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ORIGINAL PAPER

Life cycle of *Sarcocystis camelicanis* infecting the camel (*Camelus dromedarius*) and the dog (*Canis familiaris*), light and electron microscopic study

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Abstract In the present study, the heteroxeneous life cycle of *Sarcocystis* sp. infecting camels were studied. A total of 180 slaughtered camels collected from different localities in Egypt were investigated for sarcocysts. Only 116 animals were found to be infected (the infection rate was 64%). Muscle samples of esophagus, diaphragm, tongue, skeletal, and heart muscles were examined. Exclusively, microscopic sarcocysts were detected in all examined organs. The infection rates of the esophagus, diaphragm, tongue, skeletal, and heart muscles were 60%, 50%, 40%, 40%, and 10%, respectively. By means of transmission electron microscopy, details of the ultrastructure of the sarcocysts were studied. The specific architecture and ornaments of the cyst wall, its protrusions, and the cyst interior were recorded. Unique features of protrusions of the primary cyst wall, the knob-like structures, arise around each protrusion. Experimental infection of carnivores by feeding heavily infected camel muscles revealed that the dog, *Canis familiaris*, is the only final host of the present *Sarcocystis* species. Gamogony, sporogonic stages, and characteristics of sporulated oocysts were also investigated.

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Introduction

Sarcocystis cysts were first described by Miescher as early as 1843 and first named by Lankester (1882); however, their coccidian life cycle as members of the phylum Apicomplexa was first established by Heydorn and Rommel (1972). An obligatory heteroxeneous life cycle was elucidated. The genus *Sarcocystis* comprises about 130 species with differences in life cycle and pathogenicity and represents important members of the cyst forming coccidia. Many reports on *Sarcocystis* infections among different vertebrates including even man were recorded (Mehlhorn and Heydorn 1978; Dubey et al. 1983; Entzeroth et al. 1985; Abdel-Ghaffar et al. 1978, 1990a, b; Abdel-Ghaffar and Al-Johany 2002). It is now proven that the *Sarcocystis* are cosmopolitan. High prevalence of *Sarcocystis* has been reported in cattle, sheep, and swine. The pathogenicity of *Sarcocystis* species is of different gravity including a possible fatal outcome for the host (Melhorn 2008).

Although the early detection of *Sarcocystis* infection among the one-humped camels was recorded in Egypt (Mason 1910), this infection now seems to be cosmopolitan with many complications to the infected host (Boid et al. 1985; Kirmse 1986; Kirmse and Mohanbabu 1986; Ouhelli and Dakkak 1987; Abdurahman and Bornstein 1991). This disease was recorded in several semiarid and arid zones of the world, in Egypt, Saudi Arabia, Iran, Afganistan, Morocco, Sudan, and Southern Ethiopia (Woldemeskel and Gumi 2001; Valinezhad et al. 2008). Nearly all

previous studies were dealing with the detection, prevalence, and intensity of such infection of the different organs of investigated camels. Ultrastructure characteristics of sarcocysts and the heteroxeneous life cycle in the final host are the most important criteria for the specification of *Sarcocystis* species (Mehlhorn and Heydorn 1978, 1979; Mehlhorn et al. 1976; Melhorn 2008).

Therefore, the present study aimed to investigate the prevalence of *Sarcocystis* infection among slaughtered camels in Egypt and to examine the ultrastructural characteristics of the sarcocysts inside the different organs of the animals. Furthermore, the different stages and the pathway of transmission were investigated.

Materials and methods

A total of 180 muscle samples of the esophagus, diaphragm, tongue, skeletal, and heart muscles were randomly collected from freshly slaughtered camels (*Camelus dromedarius)* in the main slaughter houses of Cairo, Beni Suef, and El Minia cities, Egypt (from June to December 2008).

All muscle samples were examined for macroscopic cysts. Then fresh smears, cryosections, and tryptic digestion preparations were examined by means of light microscopy. Small pieces of highly infected muscles were immediately fixed in 3% (*v*/*v*) glutaraldehyde in 0.1 M cacodylate buffer for at least 4 h at 4°C. Fixed samples were post fixed in 2% (*w*/*v*) O_SO_4 in the cacodylate buffer for 24 h, then washed four to five times in the buffer (10–15 min each). Specimens were dehydrated in graded ethanol, transferred to propylene oxide, and finally embedded in Araldite (Sigma) embedding medium. Semi- and ultrathin sections were cut on a Reichert–Jung ultracut microtome. Ultrathin sections were stained with uranyl acetate and lead citrate before examination with a Zeiss A 902 transmission electron microscope.

In order to find the definitive host and to study gamogony and sporogony, laboratory bred and coccidian-free 13 young puppies (*Canis familiaris*) being 2–3-month old and 13 kittens (*Felis catus*) of the same age were fed small segments of highly infected muscles of the camels. Kittens and puppies used in the experimental infection were usually fed boiled milk and bread and had never been fed meat before infection. These animals were kept alive and examined daily for the shedding of any coccidian oocysts for a period of 7 weeks postinfection (p.i.). After the identification of dogs as final definitive hosts who shed sporulated oocysts and/or sporocysts. Two experimentally infected dogs were killed 12 or 24 h postinfection to study the gamogonic stages. For sporogony, dogs were killed on days 3, 5, 6, 7, 8, 9, 11 p.i. Two noninfected animals were used as controls. Fecal samples from both—infected and control animals—were examined daily for a period of 7 weeks after feeding the dogs with the infected muscles. The small intestine of the experimentally infected dogs was divided into five equally sized segments between the pylorus and ileocaecal valve. Their mucosa and submucosa were scraped, cut into small pieces, and fixed in 3% (*v*/*v*) glutaraldehyde in 0.1 M cacodylate buffer (pH 7.3), at least for 4 h. Samples were processed for light microscopic examination using a Carl Zeiss photomicroscope.

Results

Out of 180 examined animals, 116 camels were found to be infected (64%). Preliminary investigation of the collected muscle samples (examined by naked eye) indicated the absence of any macroscopic cysts of *Sarcocystis*. At the same time, examination of cryosections stained with Giemsa stain indicated the presence of microscopic cysts. This type of microscopic sarcocysts measured 120–170×50–100 μm in size. The infection rates among the muscles of the different organs varied between 60% in the esophagus muscles and 50% in the diaphragm, 40% in the tongue and skeletal muscles followed finally by 10% in the heart.

Transmission electron microscopic examination of ultrathin sections obtained from different muscle samples revealed the presence of only one cyst type.

The marginal part of the cyst showed clearly the primary cyst wall with its elongated protrusions while the interior of the cyst contained mostly cyst merozoites (cystozoites) and only a few metrocytes lying closely together. The ground substance underneath the primary cyst wall appeared rather homogeneous and extended in to the interior of the cyst forming thin septa separating the whole cyst into a number of compartments enclosing the metrocytes and merozoites (1 of Fig. 1 and 4 of Fig. 2).

It was also observed that the cyst merozoites (zoites) occupying the interior of the cyst were closely filled with amylopectin granules which represent the carbohydrate reserve materials of these stages (4 of Fig. 2).

The primary cysts wall appeared as a thick electron dense layer. This layer was folded giving rise to successive finger-like protrusions of similar length, size, and shape with a blunt apex. Their surface was noncerrated and not branched. The core of these protrusions was characterized by the presence of longitudinally extended microfibrils throughout the whole length of the protrusion. Knob-like structures were found regularly alone in the primary cyst wall of each protrusion. About 16–18 knobs were seen along each protrusion. (1 of Fig. 1 and 3 of Fig. 2). The protrusions stood in direct contact with the sarcoplasm and were usually surrounded by host cell mitochondria (1 and 2 of Fig. 1 and 3 of Fig. 2).

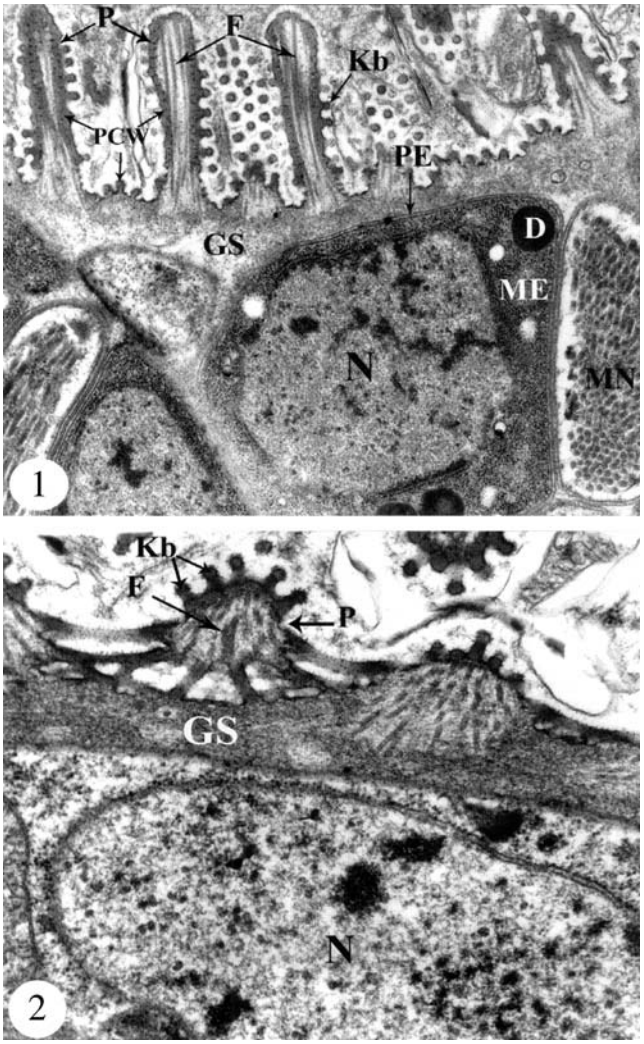

Fig. 1 Electron micrographs. *1* Primary cyst wall (*PCW*) and finger-like protrusions (*P*) with knob-like structures arising from the primary cyst wall; fibrillar structures (*F*) are observed inside the protrusions; a large metrocyte (*ME*) with a prominent pellicle (*PE*) is found directly below the ground substance (*GS*); ×20,000. *2* Protrusions (*P*) with knob-like structures (*Kb*) and fibrillar structure (*F*) arising from the ground substance (*GS*); ×25,000

It is very interesting how the protrusions arose from the ground substance. A number of arborization-like structures were observed at the base of each protrusion representing the root of this structure. The arborizations of one protrusion seemed to be connected with the base of the neighboring one (2 of Fig. 1), thus, apparently giving rise to an enormous enlargement of the surface.

The metrocytes appeared subspherical to ovoid in shape and were usually located peripherally with some exceptions where a few of them were located centrally. These stages were bordered by a clearly visible double membranous pellicle and showed inside remnants of the apical complex represented by a number of micronemes and dense bodies. Cell division resulted in the formation of two daughter cells (1 of Fig. 1 and 4 of Fig. 2).

Large numbers of elongated cyst merozoites, which were provided with all characteristics of Apicomplexa, were detected. Each cyst merozoite was characterized at the anterior end by a typical pellicle, conoid, rhoptries, micronemes which appeared somewhat elongated in longitudinal sections but rounded in cross-sections occupying the anterior third of the whole body (4 of Fig. 2). Furthermore, large numbers of osmiophilic dense bodies and many amylopectin granules were found. No micropores were observed in the present studied sections.

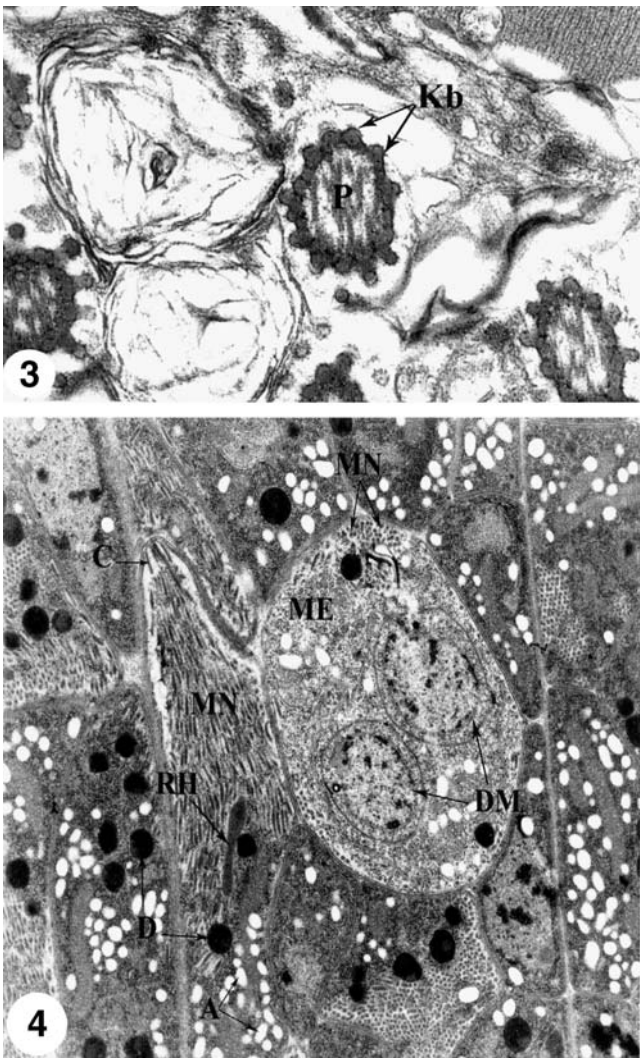

Fig. 2 Electron micrographs. *3* Cross section showing the knob-like structures of the protrusions and the destruction of the host cell close to the surface of the cyst; ×30,000. *4* Interior of a cyst showing the architecture of a dividing metrocyte (*ME*) with two daughter merozoites (*DM*) and a number of cyst merozoites with the apicomplexan organelles: conoid (*C*), rhoptries (*RH*), micronemes (*MN*), and amylopectin(*A*); ×10,000

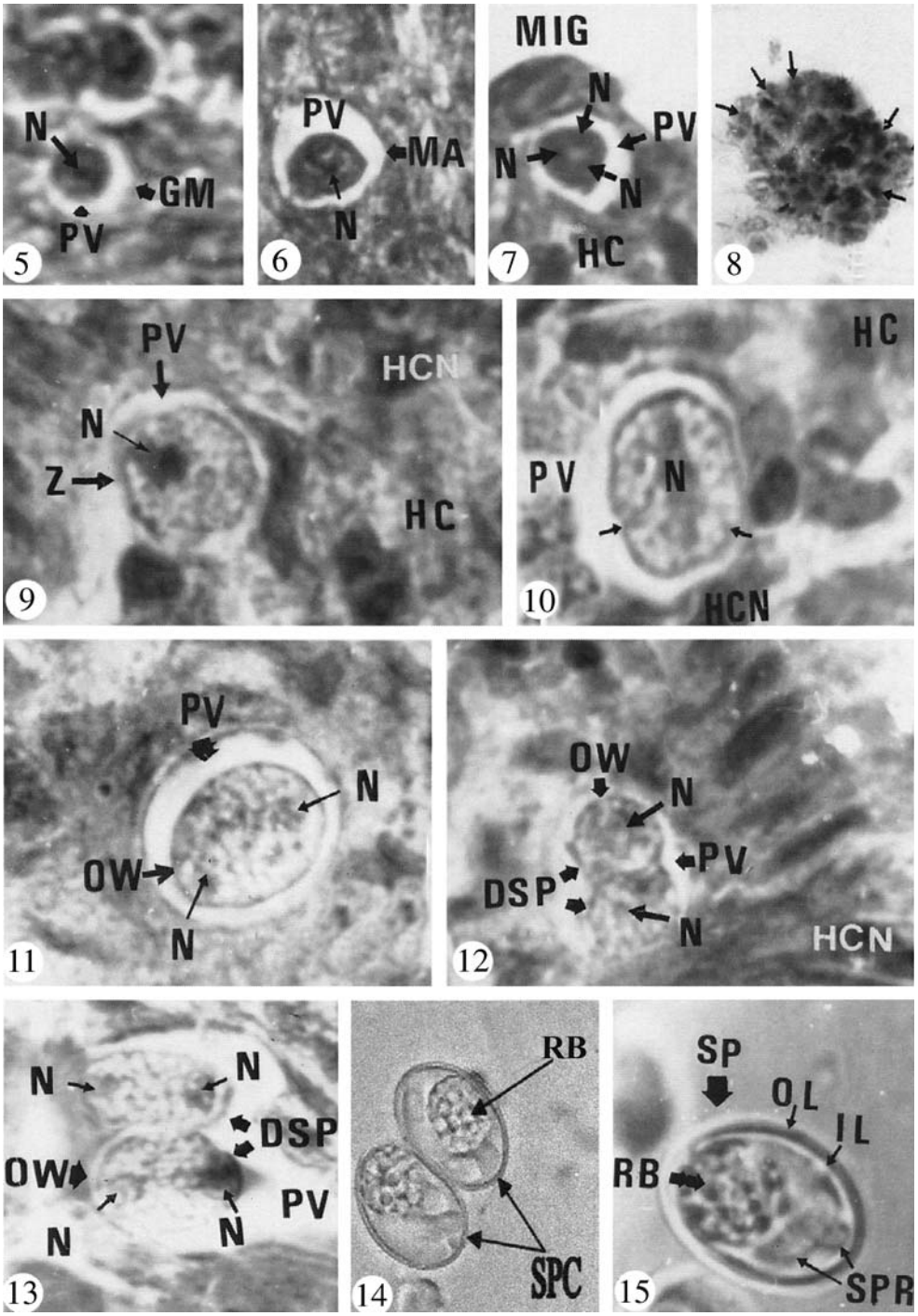

Fig. 3 Light micrographs. *5–16* Gamonts (*GM*) within a parasitophorous vacuole (*PV*) from the intestine of infected puppies, Giemsa stain; ×2,100. *7* Developing microgamont (*MIG*) with many nuclei (*N*) in a parasitophorous vacuole (*PV*); ×2,300. *8* Mature microgamont with several nuclei (*arrows*); ×3,000. *9–10* Young oocyst (zygote) in a parasitophorous vacuole (*PV*) with developing oocyst wall (*arrow*); ×2,100. *11* Elongated oocyst in PV; its former nucleus is divided into two nuclei (*N*), at 7 days p.i.; ×2,100. *12* Dividing oocyst with two developing sporoblasts (*DSP*) on day 8 days p.i. Note the presence of two nuclei (*N*) and the constriction of the cytoplasm; ×1,850. *13* Oocyst with two sporoblasts (*DSP*) on the ninth day p.i.; ×1,900. *14–15* Sporulated sporocysts (*SPC*) each containing four sporozoites and a residual body (*RB*) at the 11th day p.i.; ×2,150

Experimental infection was done by feeding dogs and cats with infected minced muscles. Histological and smear preparations of their intestine revealed that only the dogs were valid final hosts of the present camel *Sarcocystis* species. No coccidian oocysts or sporocysts were shed by cats during the experiment. Dogs, however, shed sporulated oocysts and sporocysts being characteristic for *Sarcocystis*. Beginning after 12 h p.i., examination of the mucosa and submucosa of the infected dogs showed early spherical to ovoid gamonts with central nuclei. They were located in the lamina propria of the small intestine of dogs (5 and 6 of Fig. 3). These developing gamonts measured 8.6–10×6.8–9.1 μm with a mean of 9.1×7.3 μm (n=20). No schizogonic stages were detected.

Macrogamonts appeared on the third day p.i. They were ovoid in shape and measured 6.1–7.9×7.3–9.2 μm with a mean of 7.8×8.2 μm (n=20) and contained a single large centrally located nucleus (5 and 6 of Fig. 3). As development proceeded, some dark bodies appeared in the cytoplasm probably representing the wall forming bodies.

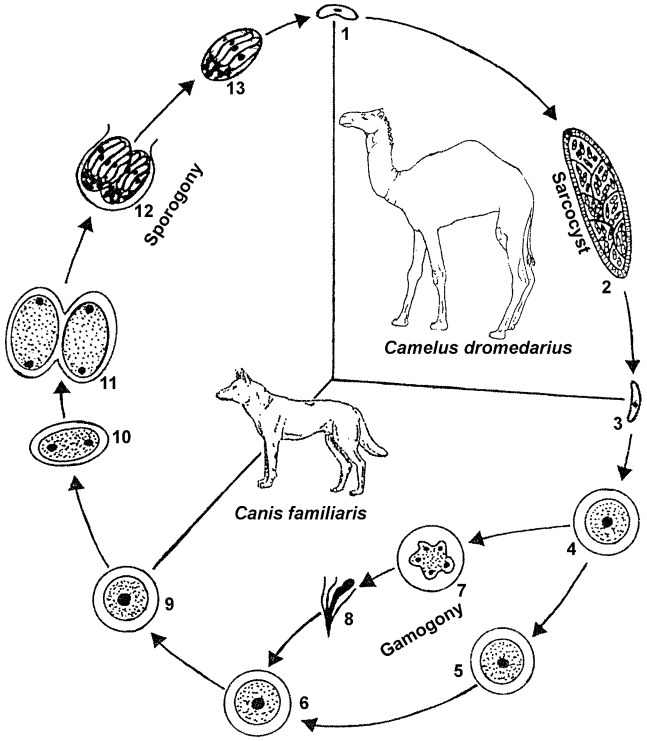

Fig. 4 Diagrammatic representation of the life cycle of *Sarcocystis camelicanis* parasitizing the muscles of the camel (*C. dromedarius)*, as intermediate host and the dog (*C. familiaris)* as final host. *1* Sporozoites (released from sporocysts) swallowed by the intermediate host to initiate schizogony in camels. *2* After formation of schizonts, cysts are formed within muscle fibers in many organs, which are surrounded by a primary cyst wall and occupied by cyst merozoites in the center and a few metrocytes located peripherally. *3* After ingestion of infected meat, free cyst merozoites from the cyst invade the intestinal epithelial cells of the final host to start gamogony. *4* Young gamonts in the intestinal epithelial cells of the final host. *5*, *6* Macrogamont and macrogamete in the intestinal epithelial cells of the final host. *7*, *8* Microgamont and microgametes in the intestinal epithelial cells of the final host. *9* After fertilization, the zygote remains located in lamina propria of the final host and develops into an oocyst. *10* An oocyst with two sporoblasts. *11* Two sporoblasts within a thin oocyst wall. *12* Sporulated oocyst with two sporocysts, each containing four sporozoites and a residual body being covered by a thick sporocyst wall. *13* Single sporocyst in the feces of the dog (after disrupture of the thin oocyst wall)

The macrogamete grew considerable in size accumulating many globules of amylopectin and lipid droplets. At the same time, microgamonts were observed also on the third day p.i. They measured 7.8–9.1×6.8–8.2 μm with a mean of 8.2×7.6 μm (n=20) and contained up to 30 nuclei (7 and 8 of Fig. 3). After maturation of the microgametes, they detached from the residual body of the microgamont. Zygotes with a thick outer wall developed into an oocyst on the fifth day p.i. (9–11 of Fig. 3). These oocysts were usually found in a large parasitophorous vacuole when they measured 9.5–11.6×7.6–9.2 μm with a mean of 11.2×8.91 μm (n=30).

Sporulation started by the elongation of the oocyst; meanwhile, the nucleus divided into two nuclei. This was followed by division of the cytoplasm, and finally, two sporoblasts were formed on the seventh day p.i. (12 and 13 of Fig. 3). On the eight day p.i., the nucleus of each sporoblast divided twice, resulting in a total of four nuclei. Each sporoblast cytoplasm finally produced four sporozoites (14 and 15 of Fig. 3). Sporulated oocysts were larger in size than nonsporulated ones and measured 21.2–22.1×18.1–19.2 μm with a mean of 21.2×18.7 μm (n=50). At the same time, sporocysts (14 and 15 of Fig. 3) measured 13.7–15.6×7.8–10.7 μm with a mean of 14.8×9.7 μm (n=50). Infected dogs began to shed sporulated oocysts and single sporocysts after 11 days of infection (prepatent period). This shedding extended for 35 days p.i. (patent period).

Discussion

Since the heteroxeneous coccidian nature of the life cycle (Fig. 4) of species of genus *Sarcocystis* was elucidated (Rommel et al. 1972), interest grew up considerably in coccidian parasites. However, little is known on the subject of the present study. An early study dealing with *Sarcocystis* species infecting camels was that of Mason (1910), within which only the sarcocyst stages were recorded. Later, the ultrastructural characteristics became one of the most important criteria for the systematics, morphology, and life cycle of parasites, especially those belonging to the subkingdom Protozoa (Scholtyseck et al. 1974; Melhorn 2008).

Regarding the ultrastructural features of cysts of the *Sarcocystis* species, it was proven that the most important criteria are the architecture and ornaments of the primary cyst wall and the protrusions that arise from it. Therefore, these features are used to separate the different species within the genus *Sarcocystis* by the majority of authors (Mehlhorn 2008; Dubey et al. 2006, 2008; Wouda et al. 2006). The finger-like protrusions of the primary cyst wall described in the present study may be similar to some other described species, but the knob-like projections that arise from the primary cyst wall in each protrusion are a clear distinctive feature. Comparison of species should only be made by using mature cysts (Abdel-Ghaffar et al. 1990a, 1994; Paperna and Finkelman 1996; Modry et al. 2000; Melhorn 2008). Comparing the results obtained in the present study with the results of Entzeroth et al. (1981), who also examined *Sarcocystis* cysts infecting camels, the architecture of the primary cyst wall and its protrusions are completely different. Entzeroth et al. (1981) described cone-like protrusions of the primary cyst wall instead of the finger-like ones with their knob-like structures presented in the present study. Meanwhile, electron micro-

scope studies have shown a rather consistent fine structure of the cyst merozoites and metrocytes in the various species of *Sarcocystis*, and their only way of multiplication by a so-called endodyogeny (Mehlhorn et al. 1976). The ultrastructure of the cyst merozoites and metrocytes in the present study corresponds closely to that observed in other studies (Mehlhorn and Heydorn 1978). The only difference may be the rich supply of merozoites with amylopectin granules as reserve material.

During the last three decades, the criteria for the identification and diagnosis of Sarcosporidia changed many times when some authors accepted the micromorphology of the cyst wall as principle criterion for species identification, while some others claimed that the study of the final host and the development of the gamogonic cycle are of basic importance. Therefore, it was of great importance to investigate the gamogonic and sporogonic features of the present parasite and to find out its final host.

The final host of each *Sarcocystis* species is expected to be among the natural predators of its intermediate host. The final host becomes infected by oral ingestion of the infected muscles of the intermediate host. After the release of the parasites in the intestine, these stages invade the lamina propria and develop into gamonts (Bashtar et al. 1992; Heydorn and Kirmse 1996; Melhorn 2008).

In the present work, gamogony occurred within lamina propria of the intestine in puppies only. Micro- and macrogamonts were observed in sections and fresh smears at 12 h to 3 days p.i., which was observed in similar studies (Mehlhorn and Heydorn 1978, 1979; Bledsoe 1979, 1980; Jian and Shah 1986; Al-Hoot et al. 2005). The shape of the wall-forming bodies in the macrogametes was in line with the findings of Mehlhorn and Heydorn (1978, 1979) and Entzeroth et al. (1985). Unlike in most other coccidia, the sporulation of oocysts in *Sarcocystis* took place within cells of the definitive host (Bashtar et al. 1990, 1992; Heydorn and Kirmse (1996); Melhorn 2008; Al-Hoot et al. 2005). Sporogony started after growth of the oocysts on the seventh day p.i., was followed by a division of the nuclei and led to the formation of two sporoblasts (8–9 days p.i.), and ended, finally, with the formation of four sporozoites within each sporocyst. Usually, sporulated oocysts had thin walls that easily ruptured when excreted in feces on the 11th day p.i. Thus, mostly single sporocysts were seen in fecal preparations. Such a sporulation was reported in many earlier reports (Mehlhorn and Heydorn 1978, 1979; Bashtar et al. 1992; Al-Hoot et al. 2005), too.

The prepatent period of the present parasite (*S. cameli*) was 11 days p.i., and the patent period extended to 35 days. Similarly, a 10-day prepatent period was reported for *Sarcocystis fusiformis* (Sakran et al. 1994). However, 15–21 days were reported for *Sarcocystis cruzi* (Fayer 1977) and *Sarcocystis chalcidicolubris* (Matuschka 1987). The patent period extended to 35 days p.i., which is shorter than that of previous records (Bashtar et al. 1992).

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