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Contribution to the Study of Digestion in Ticks: Histology and Fine Structure of the Midgut Ephithelium of *Ornithodorus moubata*, Murray (Ixodoidea, Argasidae)

OLIVIER GRANDJEAN * and ANDRÉ AESCHLIMANN *

1. Introduction

Ornithodorus moubata is known to be a vector of African Relapsing Fever (GEIGY & HERBIG, 1955). Study of its digestion should, therefore, facilitate investigation of the life-cycle of the pathogenic agents carried by the tick. The bloodmeal plays an important role in the whole biology of the tick. Every moult during the development of the tick has normally to be preceded by the intake of blood. *O. moubata* is, however, an exception to the general rule. The first stage – a hexapodous larva – ends, without previous nutrition, with a moult leading to the first nymphal stage. The larvae of *O. moubata* and *O. savignyi* neither move nor feed. As far as we know this peculiarity is limited to these two species.

The yolk reserves which are provided by the mother, are deposited in the midgut during embryogenesis in sufficient quantity for the larval needs (AESCHLIMANN, 1958). Usually there are four to seven more moults up to the adult form and all of these must be preceded by a bloodmeal. Bloodmeals are of short duration and the ticks detach themselves from their host before moulting. Generally, a host of the same species is chosen for every bloodmeal and *O. moubata* is therefore considered as a polyphasic and monotropic Argasid tick. Adult females may lay eggs several times, and normally have to take in a bloodmeal before each egg-deposition. Mating is very important indeed for the egg-laying, but it needs not to be repeated at each bloodmeal, the number of spermatophores penetrating into the female during the first mating being sufficient to assure several viable egg-layings (AESCHLIMANN & GRANDJEAN, in preparation). Experimentally, mating may be delayed until 150 to 200 days or more after the bloodmeal. In such cases vitellogenesis starts, and leads to a viable egg-deposition, if enough nutrient reserves are present within the midgut (AESCHLIMANN, 1968; AESCHLIMANN & GRANDJEAN, in press). The processes of vitellogenesis (AESCHLIMANN & HECKER, 1967 and 1969; DIEHL, 1969 and 1970; JENNI, 1971) are linked with digestion and mating. A full understanding of the digestion is therefore necessary for the understanding of the former processes.

Experimental work concerning these questions has been carried out on insects: An exhaustive review of the literature has been published by ENGELMANN (1970) about vitellogenesis, and by GOODING (1972) about digestion in haematophagous insects. Some authors have already studied the digestive system and the digestion of *Ornithodorus* (CHRISTOPHERS, 1906; TRUE, 1932; BALASHOV, 1957 and 1961), but our knowledge of digestion in *O. moubata* is still poor. This paper is a contribution to the study of digestion in this species, but further investigations are still necessary, if the processes involved in the digestive activity of the tick are to be thoroughly understood (GRANDJEAN, thesis in preparation).

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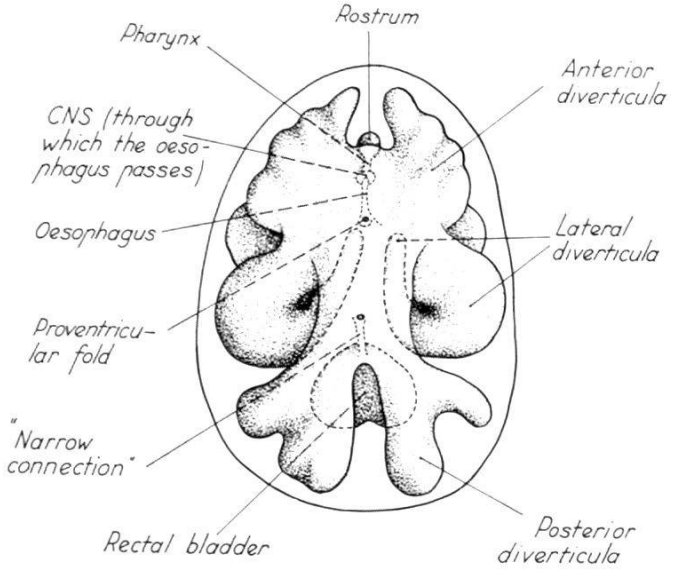


Fig. 1. Anatomy of the digestive system of the tick *Ornithodorus moubata* (dorsal vue). Schematic drawing. Magnification ca. 4 ×.

2. Material and Methods

Classical histological methods were used. Ticks [1] were sacrified every day after a bloodmeal on a guinea-pig, and their midguts fixed with Bouin-Duboscq's (0,7 % alcoholic solution of picric acid) or Carnoy's fluid and colored with haemalum-eosine or with Weigert's ferric haematoxyline. Series of ticks were also weighed every day to determine weight losses during digestion. For electron microscopy, the midguts were fixed either with 2.5 % glutaraldehyde in a cacodylate buffer, and postfixed in 2 % osmium tetroxide in a cacodylate buffer (HECKER, DIEHL & AESCHLIMANN, 1969), or with a mixture of both fixatives (HECKER, 1970: 2.5 % glutaraldehyde and 1 % osmium tetroxide in a cacodylate buffer, postfixation in 0.25 % uranyl acetate in sodium citrate). Ultrathin sections were stained with lead salts and observed with a Zeiss EM 9a and a Philips EM 300 Microscope.

3. Results

3.1. Gut anatomy

The digestive system (fig. 1) consists of a pharynx (fig. 2a) and of an oesophagus (fig. 2b), which opens into the midgut with a proventricular fold (fig. 2c). The three pairs of diverticula of the midgut – the anterior, lateral and posterior diverticula – are branched. The subdivisions of the diverticula (generally seven in number) vary in shape in the different species of *Ornithodorus* (BALASHOV, 1961). We observed that the depth of the notches, especially of the anterior diverticula, may vary within the same population of fasting *O. moubata*.

[1] The *O. moubata* came from Tanzania and were bred for several years in the Swiss Tropical Institute, according to the method of GEIGY & HERBIG (1955).

Table 1. Names for the "narrow connection" between the midgut and the rectal bladder in ticks, as used by different authors

Author	*Species studied*	*Name*
HELLER, 1858	*Argas persicus*	"Darm" (intestine)
CHRISTOPHERS, 1906	*Ornithodorus savignyi*	clear tube atrophied connection
NORDENSKJÖLD, 1908	*Ixodes reduvius*	pylorus
BLANC, 1910	*Ixodidae*	"tube connectif" (connecting tube)
ROBINSON & DAVIDSON, 1914	*Argas persicus*	rectum
TRUE, 1932	*O. coriaceus*	rectal tube
BURGDORFER, 1951	*O. moubata*	— (absent)
ENIGK & GRITTNER, 1952	*Ixodoidea*	"Dünndarm" (small intestine), (absent in *O. moubata*)
BALASHOV, 1961	*O. papillipes* *O. lahorensis*	small intestine
ARTHUR, 1962	*Ixodoidea*	narrow tube
AESCHLIMANN & RYHINER, 1970	*O. moubata*	"tube intermédiaire" (intermediate tube)
KHALIL, 1971	*Argas arboreus*	connecting tube
GUIRGIS, 1971	*Argas arboreus*	connecting tube

In most *Ixodoidea,* the midgut communicates with the rectal bladder by the means of a functional channel, which allows the tick to empty its midgut. Some confusion arises in the literature, as this channel is named differently by different authors (table 1). The posterior part of the digestive system consists of a narrow tube, leading from the midgut to the rectal bladder, the latter being connected with the outside by means of the rectum and the anus. As our knowledge concerning the physiological role of the hindgut is inadequate, we propose to use the term of "narrow connection" for the channel connecting the midgut with the rectal bladder. In *O. moubata,* the midgut has no communication with the rectal bladder, in spite of the presence of such a narrow connection (AESCHLIMANN & RYHINER, 1970), so that the midgut is functionally blind in this species.

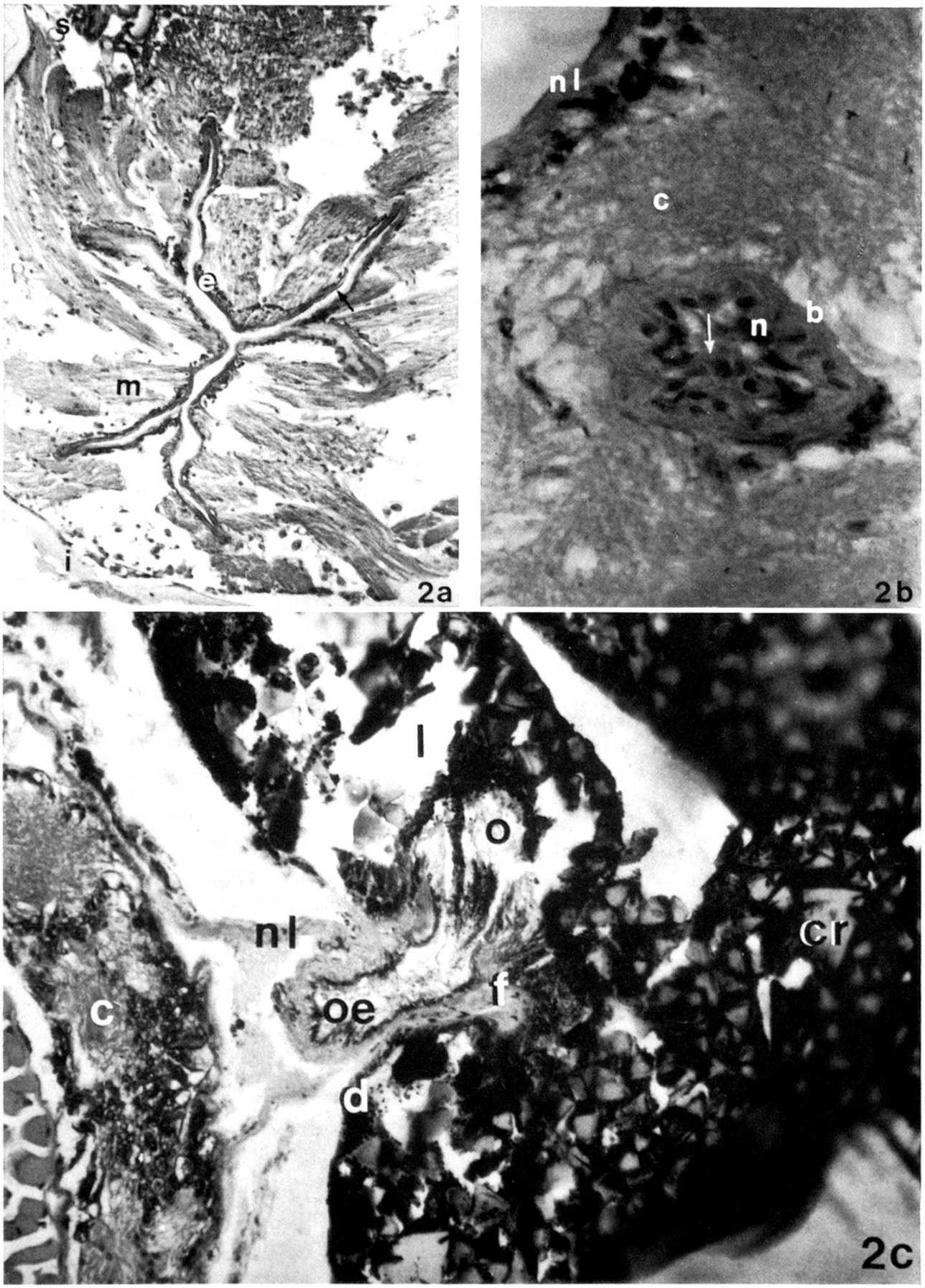


Fig. 2. Transverse sections of the foregut. *2a* Pharynx (magnification 180 ×). *2b* Oesophagus (magnification 360 ×). *2c* Proventricular fold: opening of the oesophagus into the midgut (magnification 250 ×). b = basal membrane, c = mass of central nervous system, cr = crystals of haemoglobin, d = digestive cell of the midgut, e = epithelial cells of the pharynx, f = cells of the proventricular fold, i = integument, l = midgut lumen, m = muscles, n = nucleus (oesophagial epithelium), nl = neurilemma, o = opening into the midgut, oe = oesophagus, s =

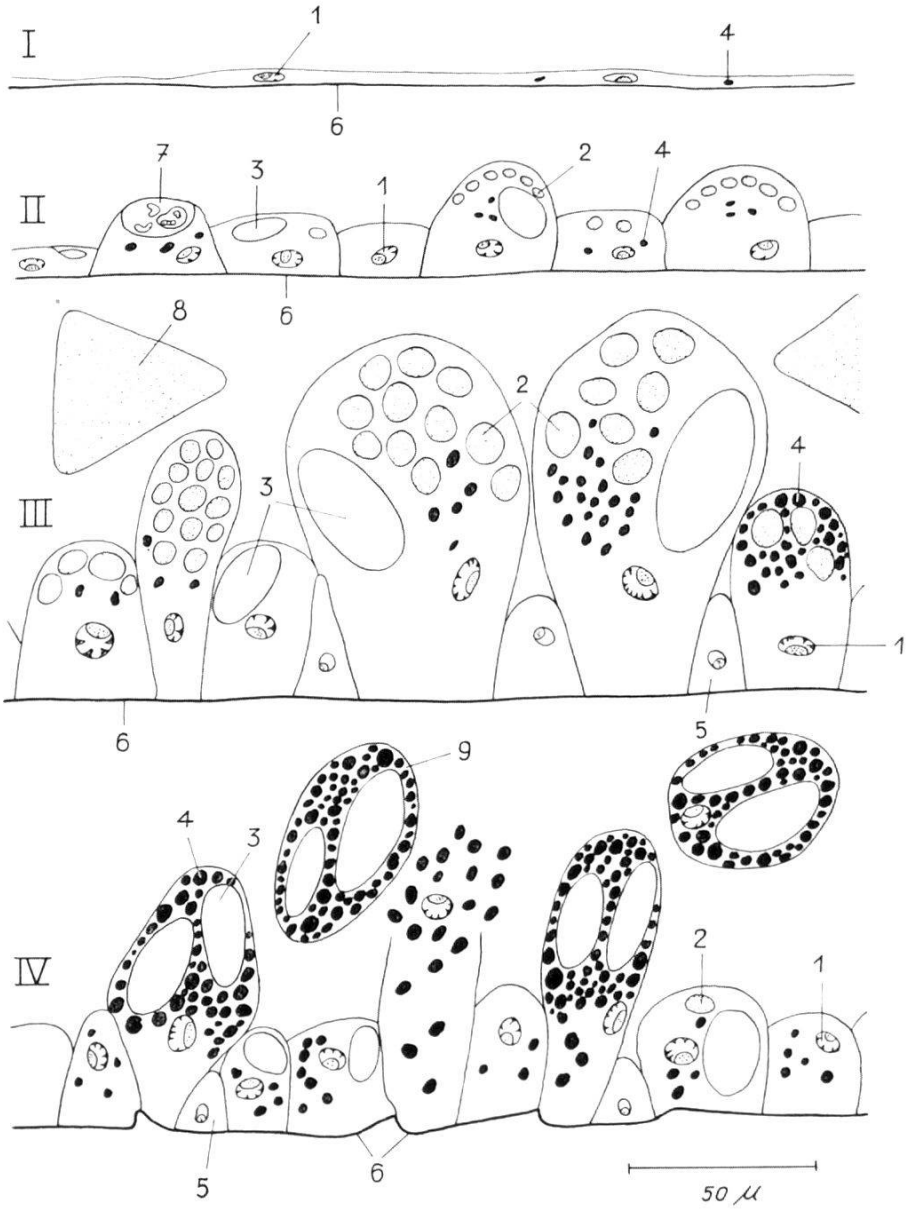


Fig. 3. Histological modifications of the midgut epithelium during digestion in *O. moubata*. Schematic drawing. I. Epithelium of a newly gorged female. II. Epithelium of a gorged female starting digestion. III. Epithelium of a gorged female, six to fifteen days after bloodmeal. IV. Epithelium of a fasting tick. 1 = nucleus, 2 = nutritive vacuoles (red with eosin staining), 3 = large vacuoles (not stained with eosin), 4 = haematin granules, 5 = replacement cells, 6 = basement membrane, 7 = phagocytosis of nuclei of leucocytes and of red blood cells, 8 = haemoglobin crystals, 9 = detached digestive cells filled with haematin granules.

3.2. Histological modifications of the midgut epithelium: cycle of the digestive cell (fig. 3)

In *O. moubata,* the midgut of the freshly hatched larva is stretched by embryonic yolk, which will slowly be digested. Traces of yolk may still be found in the first nymphal stage, fifty days after the moult (DIEHL, personal communication). The midgut epithelium consists of a single cell layer, as well in larvae as in nymphs and in adult ticks. According

to our observations and to the statement of several authors on different tick species [BATELLI (1891) *Ixodidae*; NORDENSKJÖLD (1908) *Ixodes reduvius*; SAMSON (1909) *I. ricinus*; BALASHOV (1957) *O. papillipes* and *lahorensis*, and TATCHELL (1964) *Argas persicus*], there is only one type of digestive cell besides the small replacement cells (see Remarks, 3.4. A). We did not observe the secretory cells mentioned by HUGHES (1954) and BALASHOV (1961). Yet this question needs further investigation. As a rule, digestion is an intracellular one in the *Acari* (REICHENOW, 1921; ROESLER, 1934; SCHLOTTKE, 1934; YONGE, 1937; BADER, 1938; BALASHOV, 1957). The cycle of a larval midgut cell digesting yolk is similar to that of a digestive cell of a nymph or an adult tick digesting blood. There are no morphological differences between the epithelia of the central part and of the diverticula of the midgut.

The cycle described below is based on histological observations of the midgut of adult females. Before these feed as adults, their midgut is still filled with the remains of their last bloodmeal, i.e. the blood taken in at the last nymphal stage.

Fasting tick (fig. 3, IV)

Most of the cells of the digestive epithelium of the fasting tick have a cubical or cylindrical shape, and their basal lamina are folded. The spherical nuclei are distributed evenly in apical, central or proximal positions within the cytoplasm of the cells. Numerous heterochromatic granules are seen in the nucleus. The structuration of the cytoplasm is not distinct, apart from some network-like structures.

Nevertheless some cells show either a cytolytic or a digestive activity: they protrude into the midgut lumen. The few active cells digest the nutrient reserves stocked inside the midgut; they are characteristic of a state of lowered digestive activity.

Newly gorged female (fig. 3, I and fig. 5)

Immediately after the bloodmeal the midgut epithelium is highly distended. The basal lamina is no longer folded. The few cells, which showed a digestive action, have become detached and are broken down in the midgut lumen. The now elongated nuclei each contain a nucleolus. Their aspect is granular and heterochromatic granules are present in a small number. Cytoplasmic structures are dense; cellular limits can not be distinguished with the light microscope.

Gorged female starting digestion, two to five days after the bloodmeal (fig. 3, II)

As digestion proceeds the cells swell and two types of vacuoles appear: the small nutritive vacuoles stain with eosin whereas the larger type of vacuoles do not. Nuclei of leucocytes and red blood cells of the host are absorbed by phagocytosis (fig. 3, No. 7). The nuclei of the digestive cells become rounder and larger. A network-like structuration of the cytoplasm is particularly noticeable at this stage. Haematin granules (see Remarks, 3.4. C) also appear; they are small and yellowish at first, later becoming larger (up to 5 μm) and darker.

Gorged female, six to fifteen days after the bloodmeal (fig. 3, III)

The digestive cells become still longer and take on a club-like shape, the thicker end protruding into the midgut lumen. These large cells are very numerous during the second week of digestion. They accumulate more and more haematin granules, whereas the number of nutritive vacuoles diminishes. The cell then often becomes detached from its basal lamina. Its shape becomes spherical and the cell floats between the crystals in the midgut lumen (see Remarks, 3.4. D). Disintegration of the cell then occurs and the liberated cell contents mix with the midgut reserves. Pycnotic nuclei of the degenerated digestive cells are then observed in the midgut lumen. Some cells have been observed, which remained attached to the basal lamina and which were ruptured there (fig. 3, IV). In other cases, only the apical part of the cell was detached, and the nucleus remained within the basal part still attached to the basal lamina. This behaviour of the cells could be compared to either the holocrinic or the merocrinic type of secretion in glandular cells. Yet it is not sure, whether cytolytic enzymes are released from the disintegrated cells, and whether they play a role in digestion.

The different stages of the cycle described above correlate well with recent observations on *Argas arboreus* (KHALIL, 1971).

3.3. Ultrastructural modification of the midgut epithelium

Preliminary investigations have been carried out on the ultrastructure of the digestive cells, both of gorged and of fasting ticks, in order to observe the most apparent cytologic differences between the midgut epithelia with different digestive activities.

Digestive cells of fasting females (fig. 4 and 4a)

The infolds of the basal cell membrane (bm) are much expanded. The limiting cell membranes (cm) are clearly seen. Mitochondria (m) are present. The nucleus (n) contains heterochromatin (arrow), but the nucleolus is poorly developed. Numerous strongly electron-opaque granules (h) are present in the cytoplasm as well as in the midgut lumen. They appear to be identical with the haematin granules observed with the light microscope (fig. 3, IV); they might be considered as residual bodies, after the digestion of the haemoglobin inclusions (i). In the cytoplasm a few vesicles (v) are present, which appear to be empty. The endoplasmatic reticulum is poorly developed (fig. 4 and 4a, compare with fig. 6 and 7). The apical cell membrane forms microvilli (mv), which protrude into the midgut lumen (fig. 4a). Ergastoplasmic elements or other types of vesicles, which might indicate a pinocytotic activity are very seldom at the base of the microvilli.

Digestive cells of gorged females, five days after a bloodmeal (fig. 6, 6a and 7)

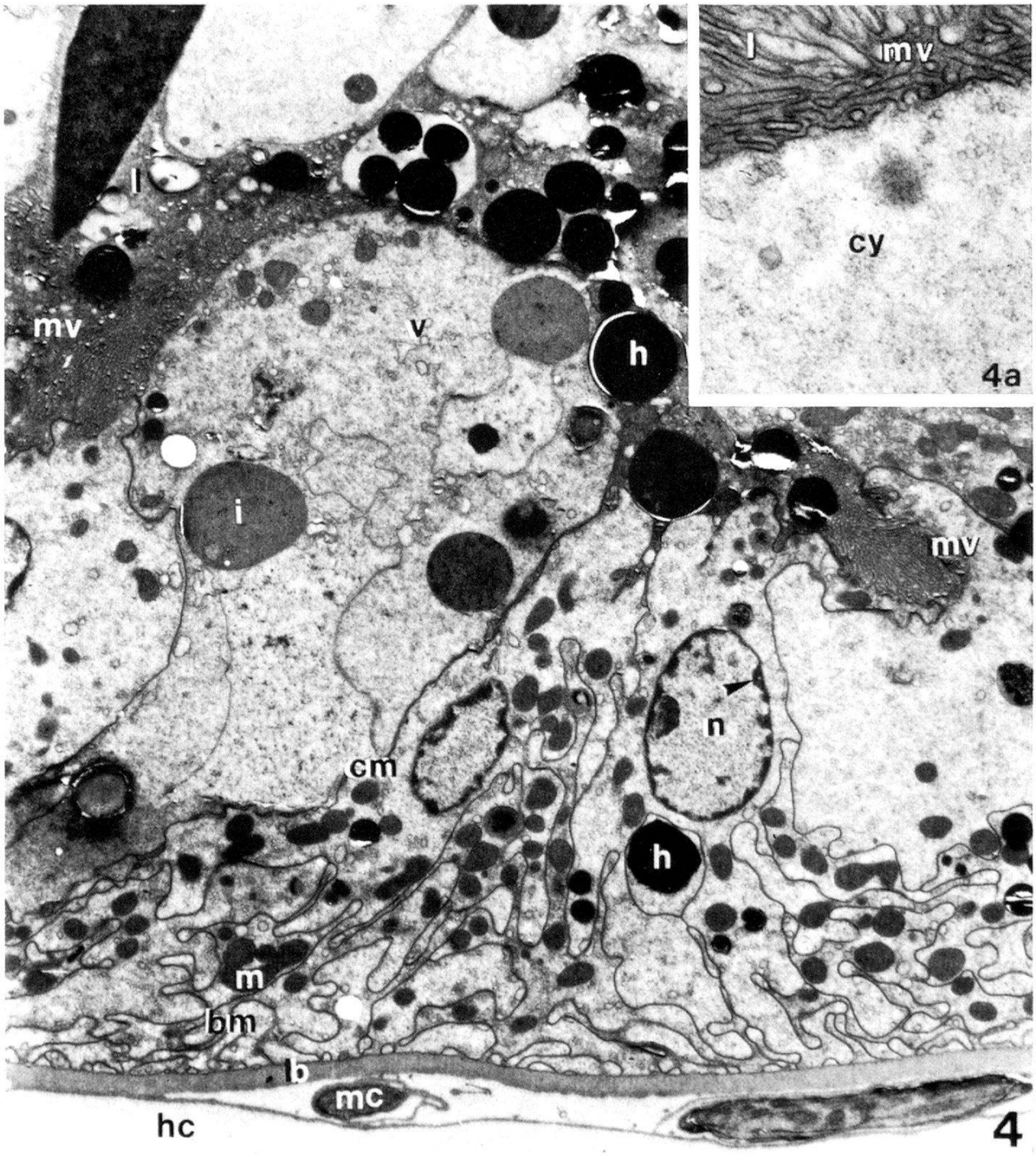
The basal cell membrane (bm) is still present: it contains mitochondria (m) within its folds. Numerous mitochondria are also present in the apical part of the cell. A nucleolus (nl) is well developed within the nucleus (n). Inclusions, such as vacuoles (va), are seen within the cytoplasm, as well as darker electron-opaque bodies (rb), which presumably are residual bodies from the digestion of the vacuole contents. A more detailed analysis of the cellular processes of digestion is being carried out (GRANDJEAN, in preparation). The rough endoplasmic reticulum (er) is highly developed (fig. 6 and fig. 7). At the bases of the microvilli (mv), micropinocytotic vesicles are seen (fig. 6a, p and arrow).

The ultrastructural modifications (appearance of a rough endoplasmic reticulum and of various inclusions, both vacuoles and pinocytotic vesicles) indicate a high metabolic turn-over of the digestive cell.

Fig. 4. Digestive cells of a fasting female. Electron micrograph, magnification 3800 ×. b = basal lamina, bm = basal membrane, forming the basal labyrinth, cm = cell membrane, er = rough endoplasmic reticulum, g = Golgi zone, h = haematin granules, hc = haemocoel, i = inclusions, l = midgut lumen, m = mitochondria, mc = muscle cell, mv = microvilli, n = nucleus, nl = nucleolus, r = rickettsia-like microorganisms (see REINHARDT, AESCHLIMANN & HECKER, 1972), rb = "residual body", v = vesicles, va = vacuoles, arrow = heterochromatin.

Fig. 4a. Detail of the apical part of the digestive cell of a fasting female. Electron-micrograph, magnification ca. 15,000 ×. cy = apical cytoplasm, l = midgut lumen, mv = microvilli.

Fig. 5. Stretched midgut epithelium one hour after blood intake. Magnification 1,380 ×. d = undetached digestive cell, h = haematin granules, hc = haemocoel, l = midgut lumen containing red blood cells, n = nucleus, t = trachea, z = zone of haemolysis.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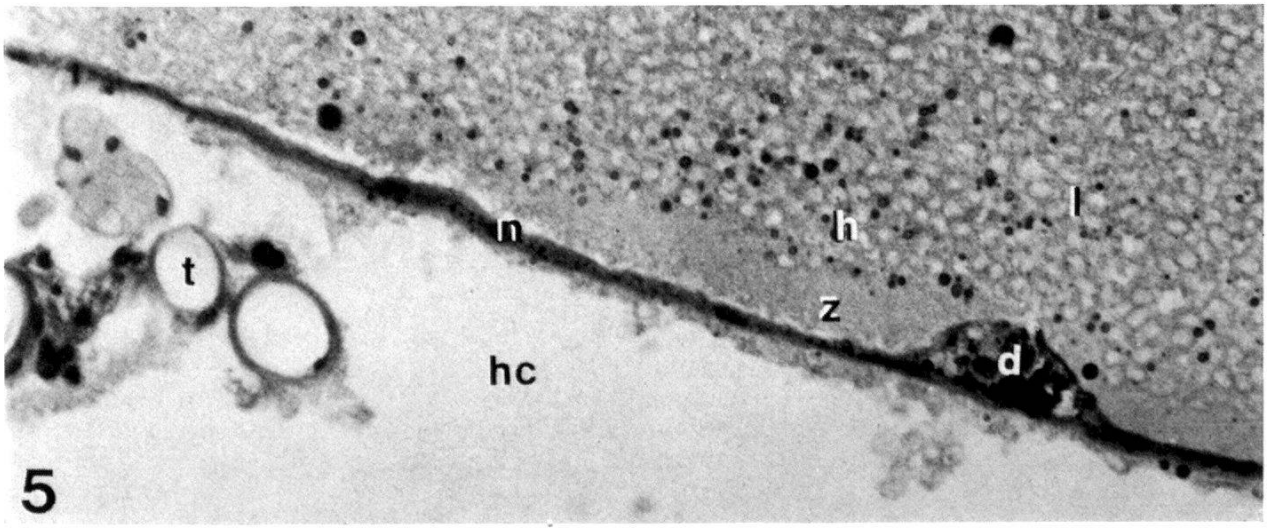
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3.4. Remarks on some detailed aspects of the digestion

A. Replacement cells

The micrograph (fig. 8) shows the only cellular division seen in several thousand cells observed. The autoradiographic evidence of midguts easily marked with tritiated thymidine[2] indicates that mitoses do occur at a higher rate than supposed from histological observation. Mitoses are therefore likely to be very rapid processes in the midgut of the tick, and it is not yet possible to give an exact statement on when and where they do occur.

B. Synchronisation of the cycle

It should be pointed out that the cycles of the different digestive cells are not synchronised in *O. moubata*. So nearly all the stages (fig. 3, I–IV) may be found in one single tick, e.g. 10 days after the bloodmeal. The absence of a strict synchronisation allows a slow digestion of the haemoglobin reserves, so that the tick may survive a prolonged period of starvation (three years and more for adult ticks).

C. Haematin granules

Due to the digestion of yolk – which consists essentially of haemoglyco-lipoproteins (DIEHL, 1969) – small brownish intracellular granules (ϕ 0.5–2 μm) are observed in the epithelium of the larva (DIEHL, personal communication). Similar dark granules (ϕ 0.5–5 μm) are found in the digestive cells of nymphs and of adult ticks having digested their bloodmeal. In both cases, the concretions contain haematin, a product of haemoglobin metabolism (WIGGLESWORTH, 1943). As the digestive cells disintegrate at the end of their cycle, the haematin granules are liberated into the midgut lumen (fig. 3, IV).

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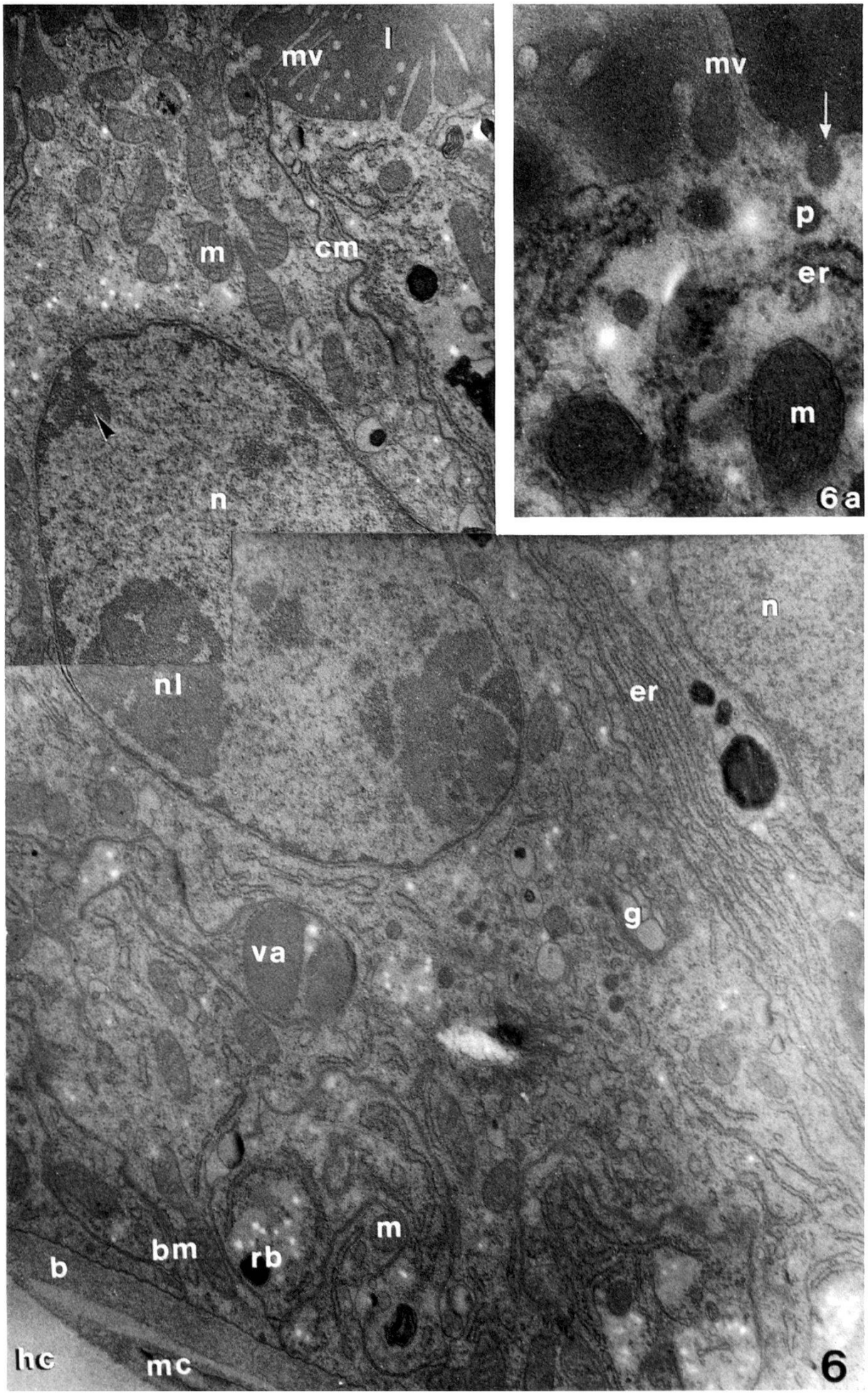
[2] We are grateful to Miss R. M. Ryhiner for her skilled technical assistance.

Fig. 6. Active digestive cell, five days after bloodmeal. Electron micrograph, magnification 11,650 × (for abbreviations see fig. 4).
Fig. 6a. Detail of the apical part of an active digestive cell, five days after bloodmeal. Electron micrograph, magnification 36,000 ×. er = rough endoplasmic reticulum, m = mitochondria, mv = microvilli, p = micropinocytotic vesicles, one of which is in the process of formation (arrow).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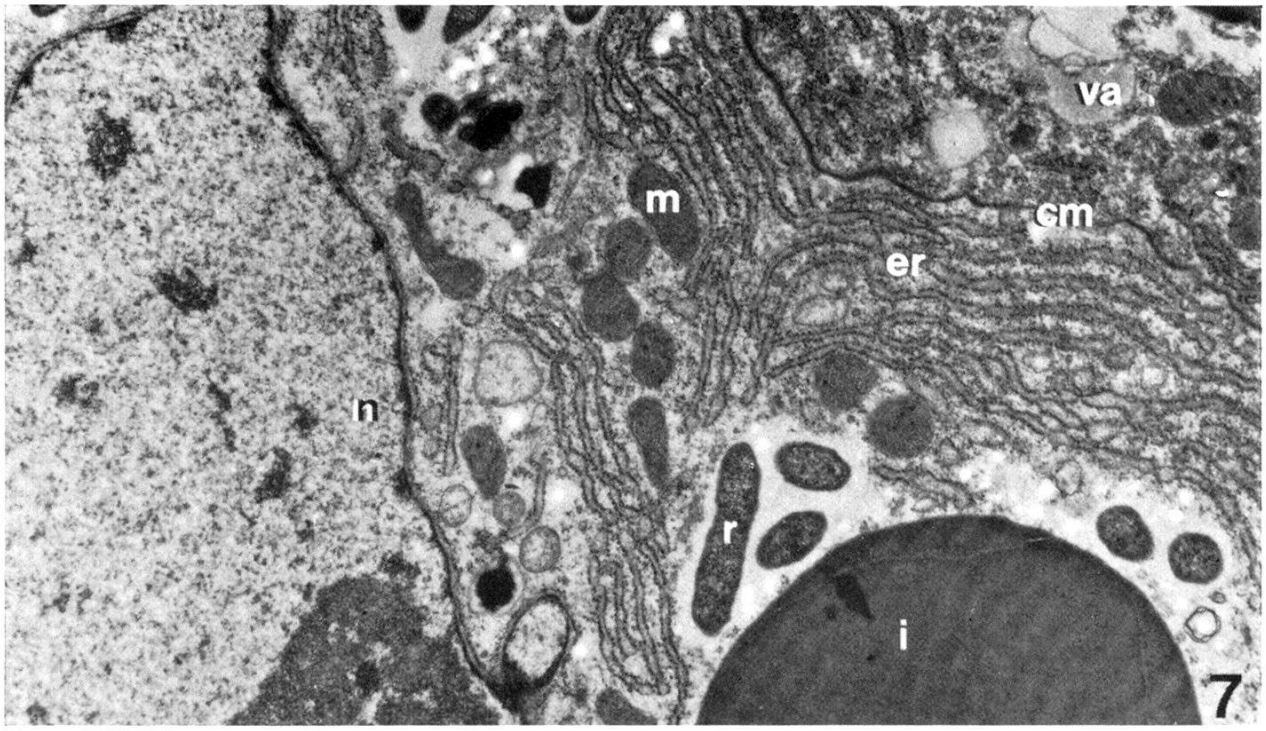

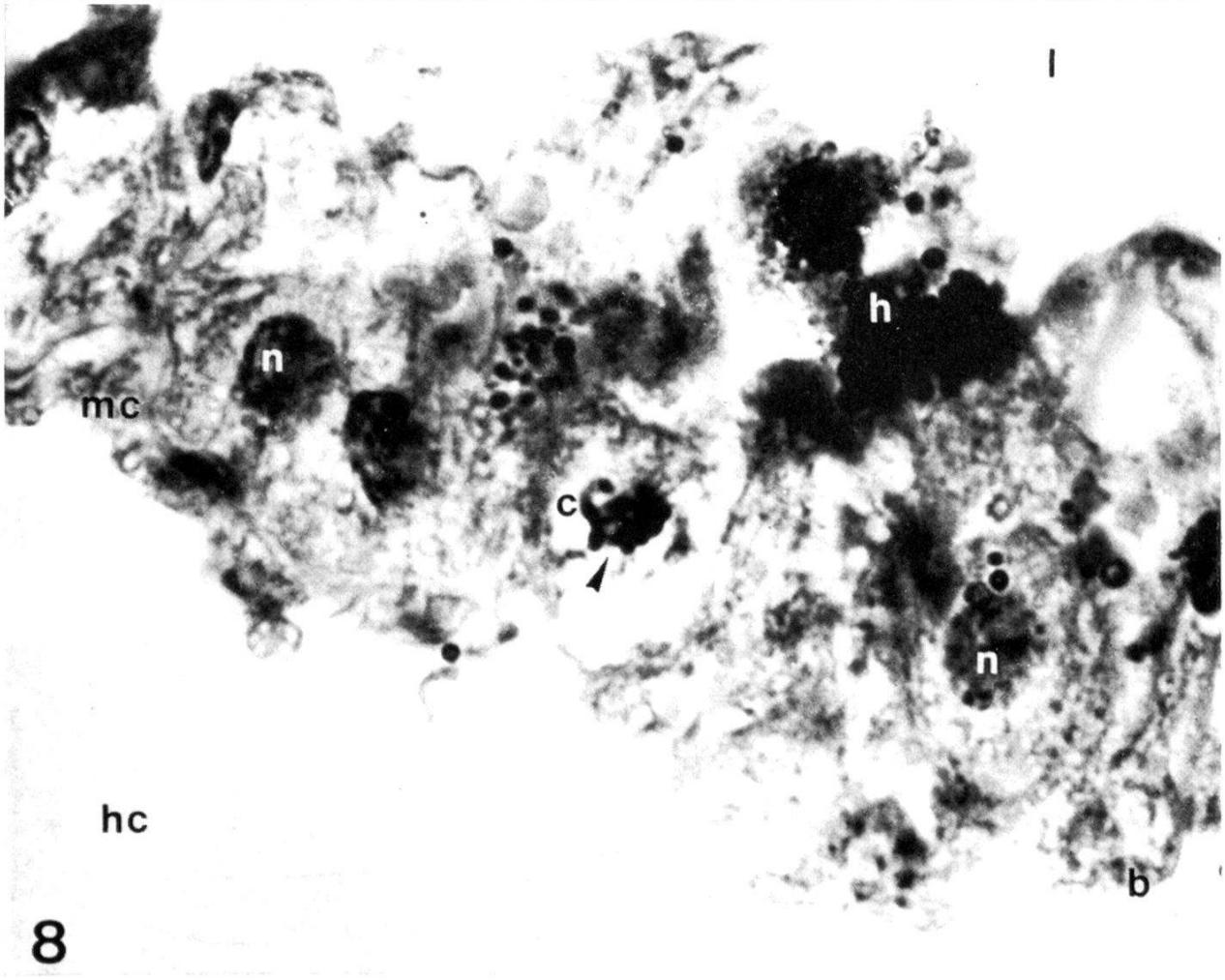

Fig. 7. Detail of an active digestive cell, five days after bloodmeal. Electron micrograph, magnification 13,000 × (for abbreviations see fig. 4).
Fig. 8. Mitosis of a midgut epithelium cell (metaphase). Magnification about 1,400 ×. b = basement membrane, c = chromosomes, h = haematin granules, hc = haemocoel, l = midgut lumen, mc = muscle cell, n = nucleus; the arrow shows the mitotic division of one nucleus.

Table 2. Gravimetric analysis of feeding in *Ornithodorus moubata*

	Nymphs I * (n = 10)	Females (n = 28)	Males (n = 8)
Mean weight before feeding	0.20 mg	50 mg	15 mg
Mean weight just after feeding	1.03 mg	210 mg	45 mg
Mean weight of ingested blood (100% = weight of fasting tick)	400%	340%	200%
Mean duration of a bloodmeal (minutes)	49′ (13–110′)	41′ (15–100′)	42′ (n = 7)

* DIEHL, personal communication.
n = Number of ticks.

D. Midgut content: Primary enzyme activity and haemoglobin crystallisation

At the beginning of blood digestion, some localised zones of granular aspect, which are deprived of red blood cells of the host, are seen in the immediate vicinity of the midgut epithelium (fig. 5). The appearance of these zones could be due to the action of haemolysines, as stated by TATCHELL (1964) to be the case in *Argas persicus*. Furthermore, the red blood cells are ruptured in the midgut lumen, and the liberated haemoglobin forms small crystals (from the 30th hour after the blood intake in the case of the first nymphal meal of *O. moubata*). It is more difficult to study the beginning of this phenomenon in later developmental stages: neither haemoglobin crystals from the last bloodmeal nor haematin granules can be eliminated by the anus in *O. moubata* and, therefore, they remain within the midgut lumen. Hence the appearance of the new crystals is masked. It may be observed that the red blood cells disappear at the latest during the fifth day after the bloodmeal. Larger haemoglobin crystals appear two weeks after the meal. The shape of the crystal would be different according to the species used as a host (AMANTEA, 1926; PICK, 1965).

3.5. Gravimetric aspects of digestion in O. moubata

a) Gravimetric analysis of feeding (table 2)

The weight of the tick often quadruples or increases fivefold during the blood intake. We must remember that the tick, when ready to leave its host, empties its rectal bladder and secretes important quantities of

Table 3. Weight loss of *Ornithodorus moubata* after bloodmeal

	Nymphs I * (n = 10)	Females (n = 28)	Males (n = 8)
Mean weight of gorged ticks (day zero)	1.03 mg = 100%	210 mg = 100%	45 mg = 100%
Mean weight of ticks, 20 days after bloodmeal	0.67 mg = 65%	175 mg = 80%	35 mg = 75%
Mean weight of ticks, 50 days after bloodmeal	0.59 mg = 57%	160 mg = 75%	32 mg = 70%

* DIEHL, personal communication.

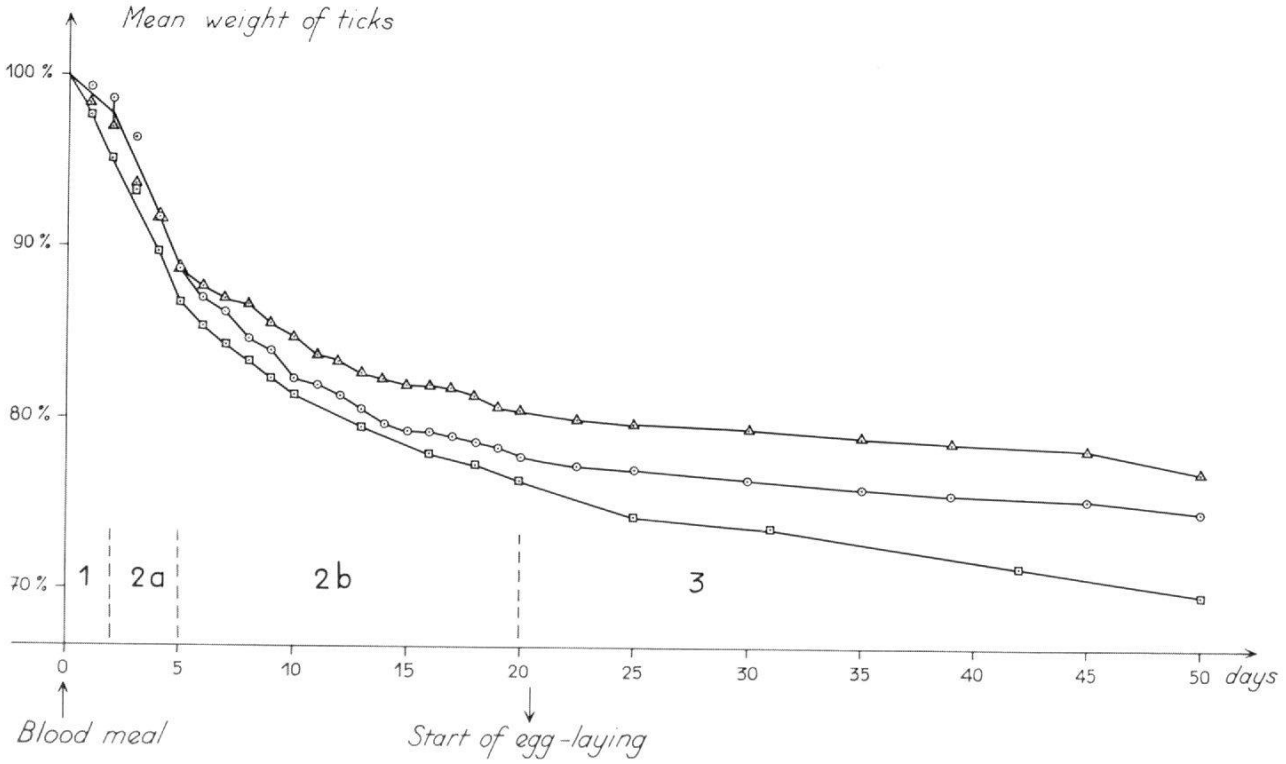

Fig. 9. Weight loss during digestion in *O. moubata* adults. Mean weight is expressed as a percentage of the mean weight of the fully gorged ticks (day zero). □ Values for males (n = 8, n = number of ticks). △ Values for virgin females (n = 14). ○ Values for mated females (n = 14). From the twentieth day, the weight of eggs layed is added to the body weight, to facilitate comparison with virgin females (see next page). 1, 2a, 2b and 3: phases of digestion.

Table 4. Analysis of the differences in the weight loss of virgin and of mated *Ornithodorus moubata* females

Days after bloodmeal	Mean weight *		Value of t-test	Tabled value (degree of freedom: $\nu = 26$)
	mated females (n = 14)	virgin females (n = 14)		
0	100	100	–	–
20	80.7 ± 1.1%	78.1 ± 0.5%	2.132	2.056 (2 P = 0.05)
50	78.3 ± 1.2%	74.6 ± 1.1%	2.217	2.056 (2 P = 0.05)
150	74.6 ± 1.7%	70.6 ± 1.5%	2.003	1.706 (2 P = 0.1)

* Each weight is expressed as a percentage of the weight of the fully gorged tick (day zero).

coxal fluid, which enables it to concentrate the ingested blood (LAVOIPIERRE & RIEK, 1955). The weights of these liquids could not be taken into account in table 2. The duration of the bloodmeal is virtually the same for the ticks of the first nymphal stage and for adult ticks.

b) Weight loss of the tick after the bloodmeal (table 3, fig. 9)

There is an initial rapid phase of weight loss, which is followed by a slower phase. The values in table 3, concerning the slower diminution of the weight of female ticks, show that these dispose of larger nutrient reserves than nymphs or males do.

c) Analysis and discussion of the differences in the weight loss of virgin and mated females (table 4, fig. 9)

Assuming a normal distribution of the values of the different weights, we used the statistical Student's t-test in order to allow a more detailed analysis of the values for the females in table 3: there is a significant difference (for values of p less than 0.05) between the weight loss of virgin females and that of mated females. The differences arise and become more pronounced from about the fifth to the tenth day after the bloodmeal. This lapse of time corresponds to the period of vitellogenesis in mated ticks (AESCHLIMANN & HECKER, 1967 and 1969). In virgin ticks, feeding also initiates a vitellogenesis. Its duration is prolonged and it is often incomplete, as the virgin ticks rarely lay eggs.

These statements emphasise the importance of digestion and of mating for allowing a normal egg-laying.

GALUN & WARBURG (1968) destroyed the midgut mucosa by irradiation and could show that the close correlation between digestion and vitellogenesis also exists in *O. tholozani*.

As we could obtain normal vitellogenesis and egg-layings in *O. moubata*, following a delayed mating of starved ticks (AESCHLIMANN, 1968; AESCHLIMANN & GRANDJEAN, in press), and as ticks have no fat body, we may conclude that they take from their intestinal nutrient reserves a large part of the yolk proteins which they incorporate into the ovocytes (AESCHLIMANN & HECKER, 1967 and 1969; JENNI, 1971; see also BRINTON & OLIVER, 1971, for *Dermacentor andersoni*, and HECKER & AESCHLIMANN, 1970, for *Rhipicephalus bursa*). These proteins are likely to be synthesised in the gut epithelium (DIEHL, 1970), as already suggested by ROTH & PORTER (1964) for *Aedes aegypti*. More detailed electron-microscopical and histochemical studies are carried out on this subject in *O. moubata* (GRANDJEAN, in preparation).

4. Discussion

Digestion in *O. moubata* may be divided into 3 phases (fig. 3 and 9). We propose the following phases, based on histological observations of virgin and mated females:

Bloodmeal (day zero).

Phase 1: Stretched epithelium (fig. 3, I); no active cells; blood haemolysis; rather large loss of weight, due essentially to secretion of coxal fluid.

Duration: about 2 days.

Phase 2: Numerous active cells appear (fig. 3, II and III); crystallisation of liberated haemoglobin.

Duration: from the third day up to the start of egg-laying by mated females.

a) Rapid loss of weight from mated and from virgin females (fig. 9: phase 2a).

Duration: third to fifth day after bloodmeal.

b) After the fifth day: slower loss of weight, much slower in virgin than in mated females (fig. 9: phase 2b).

Duration: fifth to tenth day after bloodmeal, which corresponds to the period of vitellogenesis in mated females.

After the tenth day: loss of weight similar in virgin and in mated females (if the weight of the eggs layed by the latter is taken in account).

Phase 3: Active cells less numerous (fig. 3, IV); slow utilisation of nutrient reserves (haemoglobin crystals are important for allowing the tick to survive long periods of starvation); slow loss of weight.

Duration: from 2 to 3 weeks after bloodmeal; may last several months or even years.

The succession of the phases correlates well with the various observations of other authors [BALASHOV (1961) for *O. papillipes* and *O. lahorensis*; TATCHELL (1964) for *A. persicus* and GUIRGIS (1971) for *A. arboreus*]. BALASHOV and TATCHELL studied the digestive phenomena by following the changes occurring in the blood contained in the midgut. Both authors define three phases comparable to those stated above: a phase without digestion, a phase of rapid digestion (which may be stopped in virgin *Argas* females), and finally a phase of slow digestion. The results of TATCHELL, concerning *A. persicus,* are based on the concentration of the haemoglobin stored in the midgut lumen; they give a precise parameter of digestion. His curves are comparable with those we obtained (fig. 9) by weighing living *O. moubata.* Yet the loss of weight in the first two days has no equivalent loss of haemoglobin concentration in the work of TATCHELL; it seems to be due not to digestion, but most probably to water losses caused by coxal fluid secretion and by evaporation.

We observed the red blood cells of the host to be haemolysed within the midgut during the first 5 or 6 days (phase 1 and 2a). The rate of haemolysis is not different in virgin and in mated *O. savignyi* females, apart from great individual differences (OSTERHOFF & GOTHE, 1966). These findings correlate with the equal diminution of the weight of the tick and of the haemoglobin concentration in the midgut, both in mated and in virgin females.

Differences between the digestion rates of mated and of virgin females appear five to ten days after the bloodmeal, as stated above for *O. moubata* and by TATCHELL for *A. persicus*.

In conclusion we emphasise the remarkable synchronism between loss of weight, modifications of the ingested blood mass and cyclic activity of the cells of the midgut epithelium.

References

AESCHLIMANN, A. (1958). Développement embryonnaire d'*Ornithodorus moubata* (Murray) et transmission ovarienne de *Borrelia duttoni*. – Acta trop. *15*, 15–64.

AESCHLIMANN, A. (1968). La ponte chez *Ornithodorus moubata,* Murray (Ixodoidea, Argasidae). – Rev. suisse Zool. *75*, 1133–1139.

AESCHLIMANN, A. & GRANDJEAN, O. (1973). Influence of natural and "artificial" mating on feeding, digestion, vitellogenesis and egg-laying in ticks (Ixodoidea). – Folia parasit. *20*, 67–74.

AESCHLIMANN, A. & GRANDJEAN, O. Observations on fertility in *Ornithodorus moubata,* Murray *(Ixodoidea, Argasidae).* Relationships between matings and egg-layings – Acarologia. (In press.)

AESCHLIMANN, A. & HECKER, H. (1967). Observations préliminaires sur l'ultrastructure de l'ovocyte en développement chez *Ornithodorus moubata* (Murray). – Acta trop. *24*, 225–243.

AESCHLIMANN, A. & HECKER, H. (1969). Vitellogénèse et formation cuticulaire chez l'œuf d'*Ornithodorus moubata,* Murray (Ixodoidea: Argasidae). Etude au microscope électronique. – Acarologia *11,* 180–192.

AESCHLIMANN, A. & RYHINER, R. M. (1970). Note sur une particularité anatomique du système digestif chez *Ornithodorus moubata,* Murray (Ixodoidea: Argasidae). – Acta trop. *27,* 191–192.

AMANTEA, G. (1926). Sulla cristallizzazione dell'emoglobina nell'intestino di alcuni ematofagi. – Boll. Soc. ital. Biol. spez. *1,* 66–69.

ARTHUR, D. R. (1962). Ticks and Disease, pp. 445. – Oxford: Pergamon Press.

BADER, C. (1938). Beiträge zur Kenntnis der Verdauungsorgane bei Hydracarinen. – Rev. suisse Zool. *45,* 721–806.

BALASHOV, YU. S. (1957). Histologic characteristics of digestion in ixodid and argasid ticks. – Parasitol. Sbornik (Zool. Inst. Akad. Nauk SSSR) *17,* 137–167. (English translation.)

BALASHOV, YU. S. (1961). The structure of digestive organs and blood digestion in *Argasidae.* – Parasitol. Sbornik (Zool. Inst. Akad. Nauk SSSR) *20,* 185–225 (English translation.)

BATELLI, A. (1891). Note sugli Ixodini. – Boll. Soc. Entomol. ital. *23,* 218–229.

BLANC, G. (1910). Sur la terminaison du tube digestif des *Ixodidae.* – Bull. Soc. Zool. Fr. *35,* 219–225.

BRINTON, L. P. & OLIVER, J. H. (1971). Fine structure of oogonial and oocyte development in *Dermacentor andersoni,* Stiles (Acari: Ixodidae). – J. Parasitol. *57,* 720–747.

BURGDORFER, W. (1951). Analyse des Infektionsverlaufes bei *Ornithodorus moubata* (Murray) und der natürlichen Übertragung von *Spirochaeta duttoni.* – Acta trop. *8,* 194–262.

CHRISTOPHERS, S. R. (1906). The Anatomy and Histology of Ticks. Scientific Memoirs by Officers of the Medical and Sanitary Departments of the Government of India (New Series). – *23,* 1–55.

DIEHL, P. A. (1969). Haemolymphenproteine und Vitellogenese bei *Ornithodorus moubata,* Murray. Ixodoidea: Argasidae. – Bull. Soc. entomol. suisse *42,* 117–125.

DIEHL, P. A. (1970). Zur Oogenese bei *Ornithodorus moubata* (Murray) (Ixodoidea: Argasidae) unter besonderer Berücksichtigung der Vitellogenese. – Acta trop. *27,* 301–355.

ENGELMANN, F. (1970). The Physiology of Insect Reproduction. 307 pp. – Oxford: Pergamon Press.

ENIGK, K. & GRITTNER, I. (1952). Die Exkretion der Zecken. – Z. Tropenmed. Parasit. *4,* 77–94.

GALUN, R. & WARBURG, M. (1968). Irradiation effects on respiration and blood digestion in the tick *Ornithodoros tholozani,* and their importance for the sterile-male technique. "Isotopes and Radiation in Entomology", pp. 249–258. – Intern. atomic Energy Agency, Vienna.

GEIGY, R. & HERBIG, A. (1955). Erreger und Überträger tropischer Krankheiten. – Acta trop., Suppl. 6, pp. 472.

GOODING, R. H. (1972). Digestive Processes of Haematophagous Insects. I. A literature review. – Quaest. Entomol. *8,* 5–60.

GRANDJEAN, O. Thesis. (In preparation.)

GUIRGIS, S. S. (1971). The Subgenus Persicargas (Ixodoidea, Argasidae, Argas). Histological studies on *A. (P.) arboreus,* Kaiser Hoogstraal & Kohls. – J. med. Ent. *8,* 648–667.

HECKER, H. (1970). Ultrastruktur der Symbionten in Ovozyten von *Ornithodorus moubata,* Murray (Ixodoidea: Argasidae) nach simultaner Glutaraldehyd-

Osmium-Fixierung und Nachbehandlung mit Uranylacetat (Triple-Fixation). – Experientia *26,* 874–877.

HECKER, H. & AESCHLIMANN, A. (1970). Ultrastrukturelle Aspekte der Eibildung bei *Rhipicephalus bursa* (Ixodoidea: Ixodidae). – Z. Tropenmed. Parasit. *21,* 31–45.

HECKER, H., DIEHL, P. A. & AESCHLIMANN, A. (1969). Recherches sur l'ultrastructure et l'histochimie de l'organe coxal d'*Ornithodorus moubata,* Murray (Ixodoidea: Argasidae). – Acta trop. *26,* 346–360.

HELLER, C. (1858). Zur Anatomie von *Argas persicus.* – S.-B. Akad. Wiss. Wien *30,* 297–326.

HUGHES, T. E. (1954). Some histological changes which occur in the gut epithelium of *Ixodes ricinus* females during gorging and up to oviposition. – Ann. trop. Med. Parasit. *48,* 397–404.

JENNI, L. (1971). Synthese und Aufnahme von Proteinen während der Vitellogenese in Ovocyten von *Ornithodorus moubata,* Murray (Ixodoidea: Argasidae). – Acta trop. *28,* 105–163.

KHALIL, G. M. (1971). Biochemical and physiological studies of certain ticks (Ixodoidea): Incorporation of tritiated tyrosine in the digestive system of nymphal *Argas (Persicargas) arboreus* (Argasidae). – Ann. entomol. Soc. Amer. *64,* 1149–1154.

LAVOIPIERRE, M. M. J. & RIEK, R. F. (1955). Observations on the feeding habits of argasid ticks, and on the effect of their bites on laboratory animals, together with a note on the production of coxal fluid by several of the species studied. – Ann. trop. Med. Parasit. *49,* 96–113.

NORDENSKJÖLD, E. (1908). Zur Anatomie und Histologie von *Ixodes reduvius* I. – Zool. Jb. Abt. Anat. (A) *25,* 637–656.

OSTERHOFF, D. R. & GOTHE, R. (1966). The use of red cell antigens for timing break-down of erythrocytes during digestion in *O. savigny.* – Parasitology *56,* 613–618.

PICK, F. (1965). L'utilisation du principe de xénodiagnostic de E. Brumpt pour des recherches portant sur la cristallisation biologique et pathologique de l'hémoglobine sanguine du cobaye. – Ann. Parasit. hum. comp. *40,* 1–12.

REICHENOW, E. (1921). Die Hämococcidien der Eidechsen (Vorbemerkungen und erster Teil: Die Entwicklungsgeschichte von *Karyolysus*). – Arch. Protistenk. *42,* 179–291.

REINHARDT, C., AESCHLIMANN, A. & HECKER, H. (1972). Distribution of Rickettsia-like Microorganisms in various Organs of the tick *Ornithodorus moubata,* Murray (Ixodoidea: Argasidae) as revealed by Electron Microscopy. – Z. Parasitenk. *39,* 201–209.

ROBINSON, L. E. & DAVIDSON, J. (1914). The anatomy of *Argas persicus* (Oken). II. – Parasitology *6,* 217–256.

ROESLER, R. (1934). Histologische, physiologische und serologische Untersuchung über die Verdauung bei der Zeckengattung *Ixodes* Latr. – Z. Morph. Oekol. Tiere *28* (3), 297–317.

ROTH, T. K. & PORTER, K. R. (1964). Yolk protein uptake in the oocyte of the mosquito *Aedes aegypti.* – J. Cell. Biol. *20,* 313–332.

SAMSON, K. (1909). Zur Anatomie und Biologie von *Ixodes ricinus* L. – Z. wiss. Zool. *93,* 185–236.

SCHLOTTKE, E. (1934). Unterschiede in der Entwicklung des phagozytierenden und des resorbierenden Darmepithels. – Biol. Zentralbl. *54,* 51–64.

TATCHELL, R. J. (1964). Digestion in the tick *Argas persicus* Oken. – Parasitology *54,* 423–440.

TRUE, G. H., jr. (1932). Studies of the Anatomy of the Pajaroello Tick, *Ornithodorus coriaceus* Koch. I. The alimentary canal. University of California Publications in Entomology *6,* 21–48.

WIGGLESWORTH, V. B. (1943). The fate of haemoglobin in *Rhodnius prolixus (Hemiptera)* and other blood sucking arthropods. – Proc. roy. Soc. Ser. B *131,* 313–339.

YONGE, C. M. (1937). Review of digestion in *Metazoa.* – Biol. Rev. *12,* 87–116.

Zusammenfassung

Nach einer kurzen Beschreibung der Anatomie des Verdauungstraktes von *Ornithodorus moubata* untersuchen die Autoren in der vorliegenden Arbeit die Veränderungen des Mitteldarmepithels, welche nach einer Blutmahlzeit bei dieser Lederzecke *(Argasidae)* auftreten. Insbesondere wird die auffallende zeitliche Übereinstimmung hervorgehoben, die zwischen dem Gewichtsverlust vollgesogener Weibchen, den Veränderungen des Mitteldarminhaltes und der Stoffwechselaktivität der Verdauungszellen festzustellen ist. Mit Hilfe von Licht- und Elektronenmikroskopie wird der Zyklus einer Verdauungszelle beschrieben. Bei Nymphen und Adulttieren erfolgt die Verdauung in drei Phasen: eine erste Phase ohne sichtbare Zellaktivität, gekennzeichnet durch ein stark gedehntes Mitteldarmepithel; eine zweite Phase der raschen Verdauung, während der zahlreiche Zellen eine hohe Stoffwechselaktivität aufweisen und in das Mitteldarmlumen hineinragen; ultrastrukturell sind diese Zellen durch das Auftreten eines gut entwickelten rauhen endoplasmatischen Reticulums und von zahlreichen Mikropinocytose-Bläschen gekennzeichnet; schließlich eine dritte Phase der langsamen Verdauung, welche Monate, bei Adulttieren sogar Jahre dauern kann, wobei die Aktivität des Mitteldarmepithels zwar vorhanden, jedoch eingeschränkt ist; ultrastrukturell fehlt in den Zellen das rauhe endoplasmatische Reticulum. Während der zweiten Phase erfolgt die Verdauung bei unbegatteten Weibchen deutlich langsamer als bei begatteten.

Résumé

Dans le présent travail, après une brève description de la morphologie du système digestif d'*Ornithodorus moubata,* les auteurs étudient les modifications de la muqueuse intestinale de cet Argaside enregistrées à la suite d'un repas sanguin. Ils soulignent le remarquable synchronisme observé entre la perte de poids des femelles gorgées, les modifications de la masse sanguine ingérée et l'activité métabolique des cellules digestives. Le cycle d'une cellule digestive est décrit par les méthodes de la microscopie photonique et électronique. Chez les nymphes et les adultes, la digestion s'effectue en trois phases: une première phase sans activité cellulaire visible, caractérisée par un épithelium intestinal distendu; une deuxième phase de digestion rapide, marquée par l'activité de très nombreuses cellules faisant saillie dans la lumière intestinale, le microscope électronique révélant l'apparition de nombreuses vésicules de micropinocytose et d'un ergastoplasme granulaire bien développé; enfin une troisième phase de digestion lente, pouvant durer des mois, voire des années chez l'adulte, où s'observe une activité réduite de la muqueuse intestinale; au microscope électronique, on constate alors l'absence d'un ergastoplasme granulaire. Au cours de la deuxième phase, la digestion est nettement moins rapide chez les femelles vierges que chez les femelles fécondées.