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LIFE CYCLE OF EIMERIA COECICOLA CHEISSIN, 1947

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Abstract. Life cycle of *Eimeria coecicola* was studied in experimentally infected rabbits by light microscopy and by transmission and scanning electron microscopy. First and second generation meronts developed in the vermiform appendix; third and fourth generation meronts were located in the epithelium of the ileum. Gametogony developed again in the vermiform appendix. The prepatent period was 9 days. New data were obtained by the study of asexual reproduction. First generation meronts were first observed 4 days post infection (DPI), which is relatively late in comparison with other species of rabbit coccidia. Sporozoites were found in lymphatic follicles of the vermiform appendix at 4 DPI by transmission electron microscopy. This suggests, together with selective location of first generation meronts in the epithelium adjacent to these follicles, that major part of sporozoites enter the epithelium cells through lymphatic follicles and not through the lumen of the vermiform appendix. The process of development of first generation merozoites is similar to endodyogeny. The differences are in formation of apical parts of daughter merozoites which is not coincidental with nuclear division and in formation of the outer membrane of pellicle which arises within the mother cell. Some first generation merozoites have 2—3 nuclei, second and fourth generation merozoites are only uninucleate, while third generation merozoites are only multinucleate. We found that further merozoites are formed in multinucleate third generation merozoites by endopolygeny.

The life cycles of rabbit coccidia were described almost in all valid species, with the exception of *Eimeria coecicola*, the biology of which was described only by Cheissin (1947, 1967, 1968). Cheissin (1947, 1967) described meronts found in the ileum within 15 cm from ileocaecal valvule. Meronts observed at 6 DPI measured 12—18 μm and had 8—12 merozoites. Gamonts developed in the vermiform appendix and in the caecum from 7 DPI; first oocysts appeared in the faeces at 9 DPI. In addition to these stages Cheissin (1968) described also meronts found in the vermiform appendix visible until 9 DPI. Meronts measured 12—15 μm and produced elongate merozoites (10×0.8 μm). The whole endogenous cycle of *E. coecicola* was described insufficiently; neither the number of asexual generations, nor morphology of the endogenous stages of *E. coeciola* is known.

MATERIALS AND METHODS

Oocysts were put to sporulate in a 2—3 mm deep layer of 2.5% potassium dichromate in Petri dishes at room temperature.

Material used for inoculation was obtained from spontaneously infected rabbits (*Oryctolagus cuniculus*). Suspension of sporulated oocysts was diluted appropriately and then dropped on the slides. Individual drops were examined microscopically. Each drop containing only oocysts of *E. coecicola* was collected using a thin capillary tube. A total of 100 oocysts was collected and the suspension was diluted with five drops of water. Then a 5-week-old, coccidia-free rabbit was orally inoculated. Oocysts obtained from the faeces of this rabbit were used to study endogenous cycle.

Oocysts submitted for inoculation were cleaned and concentrated. An oocysts suspension was centrifuged, oocysts were once washed. The sediment was stirred in a 3M solution of saccharose and centrifuged at 750 g. The supernatant was diluted at least with a fivefold water volume and centrifuged. In this manner oocysts remained in the sediment. The size of inoculum was counted using a counting chamber working on a Mac Master chamber principle. Rabbits were inoculated with corresponding oocysts doses into the stomach via a catheter.

Crossbreds of Chinchilla and Californian White rabbits were used in the experiments. Females were housed with their young weaned rabbits in wooden cages, regularly cleaned with boiling water. The animals were fed pellets KO 16 and received only boiled water. They were treated with Sulfa-

kombin at a dose of 25 ml/l of water, which was discontinued 3 days before inoculation. Rabbits aged 5 weeks were used in experiments and were housed individually in metal cages cleaned daily with boiling water including water bottles and food dishes. The animals were coprologically examined each day during the whole experiment.

Rabbits were inoculated with oocysts of *E. coecicola*; the doses were as follows: 10^6 oocysts for rabbits killed at 2 and 3 DPI, 3×10^5 oocysts for rabbits killed at 4 and 5 DPI, 2×10^5 oocysts for rabbits killed at 6 and 7 DPI, 10^5 oocysts for a rabbit killed at 8 DPI, and 5×10^4 oocysts for a rabbit killed at 10 DPI. The whole experiment was repeated once more in the same arrangement. Always one rabbit killed at 7 days after beginning of the experiment served as uninoculated control during the whole experiment and the repeated one.

The animals were killed by ether. Samples from the small intestine were taken immediately behind the stomach and then at 10 cm intervals along its whole length (14—19 samples). The last sample was taken at the distance of 2—3 cm from the ileocaecal valvule. Four samples were taken from the caecum (1 sample from the region of ampula coli, then from the anterior, middle, and posterior parts of corpus caeci). Three samples from the vermiform appendix were taken (from the anterior, middle, and terminal parts). One sample was taken from the cranial part of the colon and then at 10 cm intervals (5—8 samples). In addition, one sample from the ileum and one sample from the vermiform appendix were taken from each animal for examination by scanning electron microscopy (SEM).

One rabbit inoculated with 3×10^6 oocysts and killed at 4 DPI, two rabbits inoculated with 3×10^6 and 10^6 oocysts and killed at 5 DPI, and finally two rabbits inoculated with 3×10^5 oocysts and killed at 6 DPI were used for ultrastructural examination of developmental stages of *E. coecicola*.

The material was fixed in 10% neutral formaldehyde, processed by conventional paraffin technique and tissue sections, cut at 4—7 μm were stained with Harris' haematoxylin-eosin.

The material used for SEM was fixed in 4% buffered paraformaldehyde (pH 7.2—7.4), postfixed in 2% OsO_4 in cacodylate buffer and dehydrated in a graded series of ethanol. Then the material was saturated with a 1 : 1 acetone — ethanol mixture and acetone, dehydrated using CO_2 critical point, mounted on stubs and coated with gold. A Tesla BS-300 scanning electron microscope was used for examination.

For transmission electron microscopy (TEM), the material was fixed and dehydrated in the same manner as for SEM, saturated with propylenoxid, a propylenoxid — Poly/bed 812 mixture and embedded in Poly/bed 812. Ultrathin sections were contrasted with uranyl acetate and lead citrate and examined with a Philips EM 420 electron microscope.

RESULTS

a) Light and scanning electron microscopy

Oocysts which were under study (Pl. I, Fig. 1) correspond to that described by Cheissin (1947, 1967, 1968). They are oval to cylindrical, possessing a light yellow or light brown wall which is thickened around a micropyle. The sporocysts are oval, with a small Stieda body. The residual body of the oocyst is spherical, while sporocyst's residual body is of irregular shape. A total of 100 oocysts measured as follows:

Oocysts: 33—38 × 18—22 μm, with a mean value of 35.2 × 20.2 μm
Sporocysts: 15—19 × 7—8 μm, with a mean value of 16.9 × 7.6 μm
Residual body of the oocysts: 5—8 μm, with a mean value of 6.5 μm
The width of the micropyle: 2.5—5 μm, with a mean value of 3.8 μm
Residual body of the sporocysts: 5—9.5 × 3.5—5 μm, with a mean value of 7.0 × 3.7 μm

The measurements of all stages of the endogenous cycle are mentioned in Table 1. The endogenous stages were first observed at 4 DPI in the vermiform appendix. The vermiform appendix in rabbits is the organ with a special histological structure (Snipes 1978). Lymphatic follicles are there in great numbers and they are located regularly, forming approximately a square net. The follicles are covered with a monolayer epithelium. Semi-rounded formations — domes are formed in these areas

Table 1. The life cycle of *Eimeria coecicola*

DPI	Stage	Length and width (μm)	Mean length and width (μm) (n = 100)	No. of merozoites in one meront	Size of merozoites (μm)	Mean size of merozoites (μm) (n = 100)
4	1st meront	5 — 9.5×4.5— 8	6.62× 6.40	2	4.5— 8×1.5—3.5	6.50×2.62
5	1st meront	5 —11 ×4.5— 9.5	8.17× 7.01	2— 8	5 —10×2 —4	7.97×2.95
6	1st meront	8 —13.5×6 —10	11.00× 8.33	2— 8	8 —13×2 —4	9.83×2.90
6	2nd meront	11.5—22.5×7 —17	16.00×13.33	8—47	8.5—13×1 —2	11.23×1.55
6	3rd meront	7 —14 ×4 —10	10.09× 8.05	4—25	6 —11×1.5—3	8.40×1.84
7	4th meront	8 —28 ×7 —17	16.06×10.12	12—80 approx.	4.5— 6×0.5—1	5.14×0.97
8	Mature gamonts (Female)	20—28.5×11—18	24.87×14.94			
	(Male)	15—31 ×11—25	22.63×15.33			

(Pl. I, Fig. 2). In other superficial parts mucosa overlaps the domes. From the viewpoint of the life cycle of *E. coecicola* it is important to differentiate the mucous epithelium, which either possesses or not the lymphoreticular tissue immediately below it. First asexual generation of this coccidium is selectively located in the epithelium of domes below which the lymphoreticular tissue is immediately located. First generation meronts occur first at 4 DPI, and they divide into two relatively short and thick merozoites (Pl. II, Fig. 2). The same meronts are found in the same location at 5 DPI, with the difference that some merozoites appear to be binucleate and trinucleate in comparison with the situation observed at 4 DPI (Pl. III, Fig. 1). The number of meronts with multinucleate merozoites can reach even 30% at 5 DPI as well as at 6 DPI. The number of binucleate merozoites was multiple larger than of trinucleate one. From 4 to 6 DPI the mean size of first generation merozoites increases (see Table 1).

From 5 to 7 DPI, with maximum occurrence at 6 DPI, second generation meronts containing long, slender merozoites were observed (Pl. III, Fig. 1). These are usually situated in a parallel arrangement and meronts possess sporadically a small residual body. Second generation meronts are located similarly as first generation meronts in the epithelium of domes and in the epithelial cells in the immediate vicinity of domes, too. Free second generation merozoites were found in slits between domes and mucosa of the vermiform appendix by means of SEM (Pl. IV, Fig. 3).

The developmental stages in the ileum were first observed at 6 DPI. We found third generation meronts located in the epithelium on the walls and tops of the villi, less frequently in the epithelium of the crypts. They contain merozoites mostly with 4 to 8 nuclei situated in a parallel arrangement or irregularly (Pl. V, Fig. 1). This type of meronts was observed predominantly at 6 and 7 DPI, less frequently at 8 DPI.

Fourth generation meronts were observed at 7 DPI and then always until 10 DPI with maximum occurrence at 8 DPI. These meronts contained large numbers of uninucleate merozoites, arranged usually in rosette-like patterns, which are compactly clustered (Pl. V, Fig. 4). Their nuclei are situated usually near the centre of the meront. Some differences exist in a fourth asexual generation, especially in the size of meronts and number of merozoites in individual meronts. It depends on the intensity of infection in a given place. During heavy infection the size of meronts is smaller and number of merozoites in meronts is lower.

The number of asexual stages in the vermiform appendix is lower at 7 DPI; young gamonts, located in the epithelium start to appear. They are found in the whole mucosal epithelium, not selectively in the epithelium of domes as in the first asexual generation. Asexual stages were observed scarcely in the vermiform appendix at 8 DPI, only mature gamonts and first oocysts were found (Pl. VI, Fig. 1). Meronts of all generations can be located above or below the host cell nucleus, while gamonts are usually below it. By means of SEM we observed that the cytoplasmic membrane of the host cell together with an adjacent cytoplasmic layer got vaulted above the releasing oocyst. Microvilli disappeared, cytoplasmic membrane was expanded and finally broken (Pl. VI, Fig. 2).

b) Transmission electron microscopy

A part of endogenous cycle of *E. coecicola* — sporozoites and first, second and third asexual generations were examined with the TEM. Sporozoites appeared at 4 DPI in the lymphoreticular tissue, not in the epithelium, where the first generation meronts undergo their development. Sporozoites do not differ in their ultrastructure

from commonly known coccidial sporozoites. A large refractile vacuole and amylopectin serving as a spare substance were observed. Also some components of apical complex — micronemes and rhoptries were visible on well-oriented sections (Pl. I, Fig. 3). Sporozoites were always found within the host cells, apparently lymphocytes, which were surrounded by a close space formed by the parasitophorous vacuole.

Process of inner formation of two daughter merozoites was observed in first generation meronts. This process is quite different from typical endodyogeny. Formation of apical complexes of daughter merozoites and inner membraneous complexes of their pellicle is not accompanied with a nuclear division. Obviously, no connection exists at that time between both nuclei because they are considerably separated in some cases. Nuclei protract towards the apical ends of future merozoites, where in addition to the bases of the apical complex and inner membraneous complex also the outes membrane of the pellicle is formed. This membrane follows a membrane which limits a half-mooned or horseshoe space surrounding the apical end of daughter merozoites (Pl. II, Fig. 1). It is not quite certain whether this space is formed from invaginating parasitophorous vacuole or whether the limiting membrane arises within the meront. The second alternative is more probable because the whole cytoplasm is abundantly vacuolated in this stage of the meront's development. Formation of merozoites without presence of these vesicles was not observed. Merozoites release from the mother cell but they remain connected with it in their posterior part. The outer membrane of the pellicle passes from merozoites to mother cell the structure of which has only one surface layer (Pl. II, Fig. 3). Double inner membrane of the merozoites terminates in the place where a merozoite strangulates from mother cell (Pl. II, Fig. 4). At 4 DPI most of first generation merozoites are not separated from mother cell. This fact can clarify the shorter length of first generation merozoites at 4 DPI in comparison with the length examined with an optical microscope at 5 and 6 DPI (see Table 1). Except for being multinucleate, binucleate or trinucleate merozoites do not differ in their structure from typical coccidial merozoites (Pl. III, Fig. 2). They possess a typical developed apical complex, a pellicle with three layers, nuclei with nucleoli, mitochondria, endoplasmatic reticulum and spare substances. The inner formation of daughter merozoites has never been observed in multinucleate first generation merozoites which was observed in multinucleate merozoites of *Eimeria magna* (Danforth and Hammond 1972) and in multinucleate third generation merozoites of *E. coecicola* described in this paper (see later). Since we did not observe any further development in multinucleate first generation merozoites we presume that they escape as a whole from their host cell and penetrate other epithelial cells of the mucosa of the vermiform appendix.

Second generation merozoites are formed by ectomerogony. Formation of their apical complexes and inner membraneous complex of their pellicle is connected with the cytoplasmic membrane of a meront (Pl. III, Fig. 3). Merozoites are then shifted into the parasitophorous vacuole whereas the remnant of the mother cell is visible in meronts at this stage both by electron and optical microscope (Pl. III, Figs. 4,5). Subsequently, this remnant of the mother cell disappears. Second generation merozoites are relatively short and thick at first, later they are elongated. Mature merozoites are situated mostly parallel in a meront; their apical complexes are pointed in the same direction (Pl. IV, Fig. 2). The ultrastructure of second generation merozoites is typical of coccidial merozoites; conspicuous are large numbers of micronemes observed nearly along the whole length of merozoites.

Multinucleate third generation merozoites were also observed by means of TEM (Pl. V, Fig. 2), within which inner membraneous complexes and rhoptry anlagen of future merozoites are formed in a close connection with nuclei (Pl. V, Fig. 3). Further

development of these stages was not observed. We presume that a process of inner merozoite formation analogous with observations of Danforth and Hammond (1972) in *E. magna* takes place here and corresponds to endopolygony.

DISCUSSION

Only Cheissin (1947, 1967, 1968) studied endogenous cycle of *E. coecicola*. However, he did not mention the number of asexual generations. Cheissin recorded meronts measuring 12—15 μm which were found in the vermiform appendix till 9 DPI and contained elongate merozoites measuring 10 × 0.8 μm. In spite of this fact that the merozoite width taken by us was rather greater, we suppose that second asexual generation takes place here. In addition to these stages, Cheissin described stages in the ileum. At 6 DPI he found meronts measuring 12—18 μm which contained 8—12 merozoites. These meronts might correspond to third generation meronts which we observed. Cheissin asserts that endogenous development of *E. coecicola* takes place in the caecum and vermiform appendix, whereas meronts can be located also in the ileum. We observed all developmental stages in the vermiform appendix or ileum in the present study, never in the caecum. Cheissin's opinion, that all stages are located below the nucleus of the host cell, was supported only as far as gametogony is concerned. Asexual stages were also found above the nucleus of the host cell. The prepatent period being 9 days corresponds to Cheissin's description.

First stages of endogenous cycle of *E. coecicola* were found in our experiments at 4 DPI which is rather late in comparison with other species of rabbit coccidia. We recorded sporozoites of *E. coecicola* in supplementary experiment at 3 DPI in one of 3 rabbits inoculated with a dose of 5 million oocysts in small numbers only. No sporozoites of *E. coecicola* were seen in the two remaining rabbits. Sporozoites were observed in the histological material taken from the epithelium of the vermiform appendix, in which also first generation meronts develop. Other stages except for sporozoites were not found at 3 DPI. Sporozoites were observed in the lymphoreticular tissue by TEM at 4 DPI. Sporozoites are not usually visible on histological sections of lymphoreticular tissue as there are large numbers of lymphocytes. Their nuclei stain hard with haematoxylin and overlap sporozoites.

Sporozoites do not reach in a short time after the excystation the epithelial cells of the vermiform appendix, where their further development takes place. It probably causes that the first generation meronts (4 DPI) appear rather late. It is known that free sporozoites of *E. magna* can be detected in the intestinal lumen as late as at 48 hours post infection (Ryley and Robinson 1976). Streun et al. (1979) observed free or fresh-invalid sporozoites of *E. perforans* which is located in the upper part of the small intestine even at 36 hours post infection.

However, sporozoites need not occur only in the intestinal lumen. It was proved in eimerians in chickens (Kogut and Long, 1984; Perry and Long, 1987) and in rats (Marquardt et al., 1984), that sporozoites do not divide immediately after the excystation, they enter through the intestine other organs and persist in them. It is possible, even several days post infection to infect with the homogenates obtained from these organs some other hosts in the same manner as if they were infected with oocysts. The purpose of such sporozoite migration is not clear. There are also some cases when sporozoites do not penetrate outside the intestine and they need not immediately enter the cells where their further development takes place. Lawn and Rose (1982) reported that sporozoites of *E. tenella* enter first enterocytes at the mucosal surface of the caecum, then enter intraepithelial lymphocytes and are transported

by them through lamina propria into the crypt's epithelium where the development of first generation meronts takes place.

We have found some peculiarities in the life cycle of *E. coecicola* which are directly or indirectly related to sporozoites.

1. Sporozoites were hardly detected in the epithelium of the vermiform appendix, where first generation meronts develop.
2. Sporozoites were found in lymphatic follicles of the vermiform appendix.
3. First generation meronts did not appear sooner than at 4 DPI.
4. First generation meronts are selectively located in the epithelium of domes, below which the lymphoreticular tissue is immediately located.

It appears that sporozoites enter the epithelium of the vermiform appendix through the lymphatic follicles and use the host cells, probably lymphocytes for their transport. However, it is not known where and in which manner sporozoites enter the lymphatic system of the host. Similar situation occurs in other rabbit coccidium — *E. stiedai*, where the lymphatic system of the host is used for transport of sporozoites from duodenum into the liver (Dürr 1972).

It appears from the above description of the life cycle of *E. coecicola* that second generation merozoites migrate from the vermiform appendix into the ileum. The way of this migration is not clear. The two theoretical possibilities which were not experimentally verified may arise — merozoites migrate through the intestinal lumen or use the host cells — lymphocytes or macrophages for their transport.

Although endodyogeny is a process typical of heteroxenous coccidia, it also occurs in monoxenous coccidia. Scholtyseck (1973) recorded the formation of "cytomeres" arisen from concentrically arranged vesicles of the endoplasmic reticulum in *E. tenella* and *E. stiedai*. A process corresponding to endodyogeny was observed within the cytomeres. This process was observed within the meronts, Scholtyseck and Ratanavichien (1976) observed endodyogeny within the merozoites in *E. stiedai*. We observed a process corresponding to endodyogeny in first generation meronts of *E. coecicola*. However, the two main differences were found in comparison with a typical endodyogeny. The formation of apical parts of daughter merozoites is not coincidental with nuclear division and the outer membrane of a three-layer pellicle arises within the mother cell. In typical endodyogeny merozoites obtain the outer membrane of their pellicle when they leave the mother cell and cover themselves with its surface membrane. Another possibility arises — the space surrounding the apical ends of arising merozoites may be the invagination of parasitophorous vacuole. In this case it would be only a modification of ectomerogony. Owing to large numbers of follicles in the meronts' cytoplasm it is likely that the membrane which limits a halfmooned or horseshoe space surrounding the apical ends of arising merozoites is formed within the meront. This membrane also forms the outer surface membrane of the merozoite pellicle.

In general, multinucleate merozoites are an exceptional phenomenon in the life cycle of coccidia, however, their occurrence in rabbit coccidia is quite common. Multinucleate merozoites have been recorded in major part of known species — in *E. perforans* (Streun et al. 1979), *E. magna* (Cheissin 1940, Sénaud and Černá 1969, Speer et al. 1973, Danforth and Hammond 1972, Ryley and Robinson 1976), *E. intestinalis* (Pellérdy 1953, Catchpole and Norton 1975), *E. stiedai* (Pellérdy and Dürr 1970, Černá and Sénaud 1971, Heller 1971), *E. flavescens* (Norton et al. 1979). We also observed multinucleate merozoites in *E. media* and *E. vejdovskyi* sp. n. (Pakandl 1988).

Both multinucleate and uninucleate merozoites have been found in all above species.

A quite different situation was observed in *E. coecicola* in the present study. Primarily we observed uninucleate first generation meronts, which later possessed even 2—3 nuclei. Third generation merozoites are only multinucleate, second and fourth generation meronts are only uninucleate. It is evident from the chronology in which individual meronts appear that there are four different generations and not only two generations involving two types of meronts.

We observed that further merozoites start their formation within the third generation merozoites in close contact with nuclei. This process was described in *E. magna* by Danforth and Hammond (1972). It was not detected from the observations of the ultrastructure of these stages whether multinucleate merozoites escape as a whole from the mother cell and penetrate other cell or whether new merozoites separate within the same parasitophorous vacuole. Heller (1971) supposed that in *E. stiedai* uninucleate merozoites are formed from multinucleate merozoites within the same parasitophorous vacuole. Shah (1971) observed second generation merozoites in *Isospora felis*. These are first uninucleate, then, however, nuclear division takes place within the merozoites and uninucleate merozoites of the third generation are formed within the same parasitophorous vacuole. The question whether multinucleate merozoites leave or not the host cell is not important in determination of their role in the life cycle of coccidia. The results of Speer et al. (1973) indicate that both alternatives may occur. Multinucleate merozoites of *E. magna* obtained from rabbit intestines can penetrate cells in the tissue culture and transform into globular meronts which give rise to merozoites. Formation of multinucleate merozoites was also observed, (*Speer* et al. termed them as meroschizonts). Sometimes, multinucleate merozoites either leave the host cell or they persist within the same parasitophorous vacuole and give rise to the uninucleate merozoites.

In major cases the uninucleate merozoites occur in coccidia, they penetrate other host cell in which nuclear division takes place. However, this nuclear division can be considerably chronologically shifted and can take place before the merozoites separate from the mother cell (Danforth and Hammond 1972). Results obtained from the observations of the development of *E. magna* in tissue cultures (Speer and Hammond 1971, Speer et al. 1973) indicate that originally only one nucleus was incorporated within the multinucleate merozoites. It appears that multinucleate merozoites possess some properties of a merozoite and some of a meront. From this viewpoint the strict differentiation of asexual stages into meronts (schizonts) and merozoites need not be always correct.

ЖИЗНЕННЫЙ ЦИКЛ *EIMERIA COECICOLA CHEISSIN*, 1947

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Резюме. Жизненный цикл *Eimeria coecicola* изучали на экспериментально зараженных кроликах с помощью световой микроскопии, трансмиссионной и сканирующей электронной микроскопии. Первая и вторая генерации меронтов развивались в червеобразном отростке, третья и четвёртая генерации меронтов находились в эпителии тонкой кишки. Гаметогония проходила опять в червеобразном отростке. Препатентный период составил 9 дней. Новые данные получены при изучении бесполового размножения. Первая генерация меронтов была обнаружена 4 дня после заражения (ДПЗ), что сравнительно поздно в сравнении, с другими видами кроличьих кокцидий. Спорозоиты были обнаружены с помощью трансмиссионной электронной микроскопии в лимфатических фолликулах червеобразного отростка начиная с 4-го ДПЗ. Это указывает, вместе с предпочтительной локализацией первой генерации меронтов в эпителии прилегающем к этим фолликулам, что большинство спорозоитов попадает в клетки эпителия через лимфатические фолликулы, а не через просвет червеобразного отростка. Процесс развития первой генерации меронтов похож на эндодиогонию. Различия заключаются в формировании апикальных частей дочерних мерозоитов, что не совпадает с делением ядра и в формировании наружной мембраны пелликулы, которая возникает в родительской клетке. Некоторые первые генерации мерозоитов содержат 2—3 ядра, вторая и четвёртая генерации мерозоитов только моноядерные, в то время как третья генерация мерозоитов всегда многоядерная. Нами обнаружено, что следующие мерозоиты формируются в многоядерной третьей генерации мерозоитов посредством эндополигонии.

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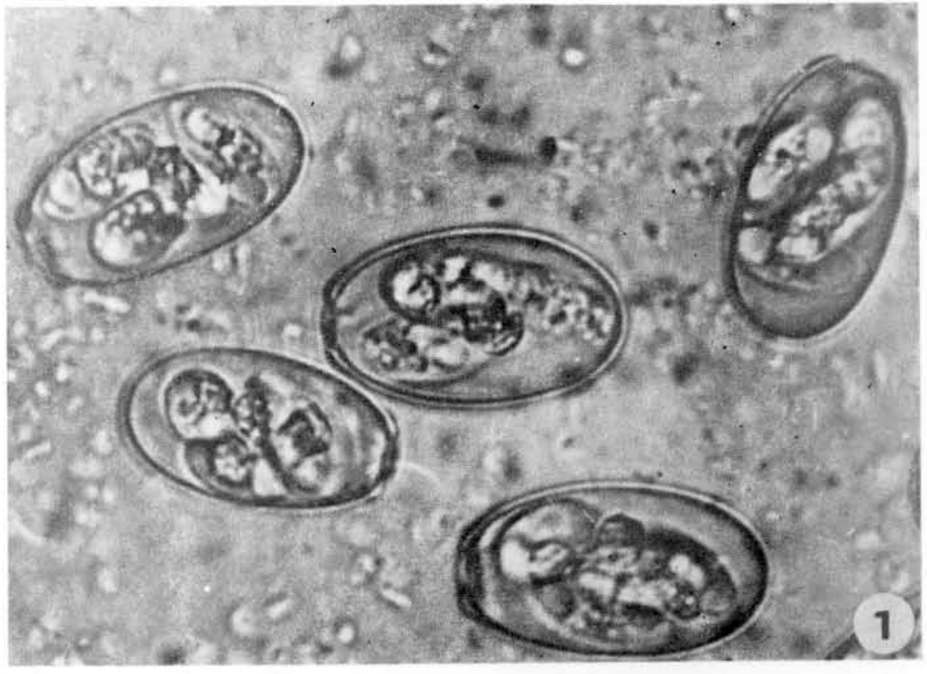
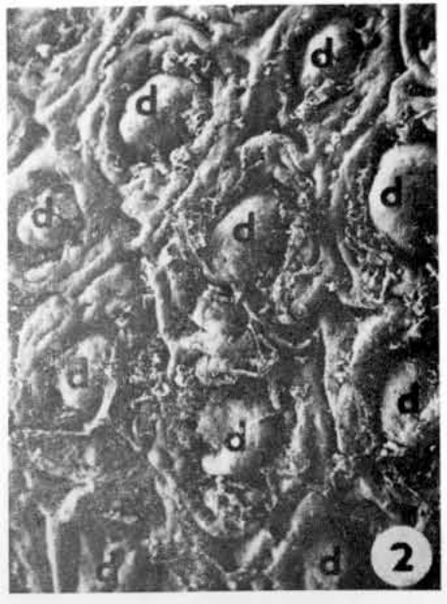




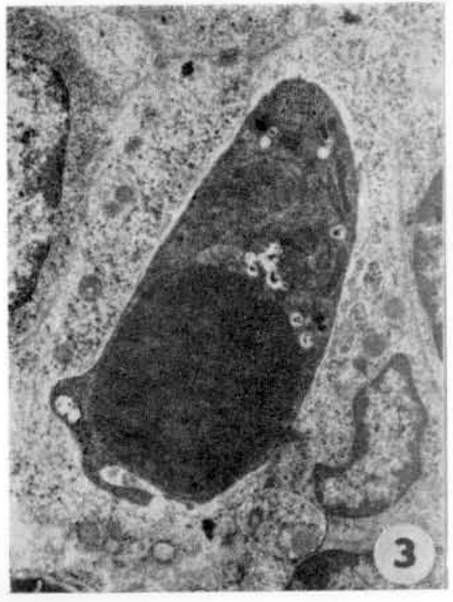
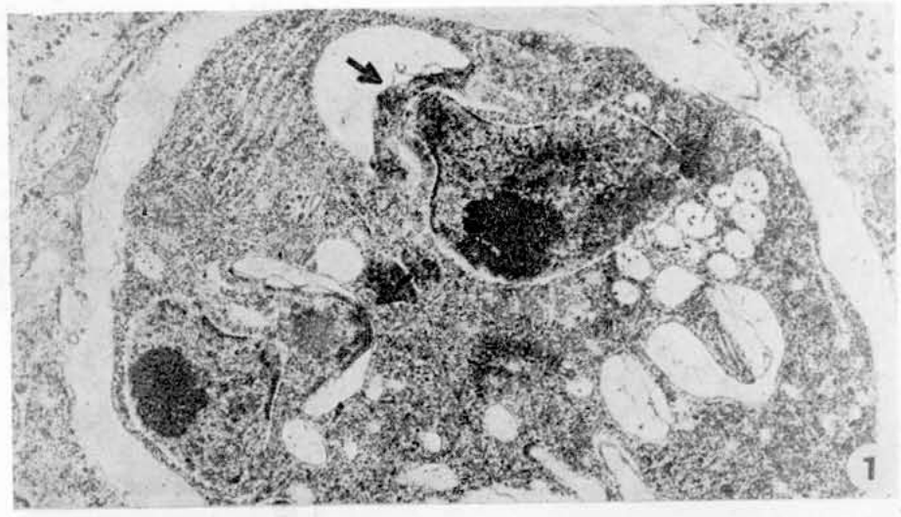
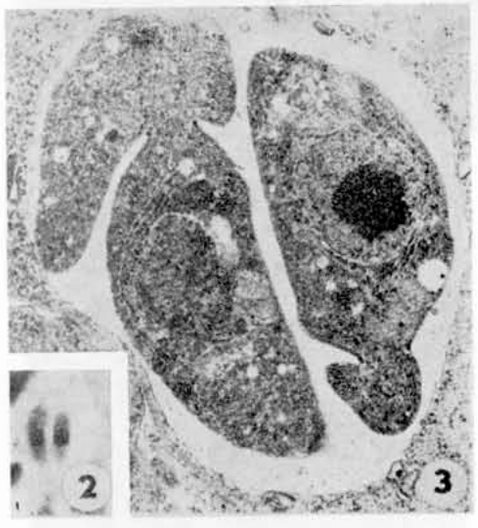


Fig. 1. Oocysts of *E. coecicola* (native, × 1 200). **Fig. 2.** Surface of the mucosa of the vermiform appendix of a control rabbit with domes (d) (SEM, × 150). **Fig. 3.** Sporozoite of *E. coecicola* (T EM, × 8 500).





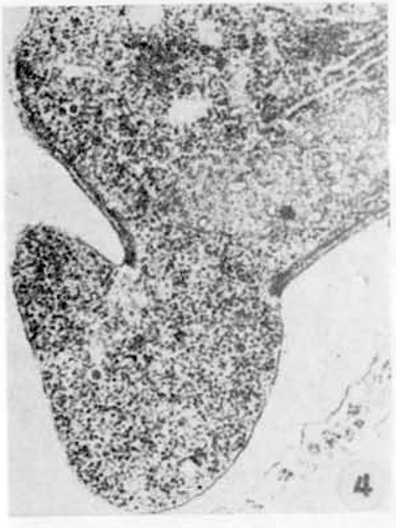


Fig. 1. Formation of first generation merozoites (arrows) (TEM, ×15 000). **Fig. 2.** First generation meront with uninucleate merozoites. Histological section stained with Harris' haematoxylin — eosin (HE, ×1 300). **Fig. 3.** First generation meront with uninucleate merozoites (TEM, × 8 550). **Fig. 4.** Detail of Fig. 3. Inner membraneous complex of merozoites' pellicle ending in the place where merozoite strangulates from mother cell (TEM, × 27 000).

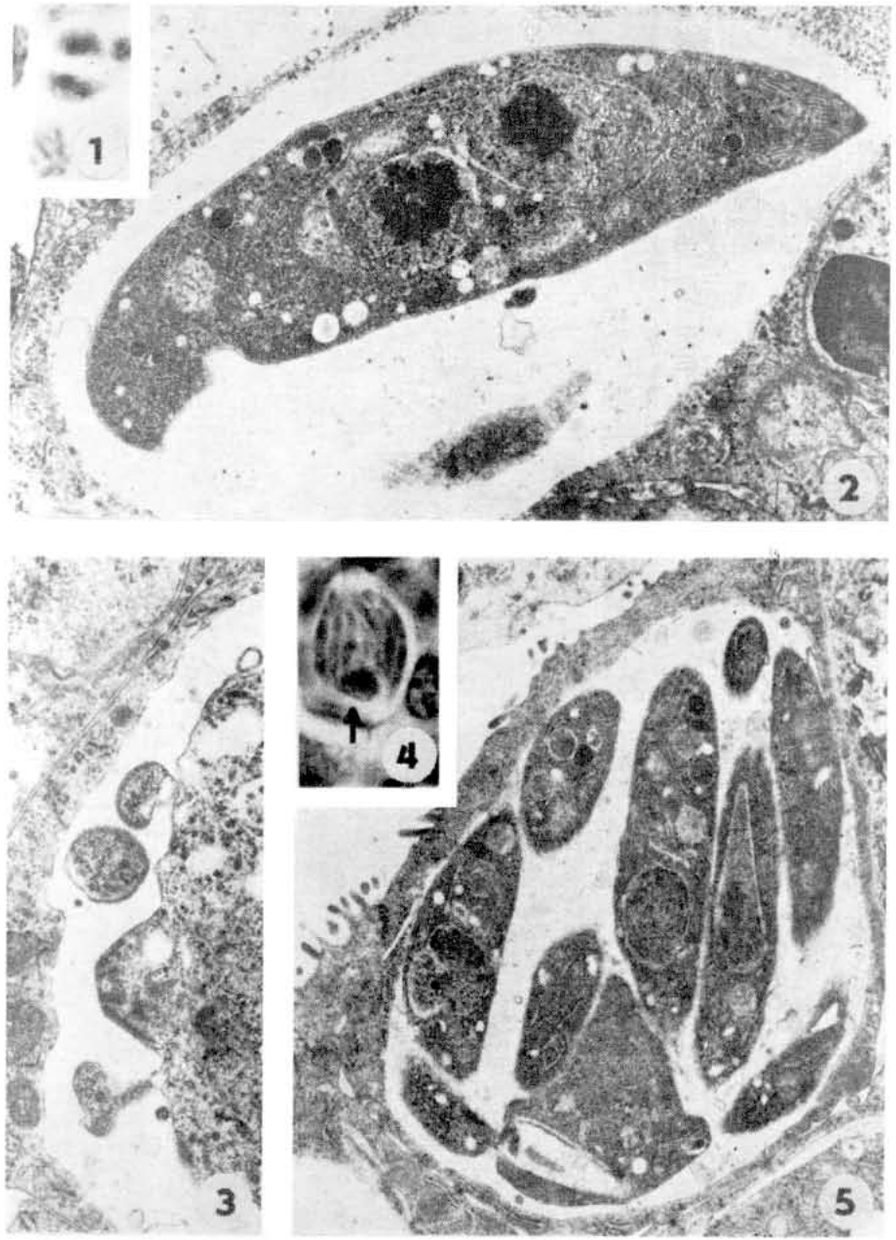


Fig. 1. First generation meront with binucleate merozoites (HE, × 1 300). **Fig. 2.** Binucleate first generation merozoite (TEM, ×10 600). **Fig. 3.** Initial stage of second generation merozoite formation (TEM, ×1 800). **Fig. 4.** Second generation meront with the remnant of mother cell (arrow) (HE, × 1 500). **Fig. 5.** Second generation meront with the remnant of mother cell (TEM, × 9 600).

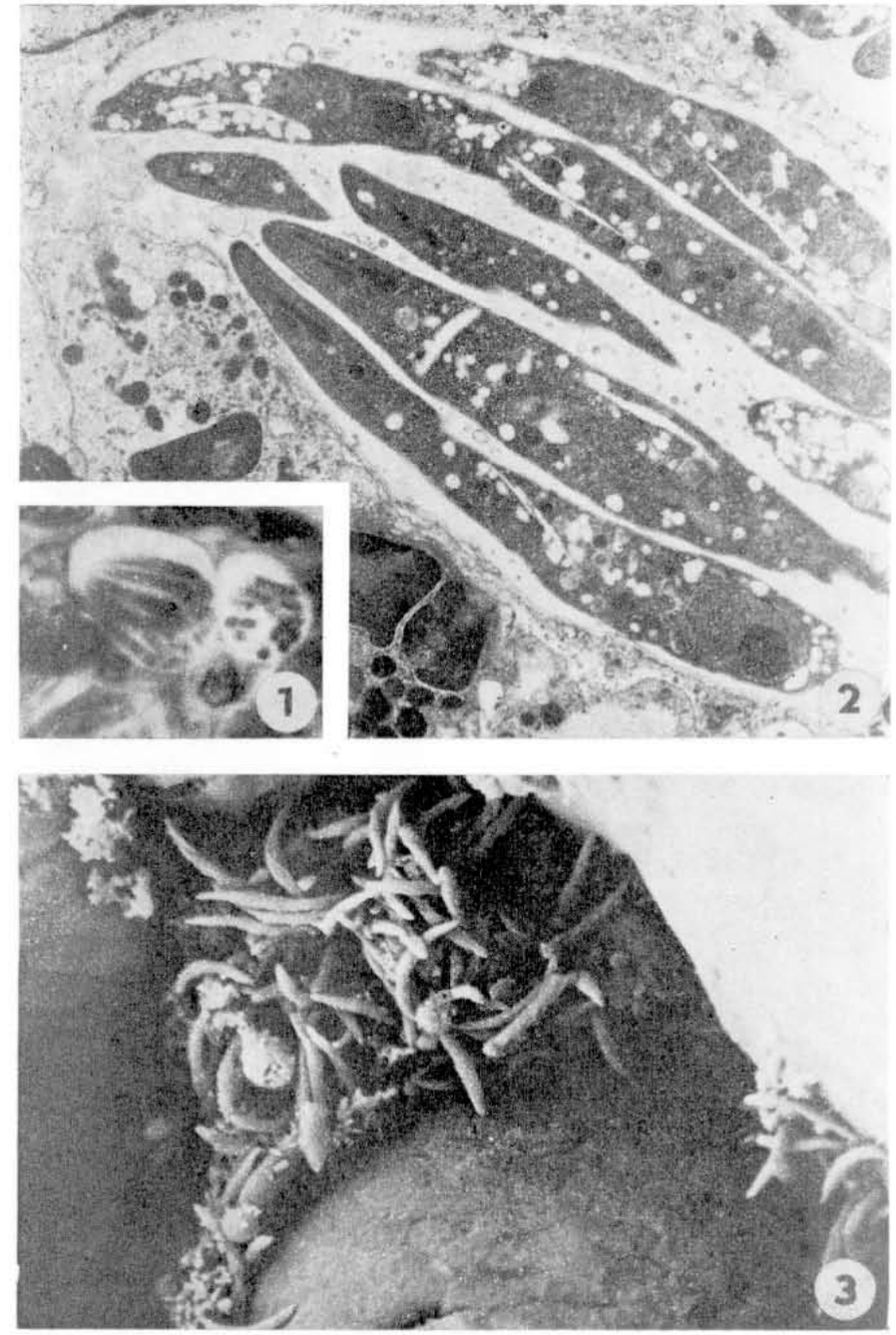


Fig. 1. Second generation meront (HE, × 1 500). **Fig. 2.** Second generation meront with mature merozoites (TEM, ×8 800). **Fig. 3.** Second generation merozoites in the slit between dome and mucosa (SEM, × 1 700).

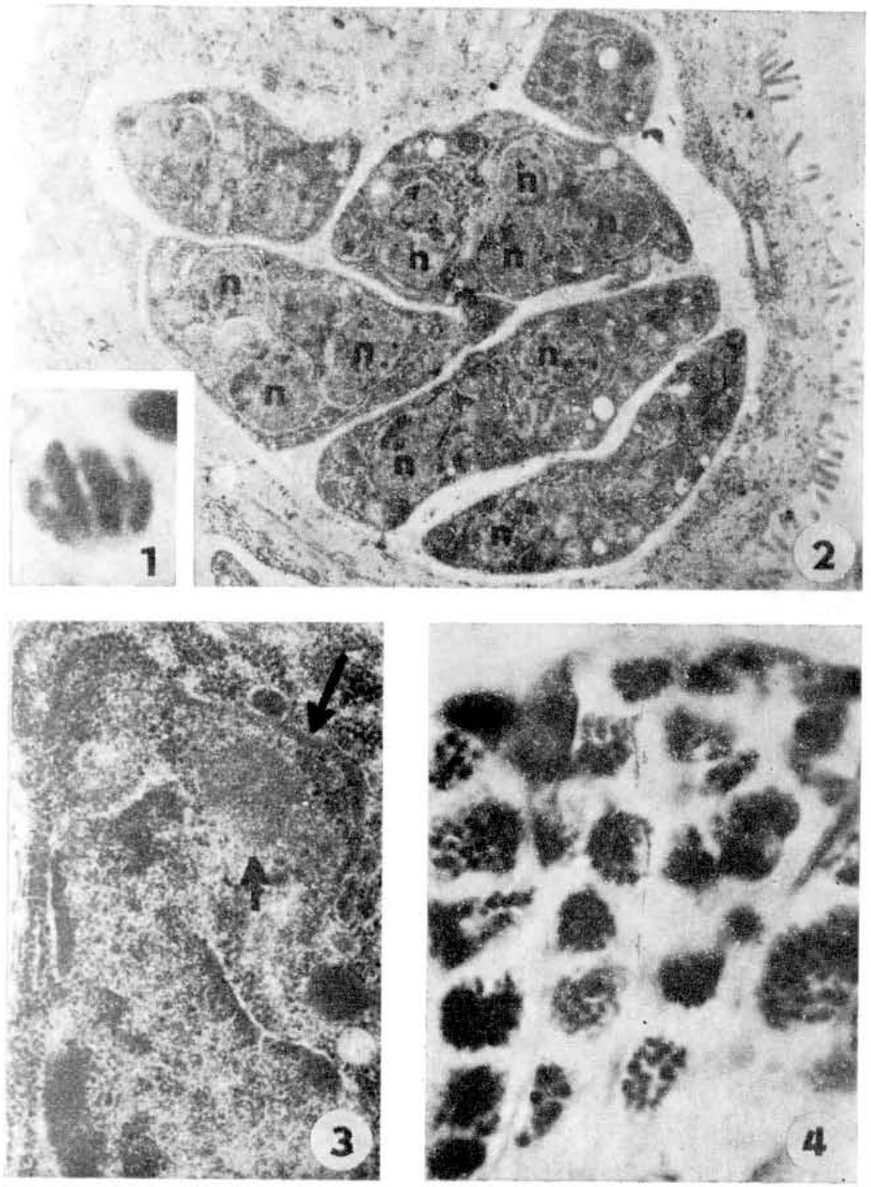


Fig. 1. Third generation meront (HE, × 1 600). **Fig. 2.** Third generation meront. Some merozoites possess more nuclei in the section level (n) (TEM, × 8 100). **Fig. 3.** Detail of Fig. 2. Apical parts of future merozoite arise in a close connection with nuclei — the inner membraneous complex of pellicle (long arrow) and rhoptry anlagen (short arrow) are apparent (TEM, × 33 300). **Fig. 4.** Fourth generation meronts in the epithelium of ileum (HE, × 1 300).

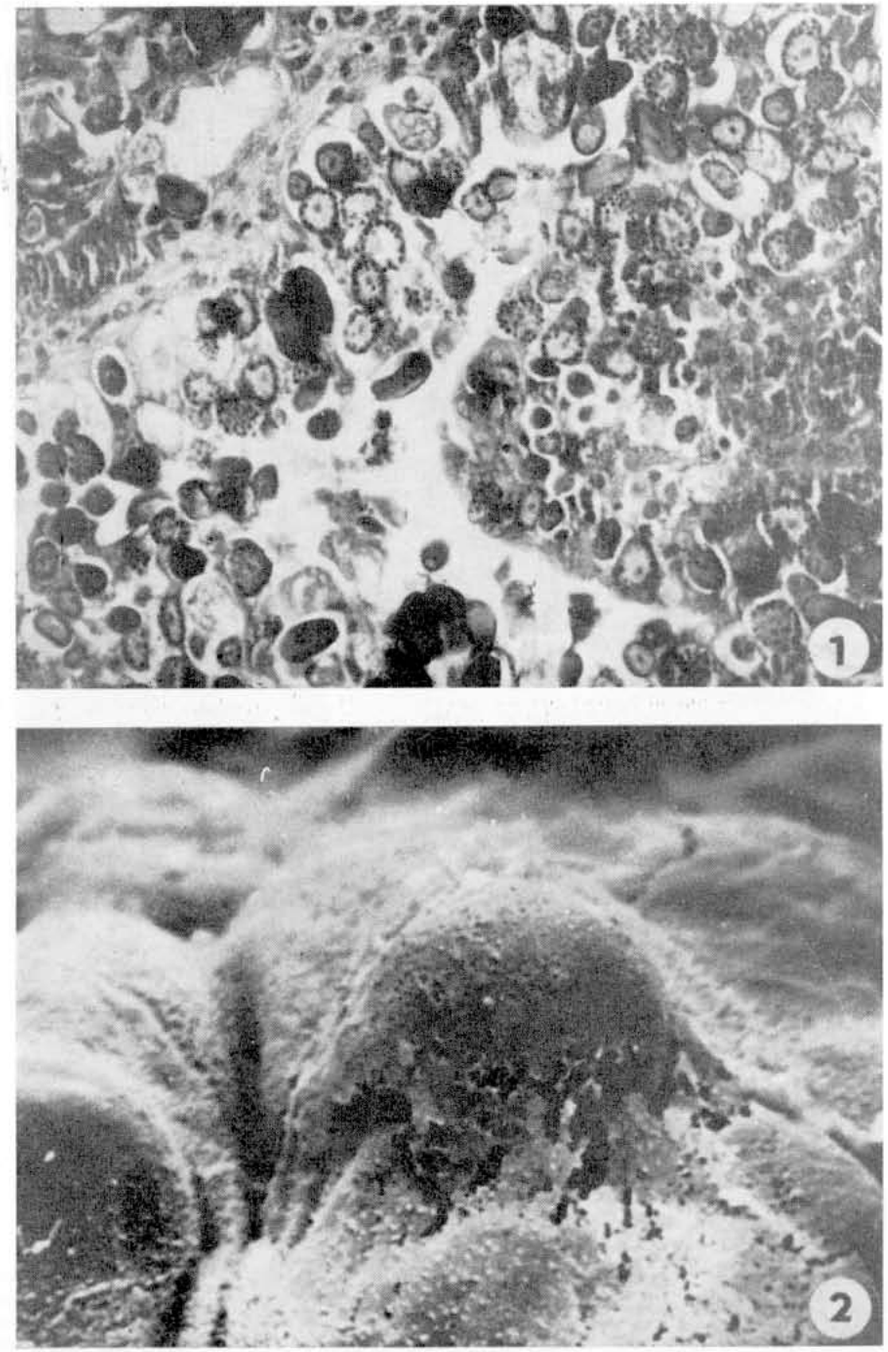


Fig. 1. Gametogony developing in the epithelium of mucosa of the vermiform appendix (HE, × 300). **Fig. 2.** Surface of the host cell above the releasing oocyst is without microvilous zone, cytoplasmic membrane of the host cell expands and breaks above the releasing oocyst (SEM, × 1 830).