Microvascular anatomy of the large intestine in adult *Xenopus laevis*: scanning electron microscopy of vascular corrosion casts and correlative light microscopy*

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Summary. The microvascular anatomy of the large intestine of the adult South African Clawed Toad, *Xenopus laevis* (Daudin), was studied by scanning electron microscopy (SEM) of vascular corrosion casts (VCCs) and correlative light microscopy. Observations showed the large intestine to be supplied by the haemorrhoidal artery and the posterior mesenteric artery and drain via the posterior haemorrhoidal vein into either the left or right posterior abdominal vein. Both arteries and veins showed a bipinnate supply/draining pattern with branches running circumferentially. Vessels embraced the gut wall while arteries and veins in most cases alternated along the gut length. Many short terminal arterioles arose from the circumferential arteries at almost acute angles and capillarized after a short distance. Capillary lengths were short and continued into numerous postcapillary venules which merged either in a leaf vein-like formation or in a rosette-like formation with up to four draining sites per supplying arteriole. The microvasculature was found to be well adapted 1) to sustain blood flow under different amounts of feces in the gut and 2) to provide optimal conditions for the resorption of water and salts from the gut lumen into the blood vascular system by the high number of venules and their conspicuous rosette-like and leaf vein-like patterns.

Introduction

The large intestine (colon) of *Xenopus laevis* is a short, wide tube which lacks longitudinal folds characteristic of the small intestine. It narrows in the pelvic region to form the rectum which then empties into the cloaca. The large intestine absorbs water and salts from the gut lumen. Aquaporins (AP-x3BL; Schreiber et al., 2000) localize in the basolateral membrane of the enterocytes of the mucosal epithelium (Mochida et al., 2008).

The histomorphology (Wiechmann and Wirsig, 2003) and gross arterial supply and venous drainage (Millard, 1941) of the large intestine of *Xenopus laevis* Daudin are well known. From Millard’s work (Millard, 1941) we read that, in *Xenopus laevis* Daudin, the large intestine is supplied from the anterior by the haemorrhoidal artery and from the posterior by the posterior mesenteric artery. The former artery is a branch of the celiac-mesenteric artery and also supplies the hind end of the ileum; the latter is a branch of the last or second last urogenital artery and ascends along the large intestine (Millard, 1941). The two arteries sometimes anastomose (Millard, 1941).

While we have thorough knowledge of the microvasculature of the colon and its functional implications in mammals (e.g. Ohtani et al., 1983; Gannon and Perry, 1989; Aharinejad et al., 1991, 1992), such is lacking on the microvasculature of the large intestine of an anuran amphibian. This study aims 1) to...
demonstrate the microvasculature of the large intestine in the adult South African Clawed toad, *Xenopus laevis* Daudin by scanning electron microscopy of vascular corrosion casts (Murakami, 1971; Aharinejad and Lametschwandtner, 1992; Motta *et al.*, 1992) and correlate light microscopy and 2) to determine for the first time if in this permanently aquatic anuran species—which lives in a hypotonic environment—the vascular bed with its microvascular patterns could play a significant role in the removal of water and salts from this portion of the alimentary tract.

**Materials and Methods**

**Animals**

Twenty-five adult South African Clawed Toads, *Xenopus laevis* Daudin, housed in aquaria (water depth: 15 cm; water temperature: 20°C) and fed three times a week fresh dried Daphnia and Gammarus were studied. Two animals (male: body weight 77 g; female: body weight: 79 g) served for histomorphology and 26 animals (males and females; body weights: 46–126 g) served for vascular corrosion casting, form which 10 high quality vascular casts of the large intestine were taken for scanning electron microscopical analyses.

**Histomorphology**

Animals were killed by immersion in an overdose of an aqueous 0,5% solution of MS 222 (Tricaine methansulfonate; Sigma Chemicals, St. Louis, MI, USA) and first perfused via ventricle-arterial trunk with Amphibian Ringer solution (20°C; for composition see Adam and Czihak, 1964) using manual pressure. After a clear reflux from the opened atria, 10 ml of Bouin’s solution (Adam and Czihak, 1964) was injected to fix the whole animal. Then the large intestine was excised and postfixed in fresh fixative (20°C). After dehydration in a graded series of ethanol, specimens were embedded in paraplast, sectioned transversally and longitudinally (7 μm), and stained (Goldner’s trichrome stain; Romeis, 1989). Micrographs taken with a digital camera (Color View III, Nikon, Tokyo) were imported to Photoshop 7.0 (Adobe) and brightness and contrast were adjusted if necessary.

**Vascular casting**

For preparatory steps preceding resin injection see the histomorphology (above). After a clear reflux from the opened atria, 10 ml Mercox CL-2B (Ladd Research Inc., Burlington, VT, USA) diluted with monomeric methylmethacrylate (Fluka Chemicals, Buchs; 4+1, v+v) was injected with manual pressure. After polymerization of the injected resin, whole animals were tempered (water bath: 60°C, 12 h), macerated (KOH, 7.5%, 12–24 h), rinsed (tap water), cleaned (5% formic acid; 10 min), rinsed (distilled water), frozen in distilled water, and freeze-dried (Lyovac GT2; Leybold Heraeus, Cologne, FRG). In dry specimens the large intestine was exposed by dissection, and specimens were mounted using the "conductive bridge method" (Lametschwandtner *et al.*, 1980), evaporated with carbon and gold, and sputtered with a thin layer of gold. Coated specimens first were investigated in situ with a scanning electron microscope (Stereoscan 250, Cambridge Ltd, UK or an Environmental Scanning Electron Microscope XL-30, FEI Comp., Endhoven, NL, USA; accelerating voltage: 10 kV). Then the ventral circumference of the cast large intestine was excised by microscissors and the luminal aspect of the subepithelial microvascular bed of the dorsal circumference was studied. Finally, the remaining dorsal circumference of the cast was excised, mounted onto a specimen stub with the serosal side facing up, coated, and re-examined in the SEM. For further details on the technique and the preparatory protocol see also Lametschwandtner *et al.* (2006).

**Results**

**Histomorphology**

The large intestine (colon) of *Xenopus laevis* consisted (from luminal to abluminal) of mucosa, external muscular layers, and serosa (Fig. 1–3). The mucosa comprised a simple columnar epithelium with many intraepithelial goblet cells, enterocytes, and basal cells (Fig. 1). The height of the epithelium approximated ~40 μm. Locally, nests of apoptotic epithelial cells were present between enterocytes and/or goblet cells. The lamina propria consisted of a ~80 μm thick layer of connective tissue with melanocytes either scattered throughout the entire lamina propria or locally concentrated directly beneath the basal lamina (Fig.1). Locally lymphoid tissue was concentrated below the basal lamina (Fig. 2) or single leucocytes and plasma cells scattered throughout the lamina propria. Also, beneath the basal lamina, were located capillaries with their feeding arterioles and draining venules placed deeper in the lamina propria (Fig. 3). In the wide portion of the large intestine, six to seven layers of circular smooth muscle cells followed. Locally,
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In the serosa and established the interface to the abdominal cavity (Fig. 1). In the rectal portion, mucosal folds extended far into the lumen making it asterisk-like (Fig. 4). Lymphoid tissue and abundant blood vessels were present within the lamina propria. Both muscular layers increased in thickness so that, in the outer longitudinal layer, large blood vessels were located between muscle cells (Fig. 4).

**Fig. 1.** Histomorphology of the large intestine in adult *Xenopus laevis* Daudin. Transverse section. 7 μm. Goldner's trichrom stain. Note the large vessels (asterisks) located between the inner circular (cl) and outer longitudinal smooth muscle layers (ll). E: columnar epithelium with basal cells, enterocytes, and goblet cells. lp: lamina propria, lu: lumen, me: melanocyte, se: serosa. Note bundles of myelinated nerve fibers located between inner circular and outer longitudinal smooth muscle layer (arrows).

**Fig. 2.** Same as Figure 1, but a longitudinal section of another area. Note the subepithelial lymphoid tissue (lt). E: epithelium, lp lamina propria.

**Fig. 3.** Same as Figure 2, but an other area. Note the large longitudinal vessel (asterisks) joining a circumferential vessel (asterisk) within the lamina propria (lp). cl: circular layer of smooth muscle cells, E: epithelium, ll: longitudinal layer of smooth muscle cells, me: melanocyte, se: serosa.

**Fig. 4.** Histomorphology of the rectal portion. Transverse section. Note the asterisk-like lumen (lu) formed by high longitudinal mucosal folds (lf). Note also the thick muscular coat composed of an inner circular layer (cl) and an outer longitudinal layer (ll) containing abundant blood vessels (empty white profiles). lt: subepithelial lymphoid tissue, se: serosa, v: vein.

A connective tissue layer separated the inner circular layer from the outer longitudinal layer of smooth muscle cells. Bundles of myelinated nerve fibers were present (Fig. 1). Melanocytes were located just beneath the epithelium in the connective tissue layer or within the adventitia of larger vessels (Fig. 1). Further, in the wide portions, some eight to ten layers of smooth muscle cells formed the outer longitudinal layer which approached ~50 μm in thickness. A ~2 μm thick squamous epithelium formed the serosa and established the interface to the abdominal cavity (Fig. 1). In the rectal portion, mucosal folds extended far into the lumen making it asterisk-like (Fig. 4). Lymphoid tissue and abundant blood vessels were present within the lamina propria. Both muscular layers increased in thickness so that, in the outer longitudinal layer, large blood vessels were located between muscle cells (Fig. 4).
Fig. 5. Microvasular anatomy of small and large intestines after removal of the overlaying right lobe of the liver. Ventral aspect. Vascular corrosion cast (VCC). Scanning Electron Micrograph. Arterial vessels are colored red, venous vessels are colored purple. Note the abrupt change in diameter at the transition from the distal ileum (il) into the proximal large intestine (li; arrows). Av: abdominal vein, dd duodenum, dv: duodenal vein, phv posterior haemorrhoidal vein, l: left lobe of liver, te: testis. Inset a: Transition site from the distal ileum (il) to the proximal large intestine (li). Ventral aspect. Note the veno-venous anastomoses between the distal ileum (il) and proximal large intestine (li; arrows). Inset b: Microvascular architecture of the dorsal aspect of the large intestine. Anterior is to the right. Note that the branches of the haemorrhoidal artery (ha) embrace the gut in a bipinnate pattern. Inset c: Microvascular pattern at the site where the ileum enters the large intestine. Luminal view as seen from the large intestine. Note the dome-like vascular papilla (encircled area) formed by the longitudinal folds (lf) extending from the ileum into the large intestine. Arrows point to wide capillaries.

**Gross arterial supply and venous drainage**

Side branches of the haemorrhoidal artery (Fig. 5) and the posterior mesenteric artery ran circumferentially and embraced the large intestine. The posterior haemorrhoidal vein drained the large intestine into the posterior abdominal vein. With its most distal branches, the posterior haemorrhoidal vein also drained the most distal parts of the ileum (Fig. 5, inset a). Larger side branches of veins ran mostly circumferentially with their smaller branches also running slightly obliquely to longitudinally at some places (Fig. 5, inset b). Arteries and veins could be clearly differentiated already at low magnification by their distinct branching patterns. Arteries revealed cylinder-like profiles, ran over longer distances without branching, bifurcated very infrequently, and were sometimes located externally to the veins. Veins were formed by abundant postcapillary venules draining the capillary bed. In most cases circumferential arteries were located between circumferentially or slightly obliquely running venules or veins (Fig. 5–7).
Microvasculature of the large intestine in adult *Xenopus* located beneath the epithelium (Fig. 8). The transitional distances from terminal arterioles to postcapillary venules were rather short (Fig. 7, inset a; Fig. 8). Depending on the amount of feces within the lumen of the large intestine at the moment of vascular casting, the subepithelial capillary beds appeared either as flat (Fig. 8) or wavy (Fig. 8, inset a). The luminal view at the subepithelial capillary bed revealed many terminal arterioles, short capillary lengths, and an abundance of postcapillary venules. A close-up view demonstrated that terminal arterioles bifurcated until their very ends where they capillarized (Fig. 8). Postcapillary venules joined either in a rosette-like pattern or in a leaf vein-like pattern (Fig. 8).

In the proximal portion, the haemorrhoidal artery regularly abutted side branches which bifurcated two to three times before they approached the serosal surface of the large intestine (Fig. 7). Here each branch again bifurcated into a left and a right branch (Fig. 7, arrows). Both branches ran circumferentially, descending from the dorsal towards the ventral circumference of the large intestine (Fig. 5–7). They gave off many short side branches which penetrated the external muscular layer (Fig. 1; Fig 6, inset a). Within the lamina propria, terminal arterioles finally gave rise to a dense capillary network located beneath the epithelium (Fig. 8). The transitional distances from terminal arterioles to postcapillary venules were rather short (Fig. 7, inset a; Fig. 8). Depending on the amount of feces within the lumen of the large intestine at the moment of vascular casting, the subepithelial capillary beds appeared either as flat (Fig. 8) or wavy (Fig. 8, inset a). The luminal view at the subepithelial capillary bed revealed many terminal arterioles, short capillary lengths, and an abundance of postcapillary venules. A close-up view demonstrated that terminal arterioles bifurcated until their very ends where they capillarized (Fig. 8). Postcapillary venules joined either in a rosette-like pattern or in a leaf vein-like pattern (Fig. 8).

**Fig. 6.** Microvascular anatomy of the transitional area from the distal portion of the large intestine (li) into the thin rectal portion (re). Lateral aspect. Anterior is to the left. ei: external iliac vein, iv: ischiadic vein, ki: kidney, phv: posterior haemorrhoidal vein, rp: renal portal vein, ur: ureter. **Inset a:** Vascular anatomy of the muscular coat of the rectal portion. Serosal view. Note that circumferentially (cc) and longitudinally running capillaries (lc) are located externally to the circumferential artery (ca) and circumferential vein (cv). Arrow points to the origin of a muscular branch feeding the capillary bed of the muscular layers.
At the site where the distal portion of the small intestine (ileum) opened into the large intestine, 8–12 conspicuous mucosal folds protruded dome-like into the large intestine (Fig. 5, inset b). These folds, however, rapidly attenuated and integrated into the large intestine subepithelial capillary bed (Fig. 5, inset c).

Figure 9 summarizes our findings on the microvascular patterns of the large intestine in adult *Xenopus laevis* Daudin and relates them to the histological structure of the intestinal wall.

Caudally, the large intestine gradually decreased in diameter and changed into the rectal portion which finally emptied into the cloaca (Fig. 6). In this portion the mucosa began to form longitudinal folds which in the partially transversely sectioned vascular cast gave the lumen an asterisk-like appearance. The much thicker muscular coat of the rectal portion revealed its own vascular bed with circumferentially and longitudinally running capillaries fed by muscular branches of the circumferential arteries (Fig. 6, inset a). Towards the cloaca the rectal mucosa folds increased in height and revealed a slightly clockwise spiral pattern.

**Fig. 7.** Initial portion of the haemorrhoidal artery (ha) located at the medial aspect of the proximal large intestine (li). Note the bifurcation of the branches of the haemorrhoidal artery into a left and a right circumferential branch (arrows). Note also the presence of both a larval-sized (lsp) and an adult-sized spleen (asp). iv: intestinal vein, pia: posterior intestinal artery, pv: portal vein, sv: splenic vein. **Inset a:** Vascular transition from a circumferential artery (ca) via a longitudinally running terminal arteriole (ta) into mucosal capillaries (c), longitudinally to slightly obliquely running postcapillary venules (vv), and into a circumferential vein (cv). Each supplying terminal arteriole drains at least via two neighboring postcapillary venular beds. Serosal view.
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**Discussion**

Present knowledge of the vasculature of the alimentary tract of anurans is limited to the gross arterial supply and venous drainage. Descriptions primarily focus on *Rana esculenta* (Gaupp, 1899), *Xenopus laevis* (Millard, 1941), and *Rana catesbeiana* (Ichimura et al., 2001) where in-depth dissection work and excellent documentations were done. Because the alimentary canal in these studies had to be stretched and pulled aside to either the left (Gaupp, 1899; Fig. 98 and 129; Millard, 1941; Fig. 6) or the right body side (Ichimura et al., 2001) before documentation, the in-situ topography of the abdominal blood vessels, their interrelations, and their relations to their target areas were lost.

The in-situ topography of the present study remained intact for the first time and spatial relations between blood vessels and abdominal organs stayed largely unchanged, though the course of individual vessels, primarily of large conducting arteries within the mesenteries, might have altered due to the injection pressure applied during manual resin injections. As a result of the whole body vascular injections, vascular relations appeared complex and dissection steps had to alternate with documentation steps of the exposed vascular patterns in the dissecting light microscope and/or in the scanning electron microscope to expose individual vessels over longer distances and to identify their origins and their area(s) of supply and drainage.

When comparing origins and branching patterns of

**Fig. 8.** Leaf vein-like patterns (lv) and rosette-like patterns (r) of the subepithelial microvascular bed of the (feces-filled) large intestine. Luminal view. Note the wheel-spoke-like arrangement of the venules in the rosette (r) and the locally very short capillary lengths. c: capillaries, v: vein. **Inset a:** Subepithelial capillary bed of a slightly feces-filled large intestine. Note the wavy vascular patterns with ridges and valleys. Luminal view.
the coeliacomesenteric artery (cma) in *Xenopus laevis* (this study), *Rana esculenta* (Gaupp, 1899) and *Rana catesbeiana* (Ichimura *et al*., 2001) it becomes evident that—though there exist great interindividual variations—the two ranid species (*Rana esculenta, Rana catesbeiana*) significantly differ in this respect from the pipid species (*Xenopus laevis*). While in *Xenopus* the cma immediately after its origin from the abdominal aorta splits up into four to five main arteries (Fig. 10a), those in *Rana esculenta* and *Rana catesbeiana* extend over a longer distance before bifurcating into two main arteries, the anterior mesenteric artery (*Rana esculenta*; Gaupp, 1899), or, respectively, the superior mesenteric artery (*Rana catesbeiana; Ichimura *et al*., 2001) and the coeliac artery (ca) (Fig. 10c).

In contrast to our findings, Millard (1941), in his pioneering work on the vascular anatomy of *Xenopus laevis* Daudin, depicted a branching pattern of the cma (Fig. 10b) similar to that found in the two ranids (Fig. 10c), with the coeliacomesenteric artery arising from the abdominal aorta and running as single stem over a longer distance before dividing into its four main branches.

It seems reasonable to assume that the higher number of somewhat smaller arteries supplying the abdominal

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**Fig 9.** Scheme of the vasculature of the large intestine in adult *Xenopus laevis* Daudin and its relations to the histological structure of the intestinal wall. Arteries are red; veins are blue. a: circumferential artery, cl: circular muscular layer, cnm: capillary network of tunica muscularis, E: epithelium, ll: longitudinal muscular layer, lp: lamina propria, se: serosa, sen: subepithelial microvascular network, v: circumferential vein. Arrows indicate direction of the blood flow; double headed arrow indicates the longitudinal axis of the large intestine.

**Fig 10.** Origin and branching patterns of the coeliacomesenteric artery in adult *Xenopus laevis* as revealed: 1) by SEM of vascular corrosion casts (a; this study); 2) by dissections of Ranvier’s carmine-gelatine or Ranvier’s Prussian blue injected specimens (b; adapted from Millard, 1941) and in *Rana esculenta* and *Rana catesbeiana* (c; adapted from Gaupp, 1899 and Ichimura *et al*., 2001). Anterior is to the left, dorsal is at the bottom. 1: left aorta, 2: right aorta, 3: abdominal aorta, 4: coeliacomesenteric artery, 5: haemorrhodial artery, 6: coeliac artery, 7: ventral gastric artery, 8: dorsal gastric artery, 9: posterior intestinal artery, 10: anterior intestinal artery, 11: anterior mesenteric artery, 12: splenic artery.
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organisms in *Xenopus* holds advantages over a supply by two larger supplying arterial trunks. Whether the distribution of blood *via* smaller arteries is energetically less costly remains a topic for future studies focussing on the vascular geometry of these vessels and the hemodynamical properties derived from it.

In *Rana catesbeiana* the large intestine (rectal portion 5 according to Ichimura et al., 2001) is supplied via the second side branches (termed B2 and B2-1) of the superior mesenteric artery. In *Rana esculenta* two anterior haemorrhoidal branches are described (Gaupp, 1899) which arise distal to the splenic artery from the anterior mesenteric artery (superior mesenteric artery; Ichimura et al. 2001) and supply ileum (first branch) and large intestine (second branch). The second anterior haemorrhoidal branch runs along the dorsal side of the large intestine towards the caudal, gives off side branches at an almost acute angle which then embrace—like those of the haemorrhoidal artery in *Xenopus*—the gut of *Rana esculenta* in a bipinnate manner (Gaupp, 1899).

In *Xenopus laevis* the largest portion of the large intestine is supplied by one of the branches which arise from the coeliacomesenteric artery. This branch, termed the haemorrhoidal artery (Millard, 1941), bifurcates into a cranially and a caudally directed branch (Fig.7). The former, which supplies the distal ileum, most likely corresponds with the first anterior haemorrhoidal branch described as supplying part of the ileum in *Rana esculenta* (Gaupp, 1899). Accordingly, in *Xenopus laevis*, the splenic artery originates from the haemorrhoidal artery while in *Rana catesbeiana* it originates as the first branch of the superior mesenteric artery (Ichimura et al., 2001) and respectively as the first branch of the anterior mesenteric artery in *Rana esculenta* (Gaupp, 1899).

The main function of the large intestine is to store feces and to absorb water and salts from them (Reeder, 1964; Duellmann and Trueb, 1986). *In-vitro* studies on the Na-fluxes from the lumen to blood and blood to the lumen in the small and large intestine of *Rana ridibunda* and *Rana pipiens* revealed that, in the large intestine, an increase in the vascular flow rate increased the lumen-blood Na-flux but had little effect on the blood-lumen flux, resulting in an increase in the net absorption of Na. In these experiments, selective vascular perfusion of the large intestine was done *via* a cannula placed in the superior mesenteric artery, and all branches supplying the small intestine were ligated. Perfusate was collected *via* a cannula placed in the portal vein (Wade, 1979). In *Xenopus laevis* the large intestine drains *via* the haemorrhoidal vein into the posterior abdominal vein and then into the ventral abdominal vein which joins the portal vein close to the liver. In *Xenopus laevis* a cannulation of the portal vein before this junction would result in wrong estimations of these ion-fluxes. It is therefore of utmost importance for any research involving the collection of blood samples to know these draining and supplying routes in great detail.

A point of interest is the microvascular anatomy at the opening of the ileum into the large intestine. A flap-like valve present in this region in some anurans is absent in *Xenopus*, as evidenced by tissue sections and the microvascular anatomy. Instead, some 8–10 folds are present which slightly protrude into the large intestine lumen. These folds, however, attenuate within a distance of ~500 μm, and mucosal fold vessels integrate into the large intestine subepithelial capillary network. Whether or not the slightly enlarged venules formed by two merging capillaries at these sites have a functional importance in the regulation of the width of the lumen of the ileocolonic junction remains undetermined. It should be noted that a very similar vascular formation is present at the site where the esophagus opens into the cardia region of the stomach (not shown). It is likely that the similar vascular formations found at the entrance sites of the esophagus (into the stomach) and the ileum (into the large intestine) are involved in the regulation of these entrance sites, but this notion needs definitive experimental proof.

The transition from the small intestinal microvascular pattern with the zig-zag running longitudinal folds (Lametschwandtner et al., 2006) into that of the large intestine brings to mind that described to occur in the human alimentary tract at the ileocecal valve. There the vascular patterns of the ileum with its characteristic villi pattern change into the honey-comb-like pattern of the colonic crypts (Berres, 1837). As the mucosa of the large intestine of *Xenopus* lacks crypts and goblet cells locate intraepithelially, the microvascular bed lacks the honey-comb-like vascular pattern characteristic for mammals. Interestingly, postcapillary venules of the subepithelial vascular network merge in leaf vein-like and rosette-like formations. These formations lead to a mosaic-like arrangement of draining sites whereby areas supplied by a single supplying arteriole may drain *via* different routes (Fig. 8) depending on the pressure conditions prevailing at a given moment.

Histomorphology of the large intestine of *Xenopus laevis* Daudin revealed prominent, diffuse lymphoid tissues located below the gut epithelium. At the light microscopical level, blood vessels found inside the lymphoid tissues lacked a high (cuboid) endothelium. This observation was corroborated by the lack of characteristic surface imprints remaining on vascular corrosion casts when high endothelial venules of lymphatic tissues are replicated (Steeber et al., 1987).

From the microvascular patterns found we conclude
that 1) the large intestine is well adapted to sustain a sufficiently high blood flow under various degrees of the storage of feces and peristaltics during defecation, and 2) that the high number of postcapillary venules together with the characteristic leaf-vein-like and rosette-like formations establish a large interface between enterocytes and subepithelial blood vessels to facilitate optimal conditions in terms of large exchange surfaces for the resorption of water and salts from the gut lumen into the blood vascular system.

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References


