ULTRASTRUCTURE OF THE CYSTS OF *SARCOCYSTIS RANGI* FROM SKELETAL MUSCLE OF REINDEER *(RANGIFER TARANDUS TARANDUS)*

Ultrastrukturen til cyster av *Sarcocystis rangi* frå skjelettmuskulaturen hos rein.

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Summary: Mature muscle cysts of *Sarcocystis rangi* from *Rangifer tarandus* were examined by transmission electron microscopy. The long and slender cysts were located within skeletal muscle cells, and were bounded by a unit membrane, the cyst membrane. The cysts were provided with closely spaced flexible, hairlike surface processes, measuring up to 12.6 µm in length and 0.3 to 0.6 µm in diameter. The projections had a smooth surface, whereas the cyst membrane formed numerous hexagonally packed vesicular invaginations between the bases of the projections. The cyst membrane was reinforced by an underlying thin layer of electron-dense material, except at the points where it was invaginated. Cyst ground substance formed a thin layer at the periphery of the cysts, filled the core of the projections, and formed thin septa that divided the interior of the cysts into numerous compartments. Most compartments contained a large number of tightly packed cystozoites, whereas a few metrocytes were forund in each of a few compartments at the periphery of the cysts. Some of the cystozoites multiplied by endodyogeny. The metrocytes displayed a vacuolation of their cytoplasm. The cysts of *S. rangi* were similar in surface morphology to the sarcocysts of certain other *Sarcocystis* species reported from other intermediate hosts.

Key words: *Sarcocystis, S. rangi*, reindeer, *Rangifer tarandus tarandus*, sarcocyst morphology, ultrastructure, transmission electron microscopy.

RANGIFER *5 (2): 43-52*

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Samandrag: Muskelcyster av *S. rangi* frå rein vart undersøkt ved transmisjonselektronmikroskopi. Dei lange cystene låg intracellulært i skjelettmuskelceller, og var avgrensa av ein elementærmembran, cystemembranen. Cystene var utstyrt med talrike hårliknande overflateprosessar, som strekte seg langsetter cysteoverflata. Prosessane var opptil 12.6 µm lange, og målte 0.3 til 0.6 µm i diameter. Prosessane hadde ei glatt overflate, medan cystemembranen danna talrike regelmessige ordna, små invaginasjonar innimellom basis av prosessane. Cystemembranen var forsterka på innsida av eit tunnt lag av elektrontett materiale, med unnatak av dei stadene der han var invaginert. Cystegrunnsubstans danna eit lag perifert i cystene, fylte det indre av prosessane, og danna septa som delte cystene inn i talrike kammer. Dei fleste kammera inneheldt cystozoitar, medan metrocytar fannst i nokre få, små kammer perifert i cystene. Nokre av cystozoitane gjennomgjekk ei todeling ved endodyogeni. Mange metrocytar hadde eit vakuolisert cytoplasma. Cystene til *S. rangi* var svært like cystene til visse *Sarcocystis*-arter frå andre mellomvertar med omsyn til overflatemorfologi.

RANGIFER *5 (2): 43-52*

INTRODUCTION

Previous light microscopic investigations have revealed that Norwegian reindeer may harbour six morphologically distinct types of fully developed sarcocysts, and thus act as intermediate hosts for six species of *Sarcocystis* (Gjerde 1984). By light microscopy the sarcocysts of the species *S. rangi* were found to be long and slender, measuring 5460 — 12700 (8994) µm in length and 95 — 280 (180) µm in diameter, and to possess numerous

8 — 10 µm long, slender, hairlike surface processes. These morphological features clearly distinguished the cysts of *S. rangi* from the cysts of the five other *Sarcocystis* species infecting reindeer (*S. grueneri, S. hardangeri, S. tarandi, S. tarandivulpes* and *S. rangiferi*) when viewed with the light microscope (Gjerde 1984). Recently, the muscle cysts of the five last mentioned species have been examined by transmission electron microscopy, and their ultrastructural features have been described in a series of papers (Gjerde 1985a, 1985b, 1985d, 1985e, 1985f). In the present paper a transmission electron microscopic study of the cysts of *S. rangi* is reported, and a more detailed morphological description of the cystic stage of this species is given. Moreover, the sarcocysts of *S. rangi* are compared morphologically with those of several other *Sarcocystis* species recovered from related intermediate hosts, and the significance of the similarity in cyst surface morphology between these *Sarcocystis* species is discussed.

MATERIALS AND METHODS

Samples of the abdominal muscles were collected from recently slaughtered domestic reindeer at abattoirs in Kautokeino and Karasjok in North Norway. The samples were kept cool during transportation to our laboratory in Oslo, arriving about 2 days after the animals had been killed. The musculature was then examined under a dissecting microscope and sarcocysts typical of *S. rangi* (5 — 10 mm long), together with a small amount of the surrounding muscle tissue, were excised and fixed in Karnovsky's paraformaldehyde-glutaraldehyde fixative. After fixation, the elongated blocks of tissue were cut transversely into several shorter pieces, which were further processed for electron microscopy as described previously (Gjerde 1985a). Ultrathin section, cut with glass knives, were examined in a JEOL JEM 100S transmission electron microscope.

RESULTS

Sarcocyst morphology

The long and slender cysts of *S. rangi* were located within morphologically altered skeletal muscle cells. There had been a substantial loss of myofilaments in the parasitized cells, so that only portions of the former myofibrils occured in the thin layer of host cell sarcoplasm that surrounded the cysts (Figs. 1, 2). The cysts of *S. rangi* had not induced an encapsulation of their host cells.

The entire cyst was bounded by a unit membrane, which was about 8 nm thick. The limiting membrane of the cyst will be referred to as the cyst membrane (Figs. 4, 5). The cysts were provided with numerous long, slender, hairlike surface processes (Figs. 2 — 5). These processes had a smooth surface (Figs. 3 — 5), whereas the cyst surface in between the bases of the projections was provided with numerous, 80 — 85 nm deep, vesicular invaginations of the cyst membrane (Figs. 4, 5). The invaginations had a hexagonal to round cross section with a diameter of 80 — 85 nm, and they were hexagonally packed on the cyst surface, having a center to center spacing of about 100 nm (Fig 5). A thin layer of electron-dense material covered the inner surface of the cyst membrane, except at the points where the membrane was invaginated (Figs. 4, 5). This submembranal dense layer was 3 — 12 nm thick at the border of the projections, and 30 — 35 nm thick in between the vesicular invaginations on the surface of the cyst proper. The limiting cyst membrane and the underlying dense layer appeared as a single structural entity at lower magnifications, and have been referred to collectively as the reinforced cyst membrane (Figs. 3, 4).

Tangential sections through the outer region of the cysts showed that the bases of the surface projections were relatively closely and regularly spaced, usually lying less than 1 µm apart. Thin sections cut perpendicularly to the cyst surface, on the other hand, often gave the false impression that the processes arose from irregularly spaced sites on the cyst surface, because the bases of adjacent projections only rarely were included in the same ultrathin section. The processes were more or less curved, so that only portions of them were lying within the thickness of a given section (Fig. 2). Hence, their true length was difficult to ascertain. What seemed to be almost complete longitudinal sections of a few projections, showed that they might attain a length of at least 12.6 µm (Fig. 3). In cross section the processes were circular to oval (Fig. 2), measuring 0.3 to 0.6 µm in diameter proximally. They tapered somewhat toward the tip, which was blunt and about 0.1 µm thick (Fig. 3). The processes were flexible and usually turned sharply sideways immediately above their bases and extended alongside the surface of the cyst

proper (Figs. 3, 4, 6), apparently because they were diverted by adjacent myofilaments. Thus, the projections became densely packed in a layer next to the cyst proper. This layer was usually less than 2 µm thick and devoid of myofilaments (Figs. 1 — 4).

Finely granular to filamentous ground substance formed a layer at the periphery of the cysts, which had an average thickness of 760 (500 — 1250) nm (n=30). From this layer, ground substance of lower electron density extended outward and filled the core of the surface processes. The cyst wall consisted of the ground substance at the periphery of the cyst, including the ground substance within the projections, the submembranal dense layer, and the limiting cyst membrane. The cyst wall could also be divided into an inner layer, made up of the peripheral layer of ground substance, and an outer layer of surface processes, both of which had a moderate thickness. Cyst ground substance also extended inward from the peripheral layer, forming on average 220 (110 —500) nm (n=21) thick partitions or septa, which divided the interior of the cyst into numerous compartments. Most compartments contained numerous densely packed cystozoites (Fig. 1), whereas a few compartments, which usually were located at the periphery of the cysts, each contained a few metrocytes (Fig. 6).

Metrocytes

The metrocytes were ovoid to cylindrical cells, measuring up to 11.1 µm i length and 5.8 µm in diameter (Fig. 6). They were bounded by a typical trimembranal pellicle, which often had one or more deep invaginations. The metrocytes possessed a conoid at the anterior end, posterior to which several electron-dense rods were lying. These rods resembled the micronemes of the cystozoites, but measured only about 100x20 nm, whereas the typical cystozoite micronemes measured about 375x60 nm. The ovoid nucleus was located in the middle region of the metrocytes and contained a prominent nucleolus. The cytoplasm of the metrocytes was rather electron-lucent and contained one or more elongate mitochondria with tubular cristae, a few amylopectin granules, a few dense globules, rough endoplasmic reticulum, and a relatively small number of free ribosomes. In addition, the cytoplasm of most metrocytes contained several membrane-bounded vacuoles of variable size. The contents of the vacuoles had a very low electron density and frequently had a flocculent appearance. Smaller vacuoles apparently coalesced with each other, forming larger vacuoles, so that the metrocytes seemed to become progressively more vacuolated.

Cystozoites

The elongate cystozoites (Figs. 1, 2) measured up to 16.3 µm in length and 4.5 µm in diameter. They were bounded by a trimembranal pellicle, which had a micropore and 22 underlying microtubules. Small membrane-bounded vesicles were frequently associated with the micropore of the cystozoites. The vesicles either occurred within larger membrane-bounded intracytoplasmic vacuoles lying next to the micropore, or within the lumen (which was often expanded) of the micropore. Numerous, identical small vesicles were also scattered alongside the cystozoites and were apparently able to pass through the cyst ground substance. However, it could not be ascertained whether vacuoles containing several vesicles were pinched off from the micropore and moved into the cell, or whether intracytoplasmic vacuoles fused with the limiting membrane of the micropore and discharged small vesicles into the environment of the cystozoites. The cystozoites seemed to possess only two rhoptries, which extended posteriorly from the lumen of the conoid. Numerous micronemes occupied most of the anterior third of the cystozoites. Immediately posterior to the micronemes numerous highly electron-dense granules were situated. Up to 15 profiles of such granules were present in sections of individual cystozoites, and thus their actual number was even higher. The middle third of the cystozoites also contained several variously sized vacuoles filled with a finely granular material of low electron density, numerous amylopectin granules, rough endoplasmic reticulum, numerous free ribosomes, an elongate mitochondrion with tubular cristae, and a Golgi complex. The nucleus was located in the posterior third of the cell. It was roughly ovoid and possessed a prominent nucleolus.

The cysts contained a small number of cystozoites undergoing endodyogeny. The multiplying cystozoites were lying among nondividing cystozoites and showed profiles of forming daughter cells (Fig. 7).

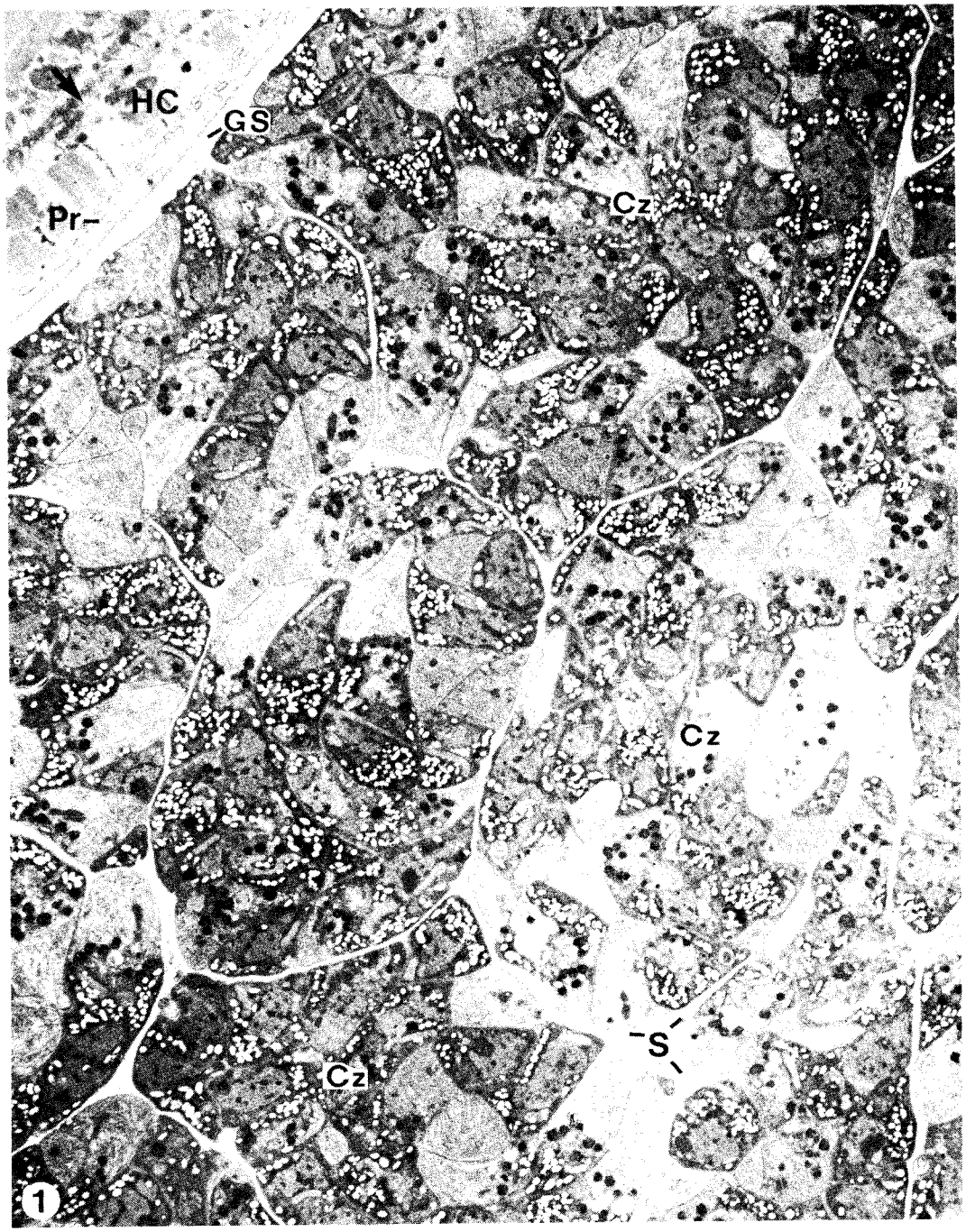

Fig. 1. Electron micrograph of *S. rangi* sarcocyst, showing groups of cystozoites (Cz) separated by thin septa (S) of cyst ground substance. The cyst has a thin peripheral layer of ground substance (GS), from which cyst surface processes (Pr) arise. HC=host cell sarcoplasm. The border of the host cell is indicated by an arrow. X 3000.

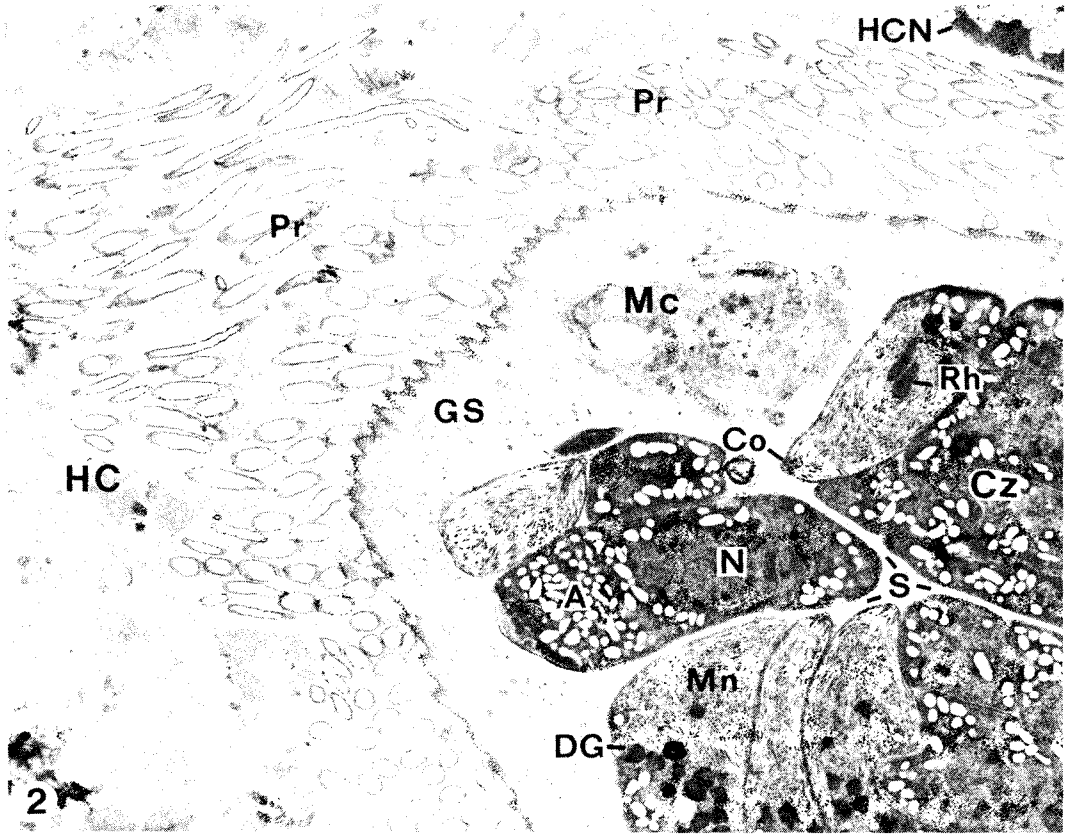

Fig. 2. Oblique section through *S. rangi* cyst, showing compartments with metrocytes (Mc) and cystozoites (Cz), and numerous portions of variously sectioned cyst surface processes (Pr). HC=host cell sarcoplasm. HCN=host cell nucleus. The cystozoites display a conoid (Co), rhoptries (Rh), micronemes (Mn), dense granules (DG), amylopectin granules (A), and a nucleus (N). X 5000.

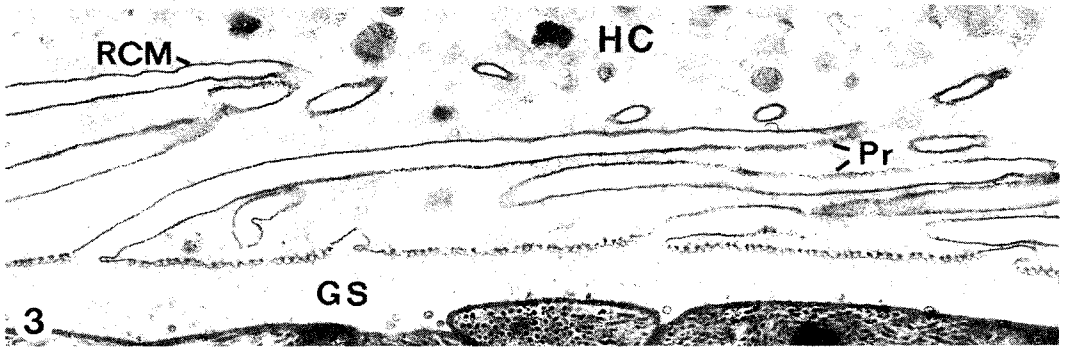

Fig. 3. Electron micrograph of longitudinally sectioned hairlike surface processes (Pr). Note the smooth contour of the projections and the serrated contour of the cyst surface between the bases of the projections. The peripheral layer of ground substance (GS) makes up the inner layer of the cyst wall. RCM=reinforced cyst membrane. X 10 000.

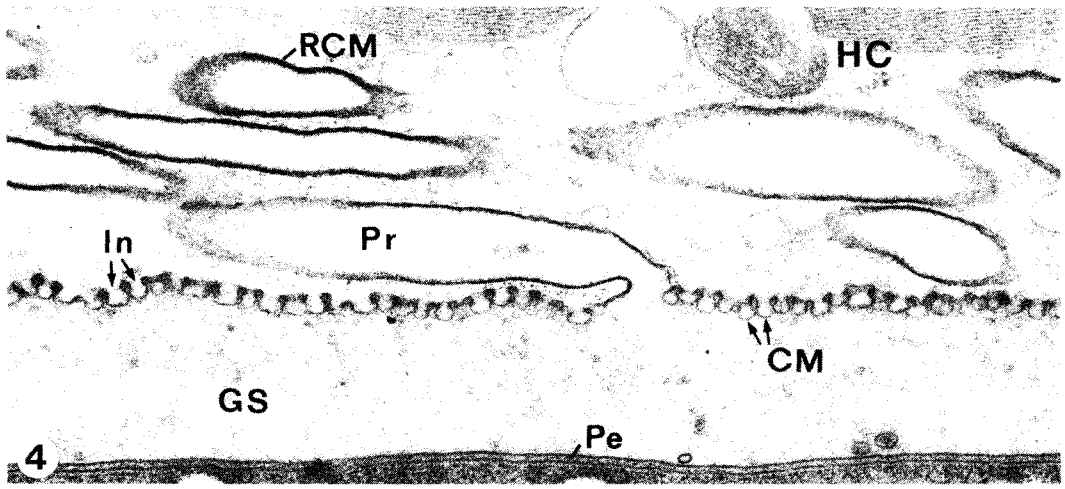

Fig. 4. Vertical section through the cyst wall, showing closely spaced vesicular invaginations (In) of the limiting cyst membrane (CM), which is visualized as a thin line at the bottom of the invaginations. Between the invaginations and on the entire surface of the projections (Pr) the cyst membrane has a thin coating of electron-dense material on its inner surface, both structural entities being referred to collectively as the reinforced cyst membrane (RCM). HC=host cell sarcoplasm. GS=ground substance of the inner layer of the cyst wall. Pe=pellicle of a cystozoite. X 28 000.

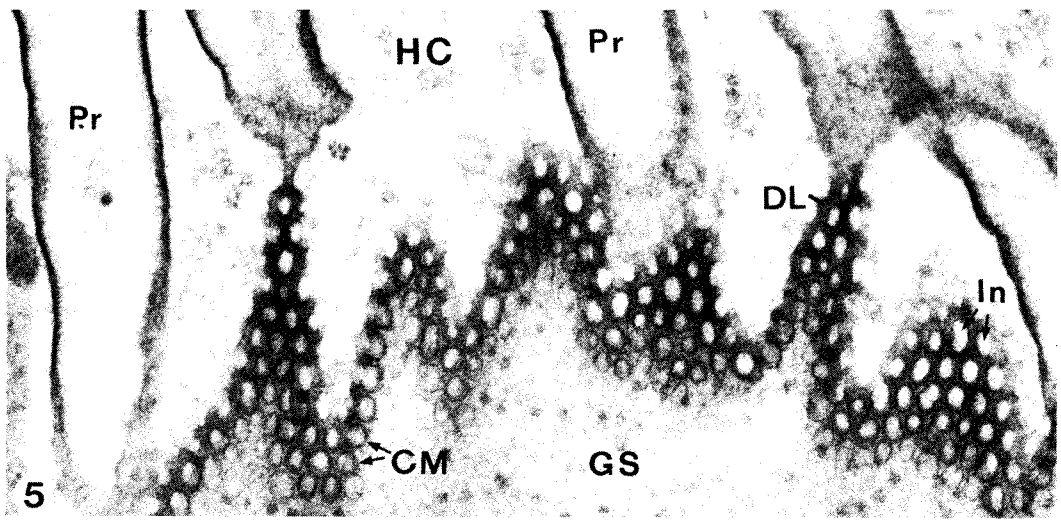

Fig. 5. Tangential section through the outer region of a *S. rangi* cyst, showing hexagonally packed invaginations (In) of the cyst membrane (CM), forming a honeycomb pattern. The dense layer (DL) subjacent to the cyst membrane is interrupted by the invaginations, but forms a continuous inner coating of the cyst membrane on the projections (Pr). GS=ground substance at the periphery of the cyst. HC=host cell sarcoplasm. X 37 500.

DISCUSSION

The present electron microscopic study showed that the sarcocysts of *Sarcocystis rangi* were provided with numerous hairlike surface processes, and had numerous hexagonally packed vesicular invaginations of the limiting cyst membrane in between the bases of the projections.

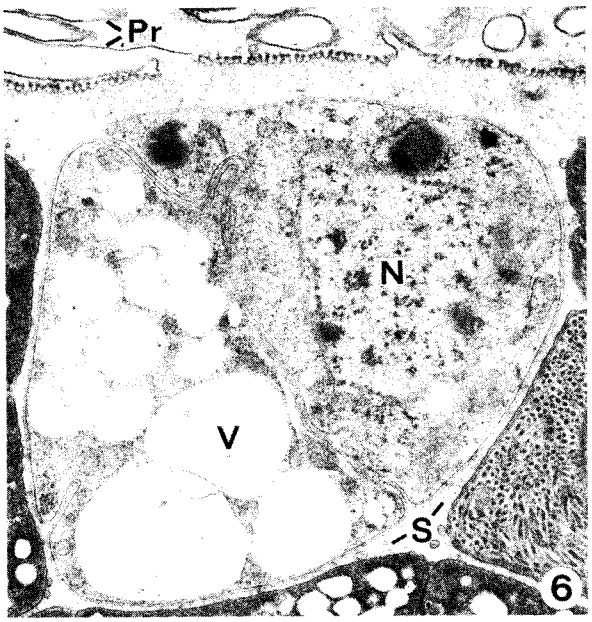

Fig. 6.

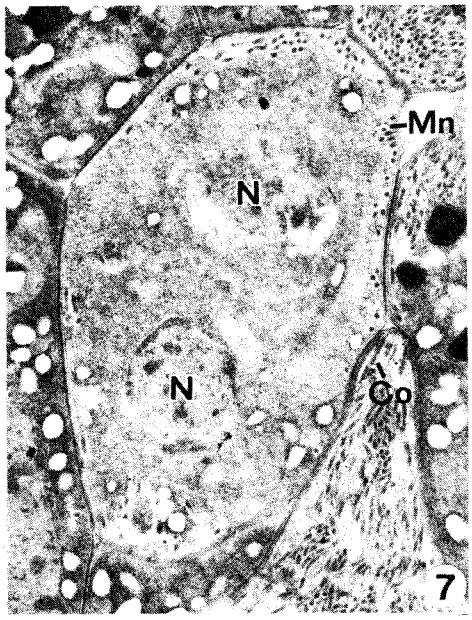

Fig. 7.

Fig. 6. Section through two metrocytes. The one on the left has an extensively vacuolated cytoplasm with many membrane-bounded vacuoles (V). N=nucleus. S=septa of ground substance. Pr=surface processes. X 10 000.

Fig. 7. Electron micrograph of a cystozoite undergoing division by endodyogeny, as indicated by the presence of two nuclei (N) and a peripheral distribution of the micronemes (Mn). Co=conoid of undividing cystozoite. X 9600.

Sarcocysts with a quite similar surface morphology have previously been recovered from six other ruminant host species by other investigators, and assigned to six separate species of *Sarcocystis*. These *Sarcocystis* species and their intermediate hosts are as follows: (1) *S. cruzi* from cattle; (2) *S. tenella* from sheep, as defined by Erber (1982); (3) *S. hircicanis* from goat; (4) *S. capreolicanis* from roe deer (*Capreolus capreolus*); (5) *S. sybillensis* from the North American elk (*Cervus elaphus*); and (6) *S. alceslatrans* from moose (*Alces alces*), as described by Colwell and Mahrt (1983). Moreover, according to the paper by Markus et al. (1984), sarcocysts from the springbuck (*Antidorcas marsupialis*), from the kudu (*Tragelaphus strepsiceros*), and from the gemsbuck (*Oryx gazella*), respectively, also have hairlike surface processes. Thus, three more host species seem to harbour sarcocysts that are similar in surface structure to the cysts of *S. rangi*.

The ultrastructure of the cysts of *S. cruzi* has been described in several papers (Simpson 1966, Bergmann and Kinder 1975b, Mehlhorn et al. 1975, Heydorn et al. 1975, Fujino et al. 1982), and the cyst surface morphology of this species seems to be closely similar to that of *S. rangi*, both with respect to the configuration of the protrusions and the occurrence of vesicular invaginations. The cyst organisms of both species are also alike in structure.

Detailed descriptions of the fine structure of the sarcocysts of the other species mentioned above are lacking, making an adequate comparison between these species and *S. rangi* impossible. By light microscopy the sarcocysts of *S. tenella* from sheep were found to measure up to 650 µm in length and to have 5 — 11 µm long, delicate hairlike projections (Erber 1982). It was probably cysts of the same species that Bergmann and Kinder (1975a) examined with the electron microscope and referred to as thin-walled microcysts. These cysts had surface processes which were similar to those of *S. rangi*. The cysts of *S. hircicanis* have also mainly been described by light microscopy, and were found to measure up to 2500 µm in length, and to have 3.6 — 6 µm long, hairlike surface processes (Heydorn and Unterholzner 1983). The

ultrastructure of the cyst border of this species was briefly described by Aryeetey et al. (1980), but this description is misleading as only obliquely to transversely cut processes were observed. Nevertheless, these processes seem to be similar to those of *S. rangi*.

The cysts of *S. capreolicanis* were originally described by light microscopy as being small cysts, up to 500 µm long, and bearing 6 — 8 µm long hairlike processes (Erber et al. 1978). It was probably cysts of the same species that Entzeroth (1982) examined with the electron microscope and referred to as type 6 cysts. These cysts also had hairlike surface processes similar to those of *S. rangi* cysts. The fine structure of the cysts of *S. sybillensis* was briefly described by Dubey et al. (1983), who found the filamentous cyst processes of this species to be ut to 6.16 µm long. In histological sections, slices of the cysts measured up to 637 µm in length, but such sections only rarely reveal the true length of the sarcocysts.

The cysts of *S. alceslatrans* from moose were originally described from histological sections (Dubey 1980), which is an unreliable method for distinguishing cysts of different species as neither the size of the sarcocysts, nor the cyst wall structure can be accurately ascertained from such sections. Colwell and Mahrt (1983) claimed that the *Sarcocystis* sp. with type A cysts in moose (Colwell and Mahrt 1981) was identical to the species *S. alceslatrans*. According to them, the cysts of *S. alceslatrans* were fusiform, measuring 1 to 7 mm in length. They had short digitiform protrusions with invaginations at their bases, and numerous, 25 nm thick membraneous extensions of the primary cyst wall, into which no granular material extended (Colwell and Mahrt 1981, 1983). However, the «digitiform protrusions» do not seem to represent structures projecting from the cyst surface. It is rather the cyst surface adjacent to them which is invaginated. The «membraneous extensions», on the other hand, are components of the real surface processes. From Colwell and Mahrt's description of these «extensions» one gains the impression that they are very thin structures, which led me to believe that they had a certain structural resemblance to the thin, striplike surface processes of *S. grueneri* (Gjerde 1985a, 1985b). However, a closer examination of the micrographs presented in the paper by Colwell and Mahrt (1981), reveals that these cysts actually have hairlike surface processes with diameters of up to about 0.4 µm, and a length of at least 5.8 µm. These processes are tightly compressed against each other and against the surface of the cyst. It therefore seems as if only the electron-dense membraneous boundaries (reinforced cyst membrane), and not the electron-lucent central core of the projections, have been recognized as extensions from the cyst, and described as membraneous extensions by Colwell and Mahrt (1981). Thus, *S. alceslatrans* also resemble *S. rangi* in cyst surface morphology.

An ultrastructural comparison between the cysts of *S. rangi* and the cysts of the five other *Sarcocystis* species from reindeer, which have been described previously (Gjerde 1985a, 1985b, 1985d, 1985e, 1985f), shows that *S. rangi* differs markedly in cyst surface morphology from *S. tarandivulpes*, *S. rangiferi*, *S. hardangeri*, and *S. tarandi*, but less so from *S. grueneri*. Thus, the cysts of both *S. rangi* and *S. grueneri* have numerous slender, flexible surface processes, which extend along the cyst surface, and a similar arrangement of the invaginations of the cyst membrane in between the bases of the projections. However, in contrast to the relatively thick hairlike processes with a circular cross section that are present on the cysts of *S. rangi*, and which are visible with the light microscope, the cysts of *S. grueneri* bear very thin (30 — 40 nm thick) and fairly narrow (about 300 nm wide) projections with a striplike configuration, which are not visible by light microscopy (Gjerde 1985a). In ultrathin sections cut perpendicularly to their surfaces, the projections of *S. grueneri* are visualized as two closely apposed, parallel reinforced membranes, irrespective of whether they are cut longitudinally, obliquely, or transversely. This type of surface processes also occur on sarcocysts recovered from other cervid hosts by other investigators, but the processes have either not been recognized (on *S. wapiti* cysts), or their configuration has been erroneously described in various papers. Thus, the width of the bandlike profiles of these processes, which actually represents the thickness of the projections, have been described as the width of supposedly extremely narrow bandlike processes, or as the diameter of extremely thin cylindrical processes. Thus Schramlová and Blăzek (1978), in their paper on sarcocysts from roe deer, seem to have illustrated cysts with hairlike processes (Fig. 1a), as well as cysts with flattened processes seen in profile (Figs. 1b — d), without being aware of the differences in the configuration of the projections. Consequently, both structural types of sarcocysts

were described collectively as a single type of cysts with fingerlike protrusions.

Böttner (1984) reported that the cysts of *S. cruzi* (syn. *S. bovicanis*) from cattle examined by him possessed two types of surface processes, and that both types of processes occasionally occurred on the same cysts. One type of protrusions had a hairlike configuration («schlauchartige»), looking similar to the processes of *S. rangi*, whereas the other type had a flattened, striplike configuration («stabförmige»), looking similar to the processes of *S. grueneri*. The cysts with hairlike processes observed by Böttner (1984) no doubt belonged to *S. cruzi*. The reported occurrence of both types of processes on individual cysts is probably due to a misinterpretation of the images seen. A similar observation has never been reported previously from the many ultrastructural studies of the sarcocysts of *S. cruzi* (Simpson 1966, Bergmann and Kinder 1975b, Mehlhorn et al. 1975), nor has it been made in the studies of *S. rangi* and *S. grueneri* by this author. I therefore think it is likely that the cysts with striplike surface processes found by Böttner in cattle belong to a *Sarcocystis* species distinct from *S. cruzi*. This would establish cattle as intermediate host for a new species of *Sarcocystis* in addition to the three previously known species *(S. cruzi, S. hirsuta, S. hominis)*. Moreover, *Bos taurus* becomes an additional intermediate host harbouring sarcocysts with surface processes similar to those of *S. grueneri*.

As reported previously (Gjerde 1985a), a *Sarcocystis* sp. from *Capreolus capreolus* (roe deer) and *S. cervicanis* (syn. *S. wapiti*) from *Cervus elaphus* (red deer, North American elk or wapiti) have cysts with processes that closely resemble those of *S. grueneri*. Moreover, according to Markus et al. (1984), sarcocysts with this type of surface projections also occur in the impala *(Aepyceros melampus)* and the waterbuck *(Kobus ellipsiprymnus)*. Likewise, from the illustrations in the paper by Entzeroth et al. (1985) it can be seen that the sarcocysts of a *Sarcocystis* sp. from fallow deer *(Cervus dama)* also bear flattened, striplike surface processes. Thus, the sarcocysts of *S. grueneri* from reindeer seem to be similar in surface morphology to sarcocysts from six other species of intermediate hosts. Moreover, the sarcocysts of *S. tarandivulpes* and *S. hardangeri* from reindeer have been found to be similar in surface morphology to the cysts of *S. odocoileocanis* from *Odocoileus virginianus* and the cysts of a *Sarcocystis* sp. from *Alces alces*, respectively (Gjerde 1985b, 1985e).

In addition to the similarities in cyst surface morphology, the species *S. rangi, S. cruzi, S. tenella, S. hircicanis, S. capreolicanis, S. sybillensis*, and *S. alceslatrans* all use canines as definitive hosts (Gjerde 1985c, Mehlhorn et al. 1975, Erber 1982, Heydorn and Unterholzner 1983, Erber et al. 1978, Dubey et al. 1983, Dubey 1980, Colwell and Mahrt 1983), but the sporocyst size differs among the species. The size of the sarcocysts of these species also seems to differ, the cysts of *S. rangi* being longer than those of the other species.

As discussed previously in connection with the recognition of morphological similarities between the cysts of certain *Sarcocystis* species from reindeer and the cysts of certain other *Sarcocystis* species from other hosts (Gjerde 1985a, 1985b, 1985e), there are two possible explanations to these similarities. The morphologically similar sarcocysts in systematically related hosts either belong to a common *Sarcocystis* species with a poor intermediate host specificity, or they belong to different *Sarcocystis* species, which are specific to each intermediate host. So far, the latter possibility has been believed to apply to most *Sarcocystis* species, even though few transmission studies involving host species that harbour morphologically similar sarcocysts have been carried out. However, Unterholzner (1983) reported that a sheep inoculated with sporocysts of *S. capracanis* and *S. hircicanis* (the latter species was referred to as *Sarcocystis* sp. (g) of goat) did not become infected with these parasites. Moreover, two goats inoculated with sporocysts of *S. ovicanis* and *S. tenella* (the latter species was referred to as *Sarcocystis* sp. (s) of sheep) did not become infected. Other transmission studies (see Aryeetey et al. 1980) have also established *S. ovicanis* and *S. capracanis* as two separate species, even though they have a very similar cyst wall structure. This shows that different *Sarcocystis* species might form morphologically indistinguishable cysts in related host species, which strongly suggests that the above-mentioned *Sarcocystis* species from reindeer really are distinct from those species in other hosts with morphologically similar sarcocysts. However, this can only be established beyond doubt by extensive cross-transmission studies, or by comparative biochemical (isoenzyme) studies of the parasites from the different hosts. Nevertheless, until proven otherwise, each of the *Sarcocystis* species described from reindeer shold be regarded as being specific to this host.

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