkaline phosphatase reaction of the stomach epithelial cells of *H. carpio* suggest that they do have this function. PRASSÉ (1967) accepts Michael's view (1901, 1903) that the digestive cells absorb materials from the caecum which are then digested intracellularly. The view held here for *H. carpio* is that although the claviform cells may initially be absorptive cells, the detachable apical portions contain enzymes which are released into the midgut when the spheres disintegrate in the lumen, an interpretation recently proposed by RILEY (1972) working on the pentastomid, *R. sternaes*. In *H. carpio* enzyme sites occur around the periphery of and within the detached spheres which lends support to the view that they play a part in the digestive process. No such spheres were, however, found by HUGHES (1950) in *T. farinae*. He speculated that the distal ends of the club shaped cells produced a digestive enzyme. This view is confirmed in *H. carpio*. Whether, as HUGHES (1950) believed, the enzyme is secreted by passage through the cell membrane or is released, as is believed to be the case in *H. carpio*, when the nipped off apical portions break down in the lumen of the midgut is not yet finally established.

A strong reaction for non specific esterase and acid phosphatase can also be demonstrated in the lumen of the midgut in specimens fixed soon after collection but this is probably largely the result of the presence of stained food rather than an indication of intraluminal digestion. However, specimens starved for seven days continue to show the presence of these enzymes in the midgut lumen. The relative importance of extracellular and intracellular digestion in *H. carpio* is thus still a matter of conjecture.

Bacteria have been identified in large numbers in the lumen of the midgut. Algae may

also form part of the diet. The animal appears to be a general browser on the zoogloal film in sewage filter beds. WOODRING (1963) indicated that most species of acarids ingest a wide range of foods including algae, fungi, yeasts and bacteria and PILLAI and WINSTON (1968) working on *Caloglyphus anomalus* showed that mites could be grown in axenic culture on species of *Bacillus*, *Escherichia* and *Pencillium* grown on artificial media.

The presence of bacillus forms in the midgut cells and isolated spheres is of particular interest. HUGHES (1959) records the presence of the same micro-organisms in the stomach wall of *Ornithonyssus bacoti* and a number of other workers have described rod shaped bodies in the gut wall of other species of mesostigmatid mites. No definite function has been ascribed to them. It is possible we have such a mycetome in the case of *H. carpio* and if this is the case it appears to be the first recorded in the Sarcoptiformes. It seems less likely that bacteria from the lumen are phagocytosed into the midgut cells prior to undergoing intracellular digestion although this possibility can not be ruled out.

The region immediately posterior and dorsal to the stomach is referred to by VITZHUM (1943) as the small intestine (Dünndarm), by BOCZEK, JURA *et al.* (1969) as the ileum and by HUGHES (1950) as the colon. In recently fed mites a food bolus is normally contained in this region and this shows strong enzyme activity as well as a positive P.A.S. reaction but the wall does not appear to secrete non specific esterase or phosphatases. The possibility remains that further digestion may occur within the bolus and that some absorption occurs in this organ. Alternatively the colon may act as a filtering mechanism, separating off and dispensing undigestible food materials. AKIMOV (1973) believes the food bolus is formed of solid substances and fragments of cells and that luminal digestion occurs in the colon. The prolonged presence of food and the pH level which is close to the optimum for the digestive enzymes of mites is quoted in support of this view.

The structure of the colon wall in *H. carpio* is quite unlike that given by HUGHES (1950) for *T. farinae* where it is described as a low flat epithelium. In *H. carpio* this is the condition only when there is a food bolus present.

BOCZEK, JURA *et al.* (1969) and ROHDE and OEMICK (1967) describe two small paired anterior gut caeca in addition to posterior caeca in *A. farvis* and *C. mycophagus* respectively. These have not been observed in the case of *H. carpio* and HUGHES (1959) makes no mention of an anterior pair in acarid mites. ROHDE and OEMICK (1967) seem to have confused the colon and rectum, referring to the latter as having a lining of cells with brush borders. The wall of the rectum in the case of all the other acarid mites studied is without a brush border and lined by a chitinous intima. As a result of this confusion they refer to the origin of the excretory tubules as being from the dorsal side of the rectum rather than between the colon and post colon (terminology of HUGHES, 1950).

The strong alkaline phosphatase reaction associated with the wall of the post colon where there is a distinct brush border, supports the view of HUGHES (1959) that this region is essentially absorptive and almost certainly involves the final absorption of water.

The Malpighian tubules of *H. carpio* have crystalline contents, are well developed and appear functional, unlike those of *T. farinae* (Hughes, 1950) or Sarcoptiform mites in general as described by HUGHES (1959) and VITZHUM (1943).

SUMMARY

The anatomy and histology of the alimentary canal is described in *H. carpio* (Kramer, 1881). Histochemical methods have revealed extensive enzyme activity in the midgut cells and lumen. In addi-

tion, the oesophagus contains acid phosphatase and the wall of the post colon shows strong alkaline phosphatase activity associated with a brush border. The midgut epithelium appears to consist of two main kinds of cell. The stomach wall is composed of cells many of which show strong alkaline phosphatase activity and have microvilli. These are thought to be absorptive in function. The posterior and outer walls of the caeca include large claviform cells with strong esterase activity and there, these cells have a digestive function. Bacteria are found in large numbers in the lumen of the midgut and the mite appears to be a general browser on the zoogloal film surrounding the medium in sewage beds. Bacteria are also found in the cells of the midgut wall and may form a mycetome. Intraluminal and intracellular digestion may occur. Although the food bolus lying in the colon shows enzyme activity, the wall of this organ does not appear to be the site for the production of these enzymes. The Malpighian tubules are well developed, have granular contents and appear functional in this species.

The nomenclature used by various authors to describe the organs of the alimentary canal in Sarcotiform mites is reviewed, illustrating a continuing lack of uniformity and confusion. The terminology adopted by HUGHES (1950, 1959) is recommended for the gut of the Sarcotiformes.

ZUSAMMENFASSUNG

Die Anatomie und Histologie des Darmsystems wird in *H. carpio* (Kramer, 1881) beschrieben. Histochemische Verfahren haben umfassende Tätigkeit der Enzyme in den Zellen des Mitteldarms und dem Lumen enthüllt. Zusätzlich enthält das Oesophagus Phosphatase-Säure, und die Darmwand des Postcolon zeigt starke alkalische Phosphatase-Tätigkeit, zugesellt ein Rhabdiorium. Die Epithelzellen des Mitteldarms scheinen aus zwei Hauptarten von Zellen zu bestehen. Die Magenwand ist aus Zellen zusammengesetzt, von denen viele starke Phosphatase-Tätigkeit zeigen, und microvilli haben. Diese Zellen sollen in ihrer Funktion resorptiv tätig sein. Die Hinter- und Aussenwände des Caecum beinhalten lange, keulenförmige Zellen mit starker Esterase-Tätigkeit, und in diesem Fall haben die Zellen eine Verdauungsfunktion. Bakterien werden in grosser Anzahl im Darmlumen gefunden und die Milben scheinen Fütterer des Zoogloalfilm zu sein, der das Medium in der Kläranlagen umgibt. Ferner werden Bakterien in den Zellen der Mitteldarmwand gefunden, diese Bakterien können ein Mycetom bilden. Intraluminäre und intrazelluläre Verdauung kann vorkommen. Obgleich der Nahrungsbolus im Kolon Enzymaktivität aufweist, haben diese Enzyme ihren Ursprung nicht an der Wand dieses Organs. Die Malpighischen Tabule sind gut entwickelt, der Inhalt ist körnig und sie sind in diesem Tier, tätig.

Die Nomenklatur, die von verschiedenen Autoren angewendet wird, um die Organe des Nahrungskanals der sarcotiformen Milben, erläutert ein fortwährender Mangel an Gleichförmigkeit und Verwirrung, so wird rezensiert. Die Terminologie — dieser Annahme ist HUGHES (1950, 1959) — wird für den Darm der sarcotiformen Milben empfohlen.

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