Scanning electron Microscopic Studies on the Microvascular System of the Spleen in the Rat, Cat, Dog, Pig, Horse and Cow.

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ABSTRACT. Structural details of the sheathed artery, arterial capillary and splenic sinus of the spleen were comparative-morphologically studied by scanning and transmission electron microscopy in the rat, cat, dog, pig, horse and cow. The network of the sheathed artery contained platelets and erythrocytes, but no other blood cells, except for macrophages in the dog. Slits with a diameter of 1-3 μm were found between the endothelial cells in all species except for the dog. The terminal portions of the arterial capillaries were sack-shaped in the rat, dog, pig and horse, and were funnel-shaped in the cow. These portions had small pores communicating with the cordal spaces. Some arterial capillaries opened into the splenic cords in the rat, but opened directly into the sinuses in the others. The endothelial cells of the sinus were rod-shaped in the rat, dog and cow, but flat stellate-shaped in the cat and horse, and in the pig they were of both types. The walls of the sinus had slits through which blood cells and macrophages passed from the sinusal lumen to the cordal space or *vice versa*. Reticular cells toughed on the outside of the endothelial cells of the sinus.—**KEY WORDS:** animal spleen, arterial capillary, sheathed artery, splenic sinus.

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Histological studies on the structure of the spleen have been made since the 19th century [2] and revealed that the spleen plays a role as a complex filter interposed in the blood stream. The vascular system in the spleen has been well studied in man and experimental animals [5, 7, 16, 18, 19, 22, 34, 42, 45], but only a few in the domestic animals, especially using electron microscope [30, 42, 48].

Schweigger-Seidel [33] reported that the sheathed artery was a capillary surrounded by the sheath consisted of adventitial cells. The structure of the sheath has been discussed by several workers [17, 18, 36]. However, some species, such as mouse, rat and rabbit, lack sheathed arteries [32, 34].

Arterial capillaries known as “terminal capillaries” run into the splenic cords. The cordal reticular cells sent their processes to reach the arterial capillary. It has been discussed by many investigators [4, 16, 21, 35, 44] whether the terminal of the arterial capil-

lary opens into the splenic cords or connects with splenic sinus. There are three interpretations on the termination of the arterial capillary; the first is the “open circulation” where the terminal opens into the splenic cords, the second is the “closed circulation” where it connects with sinuses and the third is “divided circulation” where the terminal has both “open and closed circulation” [8, 32, 42, 47].

The splenic sinus consists of rod-shaped endothelial cells with slits and argyrophilic circumferential (ring) fibers. These structures were first described in the spleen of the dog and human [3, 44]. Whereas, the sinus of cat, pig, horse and cow had not an anastomosing network of venous vessels that were encircled by ring of argyrophilic fibers and rod-shaped endothelial cells. The spleens of these species were classified as “non-sinusal (having primordial vein)” by Snook [34].

In this paper, comparative studies were made on the morphology of the sheathed

Table 1. Comparison of fine structures of sheathed arteries of cat, dog, pig, horse and cow

Species	Diameter of the sheathed artery (μm)	Endothelial cell			Sheath		
		Shape	Slit	Micro-filament	Cell layer	Macro-phage	Border on the cord
Cat	30-40	Rod	+	++	1-2	-	Clear
Dog	30-40	Rod	-	++	2-4	+	Unclear
Pig	60-90	Rod	+	++	5-6	-	Clear
Horse	40-60	Rod	+	++	2-3	-	Clear
Cow	10-20	Rod	+	+	1-2	-	Clear

Rat spleen lacks sheathed arteries.

artery, arterial capillary and splenic sinus of the rat, cat, dog, pig, horse and cow by scanning and transmission electron microscopy.

MATERIALS AND METHODS

Spleens from 15 rats, 5 cats, 5 dogs, 21 pigs, 4 horses and 3 cows were used as materials in the present study.

Before slaughter, rats and dogs were anesthetized with sodium pentobarbital solution and cats with chloroform. Pigs, horses and cows were not anesthetized.

The spleens were excised just after slaughter and perfused from the splenic artery with Ringer solution at room temperature, followed by perfusion of 0.5% glutaraldehyde or 10% formaldehyde in 0.1 M phosphate buffer at pH 7.4. The outflow of the perfusate was prevented by ligation of blood vessels at the splenic hilus. The organs were immersed in the same fixative for a few hours.

Tissue blocks measuring about $2 \times 2 \times 10$ mm were dissected out from the spleen in the fixative and fixed further for about 30 hr. According to the "modified tannin-osmium" method [29], specimens were impregnated, dehydrated in ascending series of ethanol and transferred to isoamylacetate. They were then freeze-cracked in liquid nitrogen, dried at critical point in liquid CO_2 , and coated with gold in a vacuum evaporator [38, 39].

Cast specimens were made by injection of resin (MERCOX CL) from the splenic artery, followed by maceration with 15-20% NaOH solution. These specimens were observed and photographed with a Hitachi HHS-2R scanning electron microscope under an accelerating voltage of 20 kV.

Specimens for transmission electron microscopy were fixed in 2.5% glutaraldehyde and embedded in epoxy resin (Quetol 812). Ultrathin sections were stained with uranyl acetate and lead citrate. They were examined with a JEM-100S transmission electron microscope under an accelerating voltage of 80 kV.

A part of specimens were also embedded in paraffin, sectioned at $4 \mu\text{m}$, stained with hematoxylin-eosin and observed with a light microscope.

RESULTS

1. Sheathed artery (Table 1)

The sheathed artery consisted of the endothelium and the surrounding sheath composed of several layers of reticular cells. The diameter of the sheathed arteries and layers of the sheath were different among the species. The sheath was largest in the pig, rather small in the horse, dog and cat, and smallest in the cow. The rat lacked sheathed arteries. The endothelia of these vessels in the cat, dog, pig, horse and cow were composed of rod-shaped cells arranged parallel to the long axis

Fig. 1. Sheathed artery (SA) of the cow spleen. A dense sheath consisting of reticular cells is clearly separated from the splenic cords. No macrophages are visible. $\times 1,100$.

Fig. 2. Sheathed artery of the pig spleen having oval slits (arrows) $1.0 \times 1.5 \mu\text{m}$ in size. The endothelial cells are spindle- or rod-shaped and run along the long axis of the capillary. Reticular cells of the sheath, erythrocytes (Er) and platelets (P) are observed in the reticular network. $\times 2,700$.

Fig. 3. Sheathed artery of the horse having slits (arrow) in the wall. The endothelium consists of rod- or spindle-shaped cells. $\times 4,500$.

Fig. 4. Endothelial cell of the sheathed artery of the pig containing microfilaments and a dense body (arrow). $\times 19,000$.

of the vessel, Slits with a diameter of $1-3 \mu\text{m}$ were found between the endothelial cells in all species except for the dog (Figs. 1-3). Nuclear portion of the rod-shaped endothelial cells of the cat, dog, pig, horse and cow showed ovoidal elevation protruded into the capillary lumen (Fig. 1-4). The cytoplasm of the endothelial cells contained many filaments, which were about 10 nm in diameter

and of various electron density according to the species (Fig. 4).

The network of the sheathed artery contained platelets and erythrocytes, but no other blood cells, except for macrophages in the dog (Figs. 1-3, 5 and 6). The contour of the sheathed arteries was clearly distinguished by scanning electron microscopy from the splen-

Fig. 5. Arterial sheath of the pig. It consists of reticular cells and reticular fibers forming networks to contain erythrocytes (Er) and platelets (P). The right is cordal side. $\times 1,800$.

Fig. 6. Arterial sheath of the dog. Macrophages (Mc) are observed in the sheath. The right is cordal side. $\times 2,700$.

Table 2. Comparison of fine structures of arterial capillaries of rat, dog, pig, horse and cow

Species ^{a)}	Endothelial cell		Terminal portion		Circulation system
	Elevation of the nuclear portion	Slit	Shape	Slit	
Rat	Low	Presence or absence	Sack	Visible	Open or close
Dog	Low	Absence	Sack	Visible	Open
Pig	Low	Presence or absence	Sack	Visible	Open
Horse	Low	Absence	Sack	Visible	Open
Cow	Low	Absence	Funnel	Visible	Open

a) Arterial capillaries were not observed in the cat.

ic cords in the cat, pig, horse and cow (Figs. 1, 5, 12 and 17), but not in the dog.

Reticular cells of the sheath had ovoid or irregular nuclei, and contained many mitochondria and rough endoplasmic reticula and a few lysosomes (Figs. 5 and 6). Debris of phagocytized erythrocytes were not found in the reticular cells.

2. Arterial capillary (Table 2)

The distal portion of the sheathed artery was continuous with the arterial capillaries. In the cat, the arterial capillary was not

recognized by SEM. The nuclear portion of the endothelial cells near the terminal portion were small and did not show an elevation on the surface of the cells. A few villous micro-projections were present on the surface of the endothelium. Slits were observed only in the rat and pig between the endothelial cells (Figs. 7 and 8). The reticular cells and their processes were attached on the outside of the wall of the capillary (Fig. 9).

Terminal portions of the arterial capillaries were opened into the reticular meshwork in

Fig. 7. Arterial capillary of the pig running in the splenic cords. It has some pores (arrows) about $3\ \mu\text{m}$ in diameter. The endothelium is smooth, with some microvilli-like projections. The pulp reticular cells are observed to touch on the outside of the endothelium. $\times 1,100$.

Fig. 8. Cast specimen of the pig. An arterial capillary (AC) runs from the sheathed artery (SA) and ends to be sack-shaped in the splenic cords. Resin leaked out from the sidepores into the splenic cords (arrows). $\times 360$.

Fig. 9. Arterial capillary (AC) and terminal portion of the cow. The capillary runs straight in the splenic cords and has a funnel-shaped opening. There are some sidepores in the terminal portion. $\times 2,800$.

the dog, pig, horse and cow. They were sack-shaped in the rat, dog and horse and funnel-shaped in the cow. In the dog, terminal portions ended near the sinus wall and some attached to the sinus wall. In the rat, some were opened into the red pulp and others were connected with the splenic sinus. Terminal

portions had small sidepores and endpores, but no valves and sphincters in all the species examined (Figs. 8–11).

3. Splenic sinus (Table 3)

The sinuses were wider and shorter in the cat, pig, horse and cow than in the rat and dog. In the rat and dog, the splenic sinus had

Fig. 10. Arterial capillary of the rat. The capillary (AC) connects directly with the sinus (S). An arrow indicates an anastomosing portion. The capillary has a few small sidepores, but neither valves nor sphincters. $\times 1,800$.

Fig. 11. Arterial capillary of the horse. The endothelium of the capillary protrudes a little into the lumen. Pores (arrows) are observed in the sack-shaped terminal portion. $\times 1,400$.

Fig. 12. Low power magnification of the horse spleen showing sheathed artery (SA) and sinus (S). The sheath is distinguished clearly from the cords. The area of the sinus is small and that of the splenic cords is large. $\times 250$.

rod-shaped cells arranged in parallel along the long axis of the sinus to form a lattice-like structure except in the anastomosing areas. The nuclear portions of the cells exhibited ovoid to ball-shaped protuberance protruded into the lumen of the sinus. The neighboring cells were bridged by transverse cytoplasmic processes to leave ovoid or spindle slits be-

tween them (Figs. 13, 14 and 18). In the cow, endothelial cells arranged more irregularly than in the rat and dog, and had transverse processes sometimes crossed to extend to the outside of the neighboring cells (Figs. 13 and 14). In the splenic sinus of the pig, endothelial cells were divided into two types,

Table 3. Comparison of fine structures of the splenic sinus of rat, cat, dog, pig, horse and cow

Species	Size of the sinus in the red pulp	Endothelial cell			Meshwork of reticular cell on the sinus wall
		Shape	Lateral process	Slit	
				Diameter (μm)	
Rat	Large	Rod	+	2- 6	+
Cat	Small	Stellate	-	4-16	+
Dog	Large	Rod	+	1- 3	+
Pig	Small	Rod or stellate	+ or -	4- 7	+
Horse	Small	Stellate	-	2- 6	+
Cow	Small	Rod	+	2- 4	+

Fig. 13. Sinus of the cow. The endothelial cells are rod-shaped with lateral processes which connect with neighboring endothelial cells to leave small to large slits (arrows). $\times 2,400$.

Fig. 14. Lateral processes of the endothelial cells of the cow. They do not meet with each other and extend to the outside of the endothelium. $\times 8,600$.

rod-shaped and stellate-shaped, the latter being the majority of the endothelial cells (Figs. 15 and 16). The splenic sinuses in the cat and horse were short and sometimes showed branchings and anastomoses. The endothelial cells of the cat and horse were stellate-shaped and had spindle-shaped nuclear portions protruded into the lumen. The cytoplasm of the endothelial cells were narrow and long in the cat, but wide and short in the horse (Figs. 12 and 17).

Slits of the sinus of the pig were fewer, larger and more irregular than those of the rat,

dog and cow (Figs. 13-16). In the horse, the sinus wall had a few irregularly distributed slits (Fig. 12). In the cat, the sinus wall had numerous slits largest in all the species examined (Fig. 17). Many erythrocytes were often observed to pass through the slits of the sinus wall to leave some blood cells attached to the slits. Macrophages with many projections entered into the lumen of the sinus through these slits (Figs. 12-18). The diameter of the slits was varied among the species examined.

The outer wall of the sinus was covered

Fig. 15. Sinus of the pig. The endothelium consists of rod-shaped cells with lateral processes and has large slits (arrows). $\times 1,200$.

Fig. 16. Sinus of the pig. The endothelium consists of rod- and stellate-shaped cells, and has large slits. Blood cells are attached to the slits. $\times 3,000$.

Fig. 17. Sinus of the cat. The sinus (S) in the red pulp is small and shorter than in any other species examined. The endothelium consists of flat stellate-shaped cells. Anastomosis and sheathed arteries (SA) are observed. $\times 260$.

Fig. 18. The outer surface of the sinus wall in the cat. The pulp reticular cells touch on the wall, run across the long axis of the endothelium and make meshworks. The pores in the meshwork meet with the slits of the endothelium on the whole, but some do not meet completely. A macrophage (Mc) is attached to the slits. $\times 3,600$.

Fig. 19. Sinus wall of the cow. The processes of the reticular cells (RC) touch on the outside of the endothelium and form corn- or foot-shaped ending. $\times 5,500$.

with the reticular cells of the splenic cord. The reticular cells were attached to the sinus wall by their processes ending as a foot-like expansion. The processes always overlapped on the outside of the endothelial cells, formed rings or bands around the sinus, and constituted the meshworks in the rat and dog (Fig. 18). The processes of reticular cells of the splenic cords formed meshworks on the outside of the sinus wall in the cat, pig and horse (Figs. 15 and 16). Both band and foot-like processes were found in the cow (Fig. 19). The gap in the meshwork usually meet with the slits between the endothelial cells of the splenic sinus (Figs. 10, 18 and 19).

In the present study, the sinus wall in all species examined consisted of two layers of endothelial and reticular cells, the discontinuous basal lamina being intervened between the two layers (Figs. 13, 15–20).

Fig. 20. Transverse section of the sinus wall of the horse. It consists of endothelial cells (E), basal lamina (BL) and reticular cells (RC). Reticular fibers (RF) connect with the basal lamina. Free ribosomes and vesicles are observed in the endothelial cell. $\times 11,200$.

DISCUSSION

Sheathed artery: The wall of the sheathed artery was so far called as periarterial macrophage sheath (PAMS) [5], ellipsoid [7, 11, 36], Schweigger-Seidel sheath [36] or Kapillarenhülsen [42, 43]. This structure was studied with light microscope by Billroth [2], Schweigger-Seidel [33] and others [3, 5, 17, 18, 33, 36, 37, 43, 44]. Although many reports have been published on the structure of the sheathed artery in cats, dogs and men by SEM and TEM, there have been only a few reports in the pig, horse and cow by scanning electron microscopy [30]. It was reported that sheathed arteries were not present in the rat spleen [32, 34].

The fine structure of the endothelial cells of

the sheathed artery in the pig, horse and cow were reported to be almost the same as that in cats, dogs and men by light and electron microscopy [5, 7, 12, 36, 42]. Slits were not found between the endothelial cells of the capillary walls in the dog. Blue and Weiss [7] studied the contracted vascular bed of the dog spleen and observed slits and erythrocytes attached to the slits by transmission electron microscopy. Suzuki [38], using the modified method of perfusion, observed erythrocytes attached to the slits in the dog by scanning electron microscopy. According to the present study and the previous reports [5, 7, 18, 42], it is considered that the size of the slits may change under various conditions.

Microfilaments with a diameter of 10 nm or more were found in the endothelial cells of the cat, dog, pig, horse and cow. They are believed to be a part of cytoskeleton [31], but have only been reported in the cat, dog and horse [5, 7, 11, 42, 48]. In the present study, the filaments with a diameter of 10 nm were first described in the endothelial cells of the pig and cow.

Some investigators reported the phagocytosis of the reticular cells of the sheathed artery and the presence of macrophages in the reticular meshwork [1, 5, 7, 12, 32, 36]. We think that the macrophages observed in meshwork came from the splenic cords when physiological changes such as an immunological response occurred. Mechanical and biological functions were attributed to the sheathed arteries by Imai [18]. In the present study, it is suggested that the sheathed arteries may play a role as a filter to regulate the movement of blood cells because of the existence of slits and microfilaments.

Arterial capillary: In the present study, the structure of the arterial capillaries near the terminal portion was similar to that observed by many investigators [15, 19, 20, 23, 38]. The reticular cells and their processes attached on the outside of the arterial capillary held the capillaries in the splenic cords.

The termination of the arterial capillary in the dog was described as ampulla-shaped by Mall [24] and Thoma [40]. In the present study, the termination was sack-shaped in the dog. Ohta *et al.* [30] used cast specimens of the pig spleen, but failed to observe the form of the terminal portions. We also used cast specimens, and found the terminal portion to be sack-shaped in the pig. Hartwig [14] reported in the horse by light microscope that the terminal portion was ampulla-shaped and had small pores. Snook [34], also found terminal portions to be both ampulla- and funnel-shaped with sidepores in the horse and cow. In the present study, we found that the terminal portion was sack-shaped with sidepores in the horse and was funnel-shaped with some sidepores in the cow spleen. Terminal portions in the dog, pig, horse and cow had sidepores or endpores, and blood cells in the terminal capillary were migrated into the splenic cords through slits. As the endothelium of the arterial capillary was not continuous with that of the sinus in these species, it was suggested to be open circulation system. Weiss [46] reported an open circulation system by observing crack specimens in the rat, while Murakami *et al.* [28] reported a closed circulation by observing the cast specimens. In the present study, it was demonstrated that the rat had both open and closed circulation. The present study also demonstrated that the termination of the arterial capillaries in the dog and cow showed a pattern of the "open but functional closed circulation" as reported by McCusky [25] and Suzuki [38] by electron microscopy.

Splenic sinus: Billroth [3] described the splenic sinus of the man with many slits and suggested it to be the beginning of the venous system. He called it the "cavernöse Milzvenen" or "cavernöse Milzvenensinus". Weidenreich [44] observed that the endothelium of the sinus was formed by longitudinally extended rod-shaped cells running parallel with each other to leave spaces between

them, and that transverse reticular fibers (ring fibers) bound them together from the outside. However, Mollier [27] observed lateral processes between the rod-shaped cells, which Weidenreich [44] did not find, and termed them "protoplasmatischen". Many investigators [6, 8–10, 26, 34, 38, 41, 42, 47] studied the rat, rabbit, dog and human spleens and observed carefully the shape of the endothelial cells of these species. Snook [34] divided the animal spleens into "sinusal" and "non-sinusal". The sinusoids at the beginning of the splenic system were called primordial veins in the nonsinusal spleen, consisted of rod-shaped cells and never anastomosed with each other [13]. Hataba *et al.* [15] found the presence of anastomosing vasculatures in the mouse spleen, and used the term "sinus". Snook [34] used the term "primordial vein" in his report on the mouse spleen. On the other hand, Blue and Weiss [6] used a term "venules" in the cat spleen instead of "primordial veins" of Snook [34].

In the present study, the shape of the endothelial cells of the sinus in the cat, pig and horse was considerably different from that in the rat, dog and cow. The basic structure of the endothelium of the sinus in the rat and dog were similar to that in the previous report on the rat, rabbit, dog and man [9, 10, 12, 38, 41, 42, 46]. The two types of the endothelial cells, i.e. stellate and rod-shaped were seen in the pig. They changed their forms from stellate-shaped to rod-shaped. The cow spleen was also classified as non-sinusal according to Snook [34]. Although the shape of the endothelial cells of the cow was slightly different from the rod-shaped cells of the rat and dog in the present study, it can be called rod-shaped. The lattice-like structure of the rod-shaped cells and anastomosing vasculature were also observed in the cow. The difference of the shape of the endothelial cells of the sinus among the species may suggest not only the physiological difference in the functions of

the sinus or spleen, but also the embryological and phylogenetic difference in the development of the sinus or spleen.

The pulp reticular cells and their processes were attached on the sinus wall from the outside and made meshworks on the in all species examined. The side and number of slits between the endothelial cells were different from species to species. The function and relationship of the slits of the sinus wall and networks were unknown. These slits and meshworks may or may not meet together when the spleen contracts or distends. However, the fenestrations of the sinus wall may affect to the blood flow. When the blood cells pass through the sinus wall, the narrow slits of the wall are thought to squeeze the blood cells tightly to snap off the cytoplasm containing intraerythrocytic inclusions such as Heinz bodies or malaria plasmodia [10, 22, 47].

In all species examined in the present study, the sinus walls generally consist of endothelial cells, basal lamina and reticular cells of the splenic cords. But, it is unknown whether the blood cells migrate into the splenic cords or the sinus.

Anastomosis of the sinus was found in the spleen of the rat, cat, dog, pig, horse and cow. Endothelial cells were irregularly arranged in the anastomosing area. This may be related to the sphincter mechanism of the splenic sinus [26]. In addition to this sphincter mechanism, we think that the anastomosis of the sinus may play a similar role to that of the "tuberculum intervenosum" in the heart.

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要 約

走査電子顕微鏡によるラット、ネコ、イヌ、ブタ、ウマおよびウシ脾臓の微細血管系の比較形態学: 関 あずさ・阿部光雄 (酪農学園大学獣医学科)——ラット、ネコ、イヌ、ブタ、ウマおよびウシの脾臓英動脈、動脈性毛細血管および脾洞を走査電顕と透過型電顕を用いて観察した。英動脈は杆状形の内皮細胞からなる毛細血管と、これを囲む細網細胞からなっていた。英の網眼中には血小板や赤血球が観察されたが、イヌを除いては白血球や大食細胞は見られなかった。ラットでは英動脈を欠いていた。イヌを除くすべての動物で内皮細胞間に直径1~3 μm の間隙が観察された。ラット、イヌ、ブタおよびウマの動脈性毛細血管の終末部は嚢状で、ウシでは漏斗状を呈し、すべての動物で終末孔もしくは側孔が見られ、脾索腔と通じていた。ラットでは、いくつかの動脈終末部が脾索に開放し、あるものは直接脾洞に続いていた。脾洞内皮細胞の形はラット、イヌおよびウシでは杆状、ネコとウマでは平たい星形を呈し、ブタでは両形がみられた。これらの脾洞壁には血球や大食細胞が脾洞から脾索へ、もしくは、その逆に移動する間隙があった。脾洞内皮細胞の外側には細網細胞が付着していた。