

MORPHOLOGY AND FUNCTION OF THE SPLEEN IN CAMEL: A COMPARATIVE REVIEW

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ABSTRACT

The morphology of the spleen varies among different mammalian species. In camels, it is C-shaped, while in dogs, it is elongated, dumbbell shaped, and ventrally oversized. Ruminants have a flat and oblong spleen, while in horses it is comma shaped. The spleen is located in the left upper quadrant of the caudal peritoneal cavity, behind the diaphragm, and in close proximity to the colon, kidney, lower ribs, stomach, and pancreas in camels and other mammalian species, respectively. The camel's spleen is enclosed within a thick capsule. This capsule is divided into an inner layer composed of smooth muscle cells and an outer layer primarily made of connective tissue. The two layers of the capsule are smooth muscle and dense irregular connective tissue. Species differences exist in both the overall thickness and relative quantity of smooth muscle. Collagen and elastic fibres make up trabeculae, while smooth muscle cells extend into the parenchyma from the capsule and the hilus. The spleen in camels plays a crucial role in the storage and regulation of blood supply. The central artery, which emerged from the periarterial lymphatic sheath, was branched to four penicilli and then extended as sheathed arterioles, which were found near or surrounded by blood sinusoids of the red pulp. The white pulp is surrounded by a broad marginal zone that lacks marginal sinuses but has sheathed arteries. The marginal zone macrophages, a key player in the spleen's immune response, were characterised by its large size and intimate connections between its cell processes and the nearby marginal zone B cells. Scanning electron microscopy of the camel foetus's spleen demonstrated the primary structure, including mesothelium, numerous erythrocytes, medium-sized and small lymphocytes, reticular cells, and reticular connective tissue fibres. Differential features of spleen of other animals are also discussed.

Key words: Anatomy, camel, function, histology, spleen, ultrastructure

The spleen is an intriguing organ that performs various functions such as haematopoiesis, immunological response, blood filtration, and blood storage, and these functions vary among different animal species. As the animal develops, there are exciting changes in the presence and significance of each function, with a reduction in haematopoietic activities and an increase in the specialisation of other tasks over time (Udroiu and Sgura, 2017).

The spleen, an intraperitoneal lymphoid organ, is situated on the left side of the abdomen, below the diaphragm (Dyce *et al*, 1987). During gestation, the spleen plays a significant role in haematopoiesis, (Boes and Durham, 2017). Post-birth, the spleen carries out a range of vital physiological functions, including haematopoiesis and lymphopoiesis (lymphocyte proliferation and maturation), blood filtration via recycling of senescent and damaged erythrocytes, erythrocyte and thrombocyte storage,

iron metabolism, and immune surveillance (Cheung and Nadakavukaren, 1983; Mebius and Kraal, 2005; Cesta, 2006; Eurell and Frappier, 2006; Moura *et al*, 2008; Khalil *et al*, 2009; Bello *et al*, 2019; Gnanadevi *et al*, 2019; Lewis *et al*, 2019; Xu *et al*, 2020; Abdellatif, 2021).

The spleen's structure reflects its complexity. It is primarily composed of red and white pulp (RP and WP), with a distinct marginal zone between them (Bronte and Pittet, 2013). The WP, despite occupying less than a quarter of the spleen's tissue, is its principal immunologic zone. The RP makes up the majority of the tissue and serves a different immunological function than the WP. The absence of afferent lymphatic arteries in the spleen contributes to its unique structure, as all cells and antigens enter the spleen via the blood (Lewis *et al*, 2019).

This shift from scattered lymphocytes to the segregation of the WP indicates a rise in the complexity of immunological characteristics and the

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organisation of T and B lymphocyte regions, leading to the formation of germinal centres. Additionally, different features of the RP have evolved in mammalian species, enhancing the specialisation of the filtration function of the pulp sinuses and the storage function (Udroiu and Sgura, 2017).

In adult animals, lymphopoiesis is the spleen's main haematopoietic activity, while erythropoiesis occurs during foetal life. However, splenic erythropoiesis persists in newborn horses and ruminants for several weeks postpartum (Boes and Durham, 2017). Erythrocytes and thrombocytes are typically stored in the RP and splenic cords. As animals age, the elasticity of the erythrocyte cell membrane decreases, leading to the detection and removal of old and damaged erythrocytes by the splenic cords' reticuloendothelial system and macrophages in the red pulp's venous sinuses. A reticular fibre network of macrophages and reticular cells across the reticuloendothelial system helps the spleen filter blood more effectively, resulting in numerous macrophages containing engulfed erythrocyte fragments and hemosiderin pigment in the RP (Eurell and Frappier, 2006).

Gross anatomy of the spleen in camel

The morphology of the spleen varies among different mammalian species (Fig 1). In camels, it is C-shaped, while in dogs, it is elongated, dumbbell-shaped, and ventrally oversized. Ruminants have a flat and oblong spleen, while in horses it is comma-shaped. According to Smuts and Bezuidenhout (1987) and Dyce *et al* (1987), the spleen is located in the left upper quadrant of the caudal peritoneal cavity, behind the diaphragm, and in close proximity to the colon, kidney, lower ribs, stomach, and pancreas in camels and other mammalian species, respectively. The spleen is typically not noticeable on physical inspection, but in thin adults, children, and adolescents may be detected (Nguyen and Zhang, 2020).

Accessory spleens, also known as supernumerary spleens, splenules, or splenunculi, are benign and asymptomatic. They are estimated to be present in 10% to 30% of the population, with an individual potentially having one to six accessory splenic buds. Accessory spleens are typically only a few millimetres long, but can occasionally grow to a few centimetres in length, resulting in variation in size (Nguyen and Zhang, 2020; Yildiz *et al*, 2013; Mohammadi *et al*, 2016).

Khalel (2010) conducted a comprehensive study on the gross anatomy of the spleen in Awasi

sheep, unearthing unique findings that significantly advanced our understanding in the field. The spleen, for instance, was found to possess a distinctive triangular shape with rounded corners, weighing approximately 69 ± 6.7 g and measuring an average length and width of 9.93 ± 0.3 and 6.48 ± 0.2 cm, respectively. It reached its maximum thickness near the hilus (2.48 ± 0.1 cm). The spleen also exhibited two distinct surfaces: the visceral, which was concave and had a hilus, and the parietal, which appeared to be convex. In sheep, the spleen had two ends: the ventral end, which was narrower and thinner than the base end, and the base end, which was broad and thick. These detailed observations, along with other intriguing findings such as the quadrangular shape of goat spleens (Suri *et al*, 2017; Gnanadevi *et al*, 2019) have significantly enriched our understanding of the gross anatomy of the spleen in various animal species.

The spleen, a vital organ in camels, was characterised by its dark brown colour and unique C-shape with blunt, rough surfaces and edges. It was thick at the hilus and the midline and thin at the edges (Maina *et al*, 2014). According to Nawal and Maher (2018), the spleen of a camel had four segments, two hilus, and two splenic arteries and veins. The same authors stated that the splenic blood supply had only one arterial segmentation with no anastomosis. In buffalo calves, sheep, and goats, only one tiny hilus was found, and anastomosis and venous segmentation between the dorsal and intermediate segments were absent. According to Marwa-babiker *et al* (2023), the spleen has C-shaped, rough surfaces and serrated edges in camel foetuses. It is located on the caudolateral side of the abdominal cavity, medially to the ribs and caudally to the stomach. These findings underscore the practical importance of understanding the gross anatomy of the spleen in different animal species, making a significant contribution to the field of veterinary medicine and anatomy.

The spleen of the Asian elephant was dark reddish, long and narrow. The caudal-visceral surface was concave and displayed a longitudinal hilus towards its cranial border; the cranial-parietal surface was convex with serrations on the caudal and cranial splenic borders (Rajani *et al*, 2021).

Histology of mammals' spleen

Zidan *et al* (2000) found that the camel's spleen is enclosed within a thick capsule. This capsule is divided into an inner layer composed of smooth muscle cells and an outer layer primarily made of connective tissue. The same authors showed that

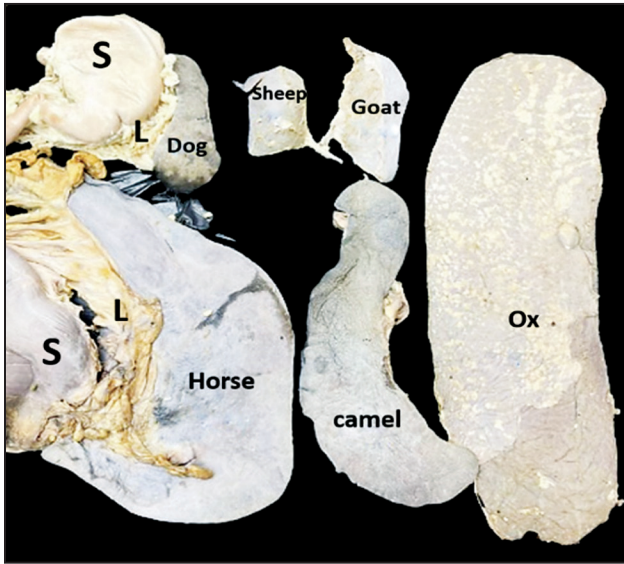


Fig 1. Photograph showing the spleen of different domestic mammalian species, S: stomach, L: gastro splenic ligament.

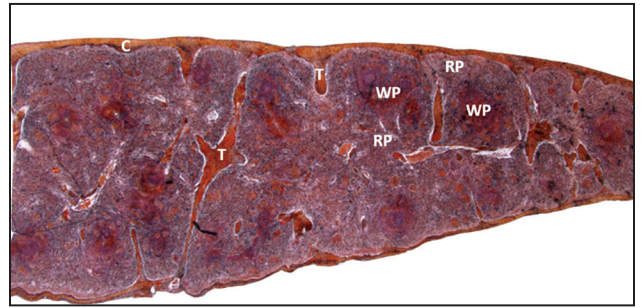


Fig 2. Photomicrograph showing general histological view of the mammalian (rat) spleen: stroma of the spleen consists of connective tissue capsule surround the spleen (C), which sends the connective tissue trabeculae (T). The parenchyma consists of white pulp (WP) and red pulp (RP).

the vascular and avascular trabeculae extending from the capsule to the parenchyma, subcapsular, and per trabecular blood sinuses around primary and vascular trabeculae are unique structures of the camel spleen. These unique structures are not found

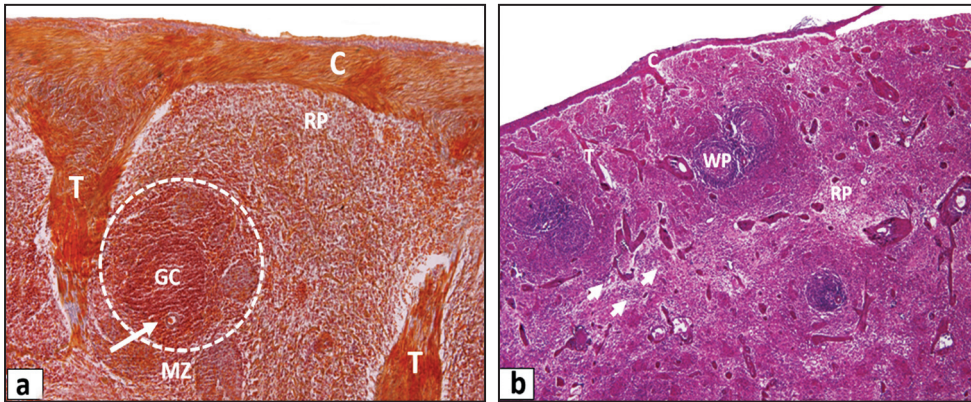


Fig 3. a and b: Photomicrograph showing the spleen; C: connective tissue capsule, T: connective tissue trabeculae, GC: germinal centre of the splenic corpuscle (dotted circle). MZ: marginal zone, which found between the white pulp and the red pulp (RP). Central arteriole (arrow) and splenic sinuses (arrows head).

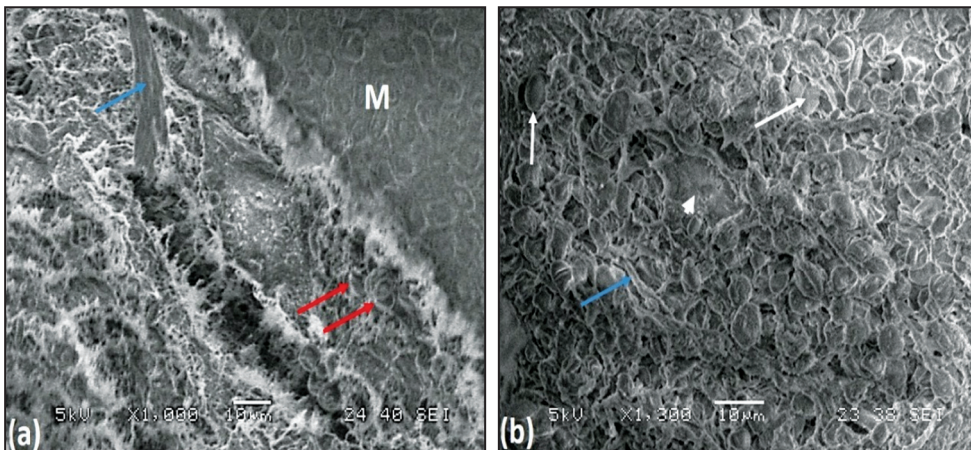


Fig 4. a and b: Scanning electron micrograph of spleen of camel foetus showing mesothelium (M) erythrocytes (white arrows), lymphocytes (red arrows) reticular cells (arrowhead) and reticular connective tissue fibres (blue arrows).

in other mammalian species, indicating a distinct evolutionary path for the camel spleen. In other mammalian species, the spleen is surrounded by a capsule of thick connective tissue invested by the peritoneum (Eurell and Frappier, 2006) (Figs 2 and 3).

The two layers of the capsule are smooth muscle and dense irregular connective tissue. Species differences exist in both the overall thickness and relative quantity of smooth muscle (Eurell and Frappier, 2006 and Marwa-babiker *et al*, 2023). Collagen and elastic fibres make up trabeculae, while smooth muscle cells extend into the parenchyma from the capsule and the hilus.

The spleen, a vital component of the body's immune system, is a complex organ. It is composed of RP, responsible for storing red blood cells, and WP, rich in lymphocytes and active in immune responses (Eurell and Frappier, 2006; Bloom and Fawcett, 1986). The RP is made up of cell cords and sinusoids, while WP is lymphoid in nature, with a marginal zone containing pores where cells can leak (Van Krieken, 1997). The WP houses two types of blood vessels: one with muscled walls, and the other with thinner walls sheathed by reticular cells. Within the reticular cells, a network of lymphoblast, small and medium lymphocytes, and dendritic macrophages is formed. This intricate network of cells and vessels is crucial to the body's defense system, underscoring the importance of studying the unique camel spleen.

According to Zidan *et al* (2000), the spleen in camels plays a crucial role in the storage and regulation of blood supply. The central artery, which emerged from the periarterial lymphatic sheath, was branched to four penicilli and then extended as sheathed arterioles, which were found near or surrounded by blood sinusoids of the RP. The WP is surrounded by a broad marginal zone that lacks marginal sinuses but has sheathed arteries. The RP was divided into cords by secondary trabeculae and contained numerous sizes of venous sinusoids. The observation demonstrated that the spleen of the camel was a sinusal type that can store blood, as well as the thick muscular capsule and trabeculae pump according to the body's need. Closed and open circulations facilitated the blood supply of the spleen. A unique venous return was drained from the venous sinusoids of the RP to the peritrabecular sinuses and subcapsular sinuses to the splenic vein. These histological structures showed no significant differences related to age.

During the first trimester of pregnancy, the spleen's capsule in camels was made of a thin connective tissue, indicating a relatively low blood

storage capacity. However, as the pregnancy progressed into the second and third trimesters, the spleen underwent significant changes. The capsule transformed into a thick, dense, irregular connective tissue with descending trabeculae of collagen fibres and bundles of smooth muscle fibres, suggesting an increased blood storage capacity. The parenchyma, which consisted of a variety of cell types in the first trimester, differentiated into white and red pulps in the second and third trimesters. The RP contained megakaryocytes in all three trimesters, indicating a continuous production of blood cells throughout the pregnancy (Marwa-Babiker *et al*, 2022).

The marginal zone macrophages, a key player in the spleen's immune response, were characterised by its large size and intimate connections between its cell processes and the nearby marginal zone B cells. It also boasts a highly developed phagocytic potential (Dijkstra *et al*, 1985). In mice, Humphrey and Grennan (1981) noted that the marginal zone macrophages were larger than the other macrophages in the spleen and had a distinct morphology. These unique characteristics of the marginal zone macrophages contribute to our understanding of the spleen's immune system and its role in maintaining the camel's health.

In a meticulous study of rats, the authors observed that the spleen, before differentiated into the periarteriolar lymphoid sheath in the interior layer of the marginal zone (MZ), migrating lymphocytes tended to gather in some places near marginal-zone macrophages (Dijkstra, 1982; Brelinska and Pilgrim, 1983). This careful observation underscores the importance of understanding the spleen's structure in different animal species.

In rats (Figs 2 and 3), in line with Suri *et al* (2017) and Gnanadevi *et al* (2019) in goats, has revealed that the spleen was enclosed in a thick capsule of irregular dense connective tissue, and red and white pulps. The WP, a crucial component, is composed of periarterial lymphatic sheath and splenic nodule, which are scattered throughout the RP. The RP, another key element, consists of splenic cords and sinusoids; the endothelial cells with prominent nuclei that protruded into the sinusoidal lumen bordered the sinusoids (Gnanadevi *et al*, 2019 and Suri *et al*, 2017).

Rahman *et al* (2016) studied the histomorphometry of spleen in human, goat, buffalo, rabbit and rat and found significant implications. Identical capsular thickness measurements were observed in goats and buffaloes, whereas the thin and thinnest capsule was measured in rat and rabbit, respectively.

In sheep, the capsule was made of collagen, elastic, reticular, and smooth muscle fibres (Thanvi *et al*, 2020). The red and white pulps, the main components of the splenic parenchyma, play a crucial role in the spleen's function. The WP, consisting of lymphoreticular tissue, lymphatic nodule and periarterial lymphatic sheath, is less abundant. The RP, made up of pulp arterioles, splenic sinusoids, splenic cords, and sheathed and terminal capillaries, is also less abundant and poorly developed (Thanvi *et al*, 2020).

A novel finding conducted by Rajani *et al* (2021), described that the spleen of the Asian elephant is surrounded by a thick capsule of dense irregular connective tissue. Most of the splenic parenchyma, a unique feature, consisted of RP, while the remaining 20.25% was WP, composed of the periarterial lymphatic sheath and splenic nodules (Rajani *et al*, 2021). Many investigators have observed numerous megakaryocytes in the RP of adult and foetal dromedary camel (Zidan *et al*, 2000; Marwa-Babiker *et al*, 2022), whereas it was observed in both the spleen and bone marrow of pregnant rats (Marien and McFadden, 1970). The findings are significant in understanding the spleen's structure in different animal species.

Ultrastructure of spleen

Scanning electron microscopy of the camel foetus's spleen demonstrated the primary structure, including mesothelium, numerous erythrocytes, medium-sized and small lymphocytes, reticular cells, and reticular connective tissue fibres (Fig 4). During the first trimester of pregnancy, a comparatively limited number of reticular cells were observed in the parietal sheath, marginal zones, and cordal gaps. Dendritic macrophages and lymphoblasts were organised into a network by the reticular cells throughout the second and third trimesters. Marwa-Babiker *et al* (2023) investigated the spleen of a camel foetus and found that it was lined with mesothelial cells and divided by reticular connective tissue fibres using scanning electron microscopy.

Weiss (1974) studied the scanning electron microscopy of normal rat spleen and demonstrated that the reticulum and vascular sinuses were made of macrophages, erythrocytes, thrombocytes, and other migratory elements. Large, bulky, irregular reticular cells with broad processes were found in the periarterial lymphatic sheath, the marginal zone and cordal spaces. Flattened reticular cells at the periphery of the periarterial lymphatic sheath formed cylinder shapes attached to the central artery and associated with unusually heavy extracellular fibres.

Vascular sinuses were suspended in the reticulum by attachments of cordal reticular cells to the adventitial surface. Adventitial cells of the sinus were branched into the cords. Endothelial cells were typically laid side by side without gaps, except as migratory cells which passed through the wall. The erythrocytes were observed in passage across the sinus wall. Sinuses and cords were often swollen, irregular, and bore blebs. Macrophages displayed rich surface folds and processes, whereas the thrombocytes were abundant and adherent to the endothelium of sinuses and the surface of reticular cells.

Polak *et al* (2009) demonstrated that the splenic cords originated from a three-dimensional network of fibroblastic reticular cells situated among branched sinuses and artery terminals in human spleen. A unique variety of rod-shaped endothelial cells that were oriented perpendicular to the longitudinal axis of the sinuses lined their interior walls. The fibroblastic reticular cells were transformed into fixed phagocytes with no phagocytosis properties. The capsule and trabeculae were composed of random smooth muscle fibres.

The reticular cells in the spleen were three-dimensional stellate shapes with smooth surfaces that extended slender processes. Although the reticular cells they exposed in some places, the reticular fibres were typically covered by reticular cell processes (Fujita and Ushiki, 1992).

Electron microscopy of albino rabbit's spleen revealed that the white pulp was arranged in clumps or nests separated by a loose-irregular meshwork composed of basement membrane-like material, collagen, and the cellular prolongations of fibroblasts and stellate cells, lymphocytes, and numerous reticular cells. The plasma cells, macrophages, erythrocytes, and thrombocytes were situated at the periphery of the white pulp and adjacent to the marginal zone. The lymphocytes of the white pulp varied in size and was difficult to differentiate from the polymorphic reticular cells (Burke and Simon, 1970).

According to Kashimura and Fujita (1987), the central arteries in human were continuous and without branching into follicular arteries in the white pulp, while developing into penicillar arteries in the red pulp. Although some penicillar arteries retreated in the marginal zone, others travelled through it, penetrating the white pulp and developing into follicular arteries.

In humans and rats, the spleen was examined using scanning electron microscopy (Sasou *et al*, 1986). Both species had the marginal zone and white and red

pulps; however, there were considerable differences in the artery termination in the marginal zone. In rats, the follicular arteries formed the marginal sinus, a circulatory net that terminated at the edge of the white pulp. Numerous vascular termini of the follicular and sheathing arteries were dispersed throughout the human's marginal zone. Despite these differences, both in humans and rats, the central artery was found to be surrounded by flat reticular cells, a reassuring similarity. In the red pulp of rats, the vascular termini were funnel- or tubular-shaped. The sheath of human arteries had a circumferential lamellar structure consisting of flat reticular fibres (Sasou *et al*, 1986).

Conclusion

The spleen, a vital organ in various mammals, exhibits significant variations in shape. For instance, it was bigger ventrally and bell-shaped in dogs, comma-shaped in horses, C-shaped in camels, and elongated in ruminants. The celiac plexus provides precise innervation and blood supply via the splenic artery and vein. This intricate network ensures the organ's optimal functioning. The spleen is a soft, reddish-purple organ with two surfaces, visceral and diaphragmatic, and its limits are divided into three areas: cranial, caudal, and intermediate. The splenic hilum, located on the caudomedial side of the gastric impression, contains nerves, splenic vessels, splenorenal, and gastrosplenic ligaments and is enclosed in an elastic and fibrous tissue capsule that extends into the parenchyma as trabeculae. The parenchyma, supported by an exemplary network of reticular fibres, comprises two types of tissue: white pulp and red pulp, separated by marginal zones.

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Conflict of Interest

The authors declare that they have no conflict of interest.

Data Availability Statement

The data presented in this study are available on request from the corresponding author.

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