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Lamina propria of intestinal mucosa as a typical reticular tissue

A scanning electron-microscopic study of the rat jejunum

Hiromi Takahashi-Iwanaga and Tsuneo Fujita
Department of Anatomy, Niigata University School of Medicine, Niigata, Japan

Summary. The three-dimensional architecture of the lamina propria in the jejunal mucosa of the rat was studied by scanning electron microscopy. The lamina propria is a typical reticular tissue with fine nets of reticular fibers and free and fixed cells lying among them. However, the lamina propria in the core of villi displayed structural features closer to other reticular or lymphoid tissues than that among the crypts. In the villi, the tissue was supported by a spongy framework of interconnecting fibroblasts, and densely infiltrated by free cells. Among the crypts, cellular elements were rather sparsely dispersed in a complex network of reticular fibers. A thin layer of reticular fibers lined the basal lamina of the epithelium. This layer contained a network of flattened cells which anastomosed with each other via slender processes. The basal lamina and the fibrous layer were perforated with round pores, through which free cells or basal processes of the epithelial cells passed. Many macrophages were found resting on the reticular framework of the lamina propria, frequently in close association with immunoblast-like cells. This paper further includes scanning electron-microscopic observations on the central lacteal with special reference to its luminal projections and trabeculae.

Key words: Lamina propria – Intestinal mucosa – Reticular tissue – Scanning electron microscopy – Rat

The lamina propria of the small intestinal mucosa has many of the morphological attributes of reticular or lymphoid tissues. It contains numerous IgA-secreting plasma cells (Crabbé et al. 1965). In addition, it is the site where lymphocyte infiltration and lymph nodules, collectively called the gut-associated lymphoid tissue (GALT), may appear. The lymph nodules are covered with a specialized epithelium containing M cells, which effectively sample luminal antigens (Owen and Jones 1974). The basic structure of the lamina propria is believed to cooperate with the GALT and intestinal epithelium in the protection of the individual against orally-aquired antigens (Parrott 1976).

Although several transmission electron-microscopic (TEM) studies have been performed on the fine structure of the intestinal mucosa (e.g., Palay and Karlin 1959; Papp et al. 1962; Trier and Rubin 1965), very little attention has been directed to the lamina propria as a lymphoid tissue. One exception is the work of Deane (1964), who observed the thin investment of fibrocyte processes around crypts and vessels, and the close association of macrophages and other types of free cells in the lamina propria.

Concerning scanning electron-microscopic (SEM) studies, Fujita et al. (1981) described the lamina propria of the duodenum in the dog as a reticular tissue, although they were not able to detail the cytoarchitecture of the tissue due to their use of only the conventional freeze-fracture method. Nakamura and Murakami (1981) observed central lacteals. Desaki et al. (1984) showed a flat cellular reticulum of fibroblast-like cells which lined the villous epithelium after removal of collagen by the HCl-digestion method. However, no systematic SEM observation has yet been made of the intestinal lamina propria. On the other hand, the application of SEM to the investigation of other lymphoid tissues, such as the lymph nodes (Fujita et al. 1972, 1981; He 1985) and the spleen (Fujita 1974; Fujita and Kashimura 1983), effectively demonstrated the three-dimensional architecture of these tissues (Fujita 1978; Owen and Bhalla 1983).

In the present study, the lamina propria of the rat jejunum was examined by SEM to clarify the three-dimensional structure of the reticular framework and the behavior of the free cells in this tissue. The conventional freeze-fracture method was mainly used to prepare the specimens. Some of the specimens were treated with ultrasonic vibration to remove the free cells from the reticular framework. Highison and Low (1982) successfully removed the jejunal epithelium by prolonged fixation of tissue samples in OsO_4. To observe the adepithelial surface of the lamina propria, we eliminated the epithelium of the intestinal mucosa by hyperosmification of the specimens, or alternatively removed the basal lamina and collagen by use of Evan's HCl-digestion method.

Materials and methods

Adult Wistar rats of both sexes weighing 150–200 g were used after overnight fasting. The rats were perfused through the ascending aorta with Ringer's solution and then with 2.5% glutaraldehyde in 0.1 M phosphate buffer, pH 7.3. The jejunum was excised and cut into small pieces, measuring 1.5 × 3 mm. The tissue pieces were divided into four groups and treated by the four methods described below,

Send offprint requests to: H. Takahashi-Iwanaga, Department of Anatomy, Niigata University School of Medicine, Asahimachi 1, Niigata 951, Japan

respectively. Specimens from each group were conductive-stained by the tannin-osmium method of Murakami (1974), dehydrated in a graded series of ethanol, transferred to isoamyl acetate, critical-point-dried using liquid CO_2, evaporation-coated with gold-palladium and examined in a Hitachi S-450 LB scanning electron microscope at an accelerating voltage of 10 kV.

1. Freeze-fracture method. The tissue pieces were immersed in the same fixative for a few hours after the perfusion fixation. The specimens at the stage of immersion in isoamyl acetate were frozen in liquid nitrogen and fractured by mechanical impact.

2. Elimination of free cells in the lamina propria. The perfusion-fixed specimens were thoroughly rinsed in phosphate buffer (pH 7.3). After conductive-staining and dehydration, the tissue pieces were freeze-fractured in isoamyl acetate and exposed to ultrasonic vibration for about 10 s to dislodge the free cells from the cut surfaces.

3. Removal of intestinal epithelium. Perfusion-fixed specimens were rinsed in phosphate buffer and immersed in 0.1% buffered OsO_4 for 3 days. The intestinal epithelium was removed with forceps under a binocular microscope after critical-point drying.

4. HCl-digestion method. The perfusion-fixed tissue pieces were immersed in 2.5% glutaraldehyde for 3 h or more. The specimens were placed in 8N HCl at 60° C for 50 min, digested in a collagenase solution (Sigma type II) at a concentration of 50 mg in 10 ml 0.1 M phosphate buffer (pH 6.8) at 37° C for 6 h, and washed in 0.01% aqueous solution of Triton x-100.

Results

1. General architecture

SEM observation of the freeze-fractured specimens shows that the lamina propria of the rat jejunal mucosa is composed of fine meshes of collagen fibrils and numerous fixed and free cells (Fig. 1).

The architecture of the lamina propria in the intestinal villi (intravillous lamina propria) was different from that among the crypts (intercryptal lamina propria). The intravillous lamina propria was composed of two layers: a subepithelial thin layer and a deeper layer that filled the villous core. The former consisted of a dense sheet of collagen fibrils lining the epithelial basal lamina. The latter showed sparse amounts of collagen fibrils and large amounts of cellular elements. Fibroblasts anastomosed with each other via their attenuated processes to form a meshwork in the extravascular space, where free densely infiltrated cells (Fig. 2) were found.

On the other hand, the intercryptal lamina propria was not clearly divided into two layers (Fig. 3). Fibrous elements were more conspicuous there than in the villi, and fixed and free cells were dispersed among the collagen fibrils.

2. Subepithelial portion of the lamina propria

At the upper two thirds of the villi, the subepithelial collagen layer measured 0.5–1 μm in thickness, becoming thicker

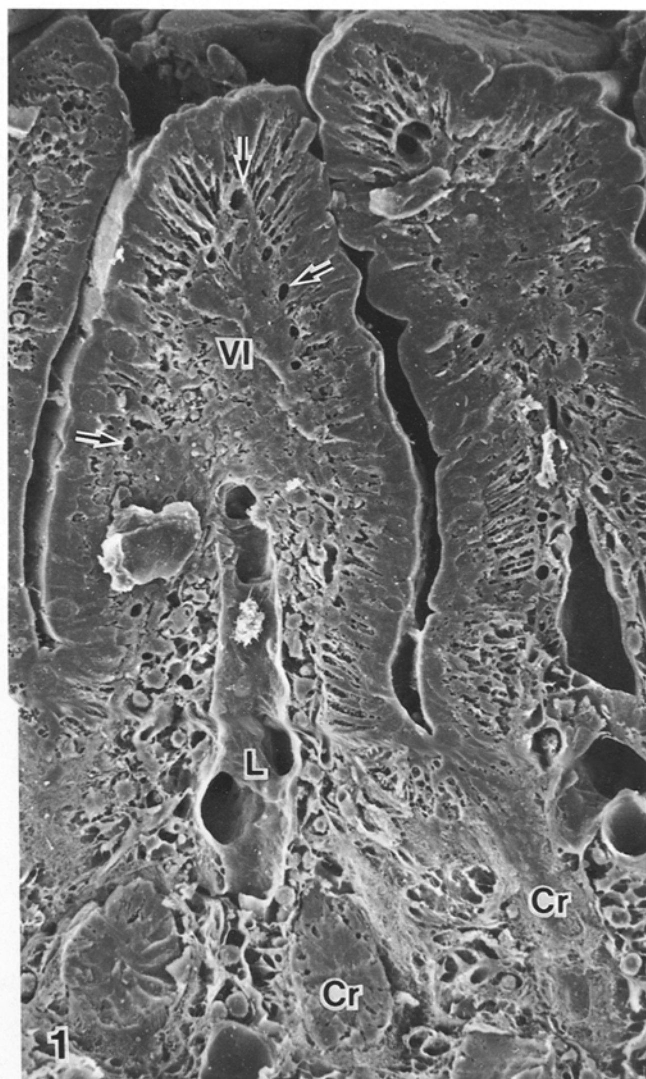

Fig. 1. SEM survey view of mucosa of rat jejunum. Intravillous lamina propria (*Vl*) contains more numerous cellular elements than intercryptal lamina propria. *Arrows* indicate subepithelial blood capillaries. *Cr* crypts; *L* central lacteal. ×430

at the lower levels. Surrounding the crypts, the layer measured 3–4 μm in thickness. However, the pericryptal collagen sheets were looser and less distinct than those in the villi (Fig. 3). Flattened cells were embedded in the collagen sheets. The epithelial basal lamina and the collagen sheet were perforated with round pores (Fig. 4a–c).

The round pores were numerous on the epithelial basal lamina at the middle portion of the villi, where one pore occurred each square 10 μm. The pores measured about 3.0 μm in diameter, ranging in size from 1.0 to 6.5 μm. Both near the tips and the bases of the villi, the pores were small in number and size. No pores were found on the cryptal basal lamina. Through the pores, free cells in the lamina propria often protruded their clubbed microprojections or parts of their cell bodies to the epithelial side (Fig. 4b, c). Occasionally, thread-like microprocesses were extended from the bases of the epithelial cells into the pores (Fig. 4a).

The flattened cells in the collagen sheet were stellate

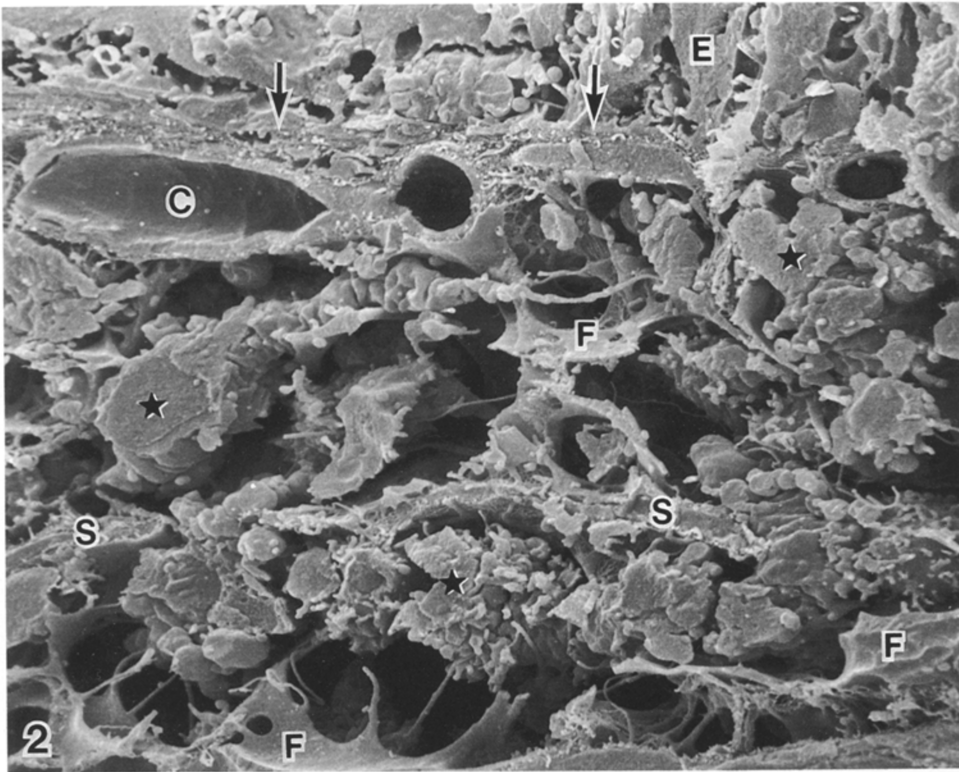

Fig. 2. SEM survey view of intravillous lamina propria of rat jejunum. A thin layer of collagen fibrils (*arrows*) lines the epithelium (*E*). The deeper portion of the lamina propria is composed of a framework of anastomosing fibroblasts (*F*) and dense infiltration of free cells of various shapes (*asterisks*). Blood capillary (*C*) is covered by fibroblast processes. *S* smooth muscle cells. ×4700

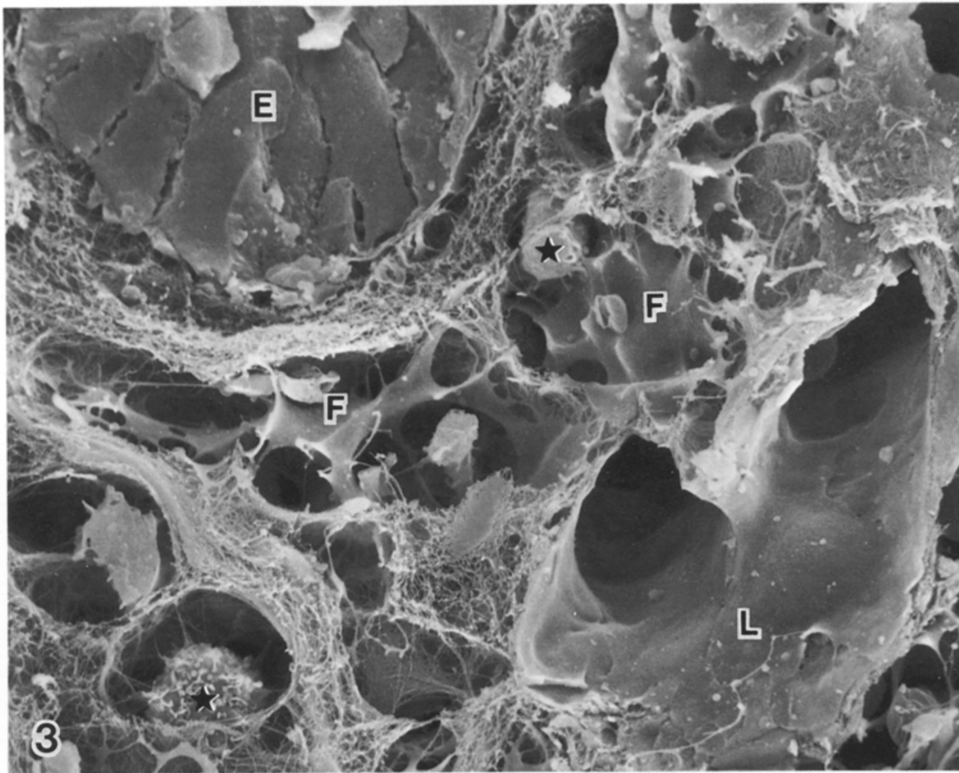

Fig. 3. Survey view of intercryptal lamina propria, comprising a complex network of collagen fibrils, fibroblasts (*F*) and free cells (*asterisks*). Cryptal epithelium (*E*) is loosely surrounded by a collagen sheet. *L* lacteal lumen. ×2200

in shape, and arranged at regular intervals (Fig. 5a). They anastomosed with each other via slender cytoplasmic processes, forming a continuous plane network which lined the base of the villous and cryptal epithelium.

In the villi, the flattened cells were occasionally found displaced and distorted around the pores, some of which were penetrated by the processes of free cells in the lamina propria (Fig. 5b). The subepithelial blood capillaries were located immediately beneath the cellular network in the villi. The flattened cells revealed a close connection to the capillary walls with their cytoplasmic processes. Each crypt was tightly surrounded by the cellular meshes (Fig. 5c, d).

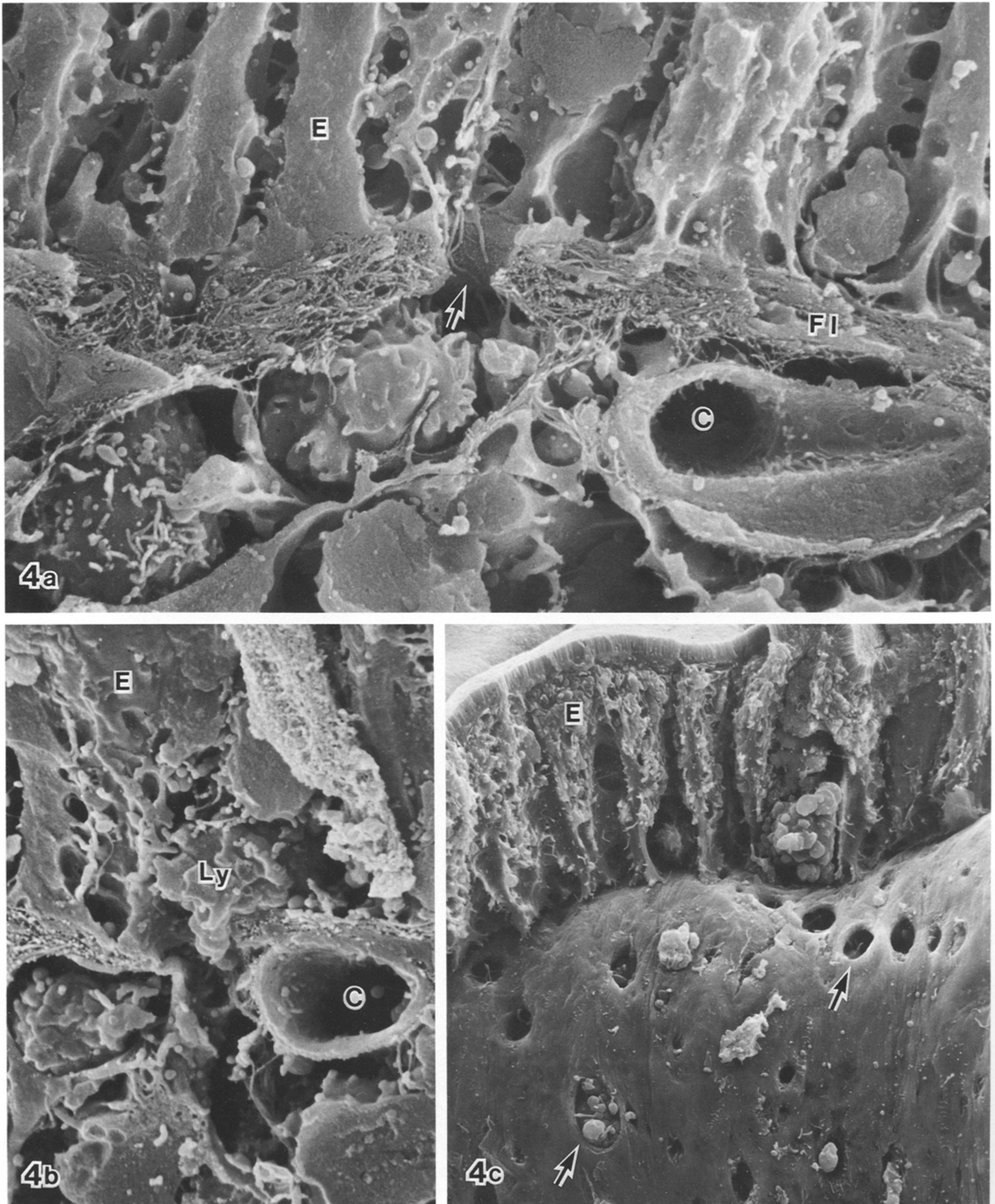

Fig. 4. **a** Detailed view of subepithelial collagen layer near the base of villus. A slender process of an epithelial cell (*arrow*) extends through a pore in the collagen layer. *Fl* flattened cells embedded in collagen. ×5600 **b** Another pore in the collagen layer near the tip of a villus. Lymphoid cell (*Ly*) in the epithelium extends a pseudopod through the pore. *C* blood capillary. ×5500. **c** Overview of basal lamina of epithelium at the middle portion of villus. Numerous round pores of varying sizes are seen. Cytoplasmic processes of free cells in the lamina propria (*arrows*) protrude to the epithelial side through the pores. *E* epithelium. ×2100

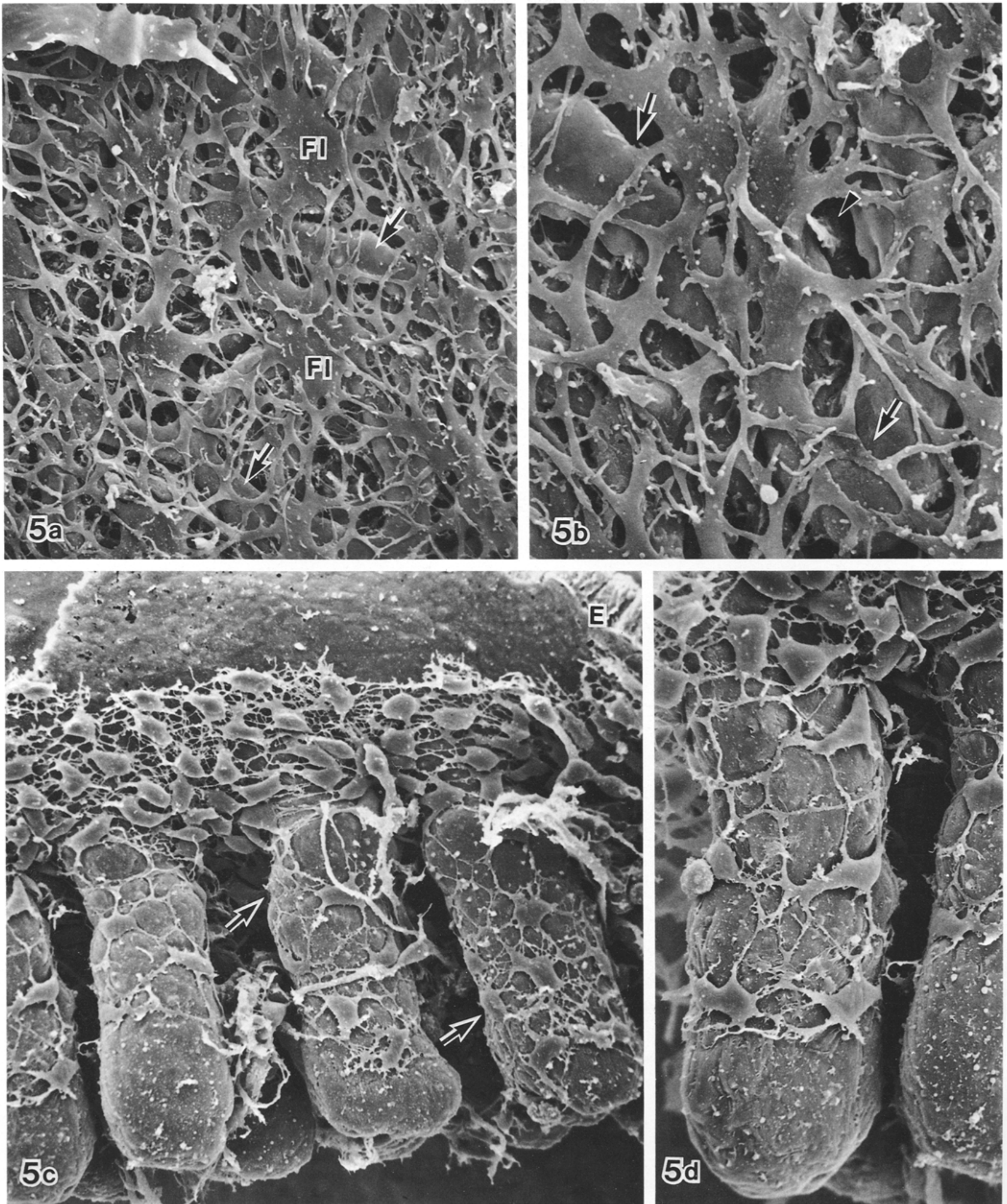

Fig. 5a–d. SEM images of flattened cells embedded in subepithelial collagen layers, after removal of collagen by the HCl-digestion method. **a** Adepithelial surface of the intravillous lamina propria. Flattened cells (*Fl*) anastomose with each other via their slender processes to form a cellular network, through which underlying blood capillaries (*arrows*) are seen. ×2000. **b** Detailed view of a flattened cell compressed by a cytoplasmic process (*arrowhead*) extending from free cells in a deeper layer of the lamina propria. Slender processes of the flattened cells closely attach to a blood capillary (*arrows*). ×4300. **c** Overview of a cellular network around crypts (*arrows*), which is continuous with the network beneath the villous epithelium (*E*). Flattened cells were eliminated by digestion at the bases of most crypts. ×730 **d** Detailed view of a network of flattened cells tightly surrounding a crypt. ×1200

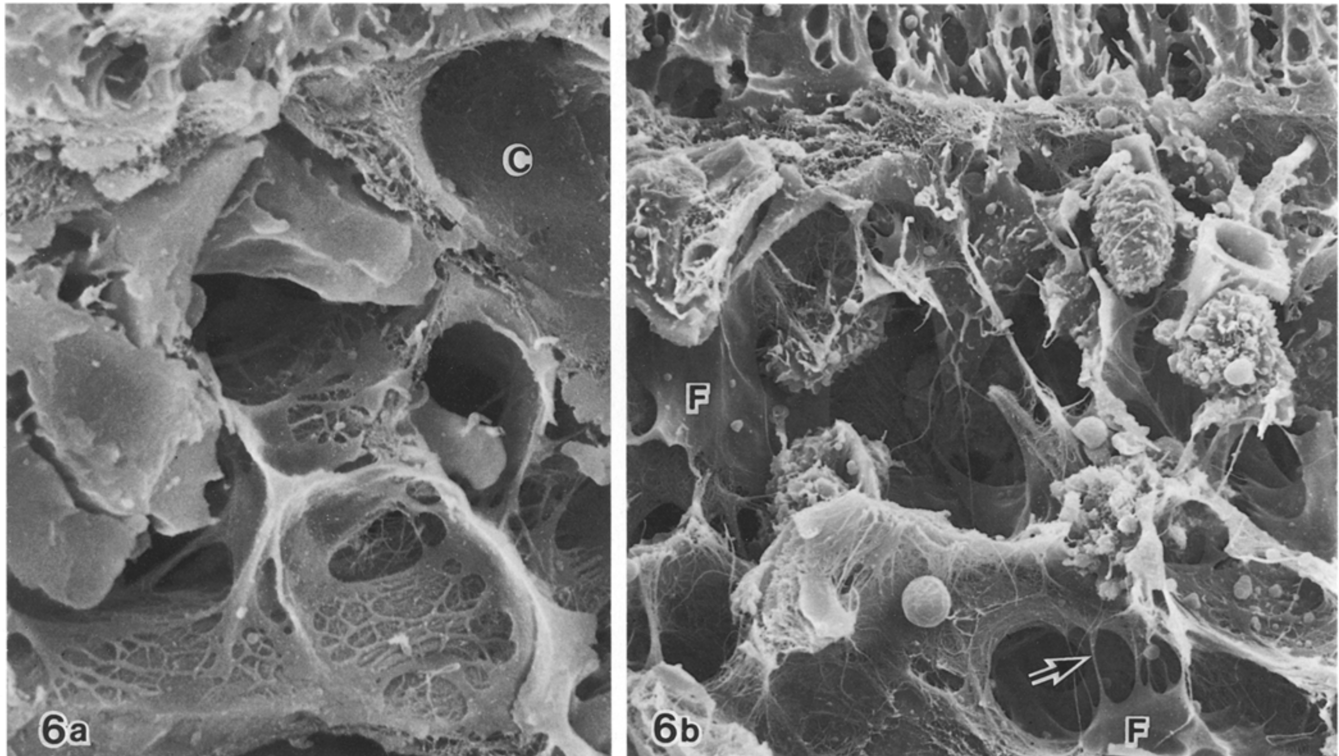

Fig. 6a, b. SEM images of reticular frameworks in the lamina propria. **a** Detailed view of the lamina propria in the middle portion of a villus. Collagen fibrils are covered by thin fibroblast processes with frequent fenestrations (treatment with ultrasonic vibration). *c* Subepithelial blood capillary. ×4100. **b** Lamina propria near the base of a villus. The reticular framework is coarser here than in the upper portion of the villi. Some collagen fibrils are devoid of coverage by fibroblast processes. Fibroblasts (*F*) extend filopodia (*arrow*). ×2200

3. *Reticular framework*

In the upper three quarters of the villi, fibroblasts, accompanied by small amounts of collagen fibrils, anastomosed with each other to form a sponge-like meshwork (Fig. 6a). The fibroblasts were stellate in shape, with smooth surfaces. All aspects of their cell bodies showed large concavities, which probably corresponded to impressions of the free cells. Their cytoplasmic processes, which constructed the reticular framework, were so short and broad that the lamina propria was incompletely separated into small compartments, each of which had room for only a few free cells. Collagen fibrils were covered by the fibroblast processes and hindered from direct contact with the free cells (Figs. 2, 6a).

In the villi, the attenuated processes of fibroblasts lined the subepithelial connective tissue layer and adventitia of the vessels. These cellular linings showed numerous pores, measuring 0.5–1 μm in diameter (Fig. 6a).

Near the bases of the villi, some collagen fibrils lost the investment of the fibroblast processes (Fig. 6b). The reticular meshes became coarse, because the fibroblasts anastomosed with each other via long filopodia arising from the ridges of their cell bodies.

In the cryptal region, collagen was more abundant than in the villus. Numerous collagen fibrils without any cellular coverage extended randomly to form a complex network, leaving collagen-free spaces around the fibroblasts (Fig. 3). The cytoplasmic processes of fibroblasts were not broad but tapered. Some processes anastomosed with each other, while others terminated in free ends.

4. *Free cells in the reticular framework*

Macrophages were distinguishable from other free cells by their large size and irregular shape (Fig. 7a, b). They extended large long processes, and possessed an undulated surface with a number of bubble-like microprojections and slender filopodia. They were often found adhering to the interstitial side of the subepithelial collagen sheet, extending their processes into the pores of the epithelial basal lamina or enfolding round cells with their processes (Fig. 7a).

Eosinophils, showing numerous small round granules on their cut faces, were often found in the lower portions of the villi and among the crypts (Fig. 7c). They were covered by plate-like microprojections.

The other free cells in the lamina propria probably corresponded to plasma cells or lymphocytes. Most of them were not regularly spherical but distorted with undulated surfaces. They were covered with sparse microvilli, a few blebs and small ruffles (Figs. 2, 7a). Some lymphocytes displayed microvilli at one pole of the cell surface (Fig. 6c).

5. *Vessels in the lamina propria*

The central lacteals occupied a large area in the villous core. Their luminal surface was characterized by undulating boundaries of endothelial cells and round elevations corresponding to the nuclei of the cells (Fig. 7a). Noteworthy was the frequent occurrence of thread- or ribbon-like processes of the endothelial cells spanning the lumen (Fig. 8a). They sometimes branched or crossed each other in the distal portion of the lacteals. At the bases of the villi, the lacteals

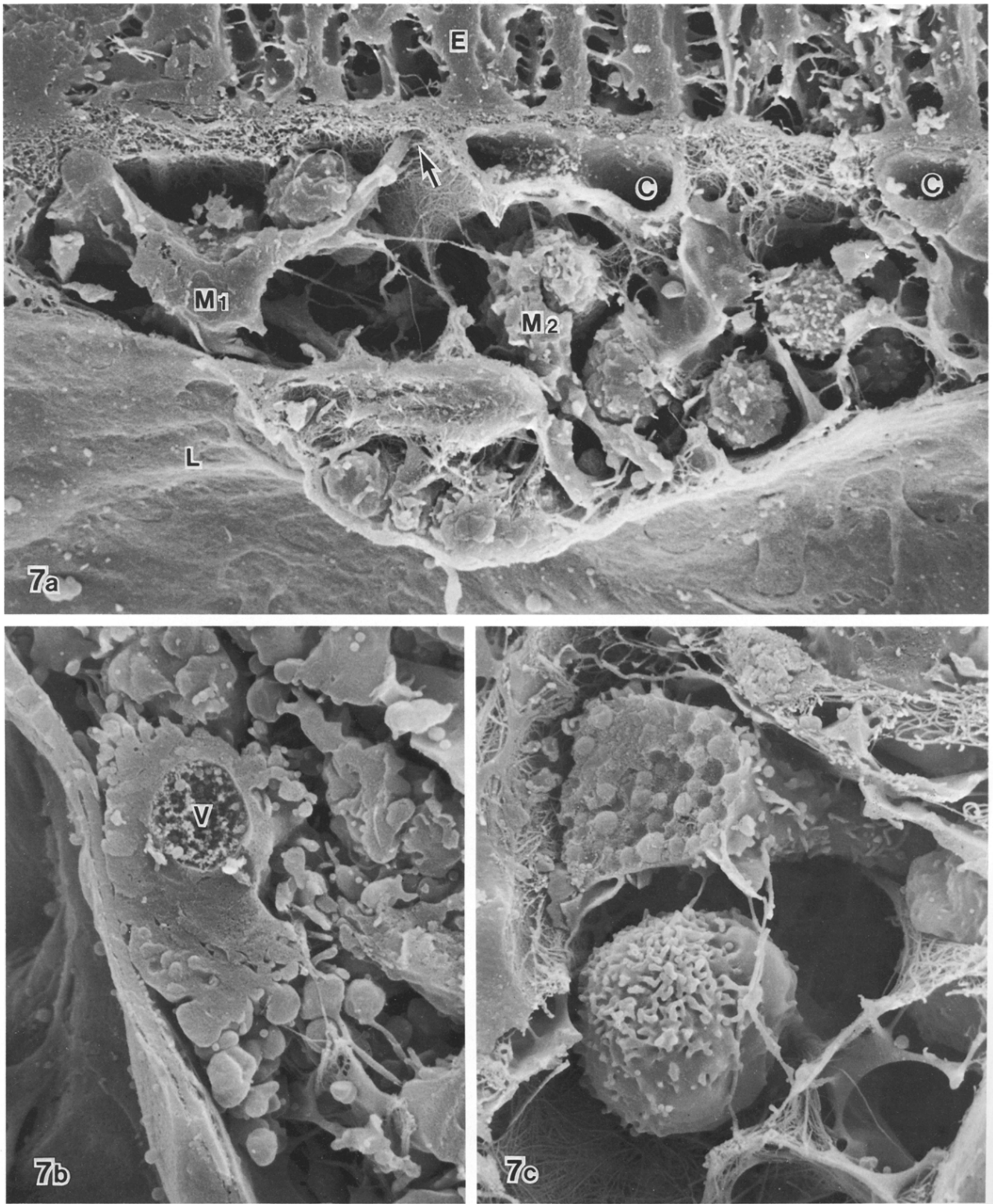

Fig. 7a–c. SEM images of free cells in the lamina propria. **a** The lamina propria near the base of a villus. One macrophage (M_1) beneath epithelium (*E*) extends a long pseudopod into a subepithelial collagen sheet (*arrow*). Another macrophage (M_2) closely attached to a lymphoid cell. *C* blood capillaries; *L* central lacteal. ×3100. **b** Macrophage, adhering to basal surface of central lacteal, shows numerous bubble-like microprojections and a large vacuole (*V*). ×4200. **c** Presumed eosinophilic leukocyte in the upper portion of the photograph, showing small granules on the cut face and plate-like microprojections. A capping lymphocyte is seen in the lower portion of the photograph. ×5700

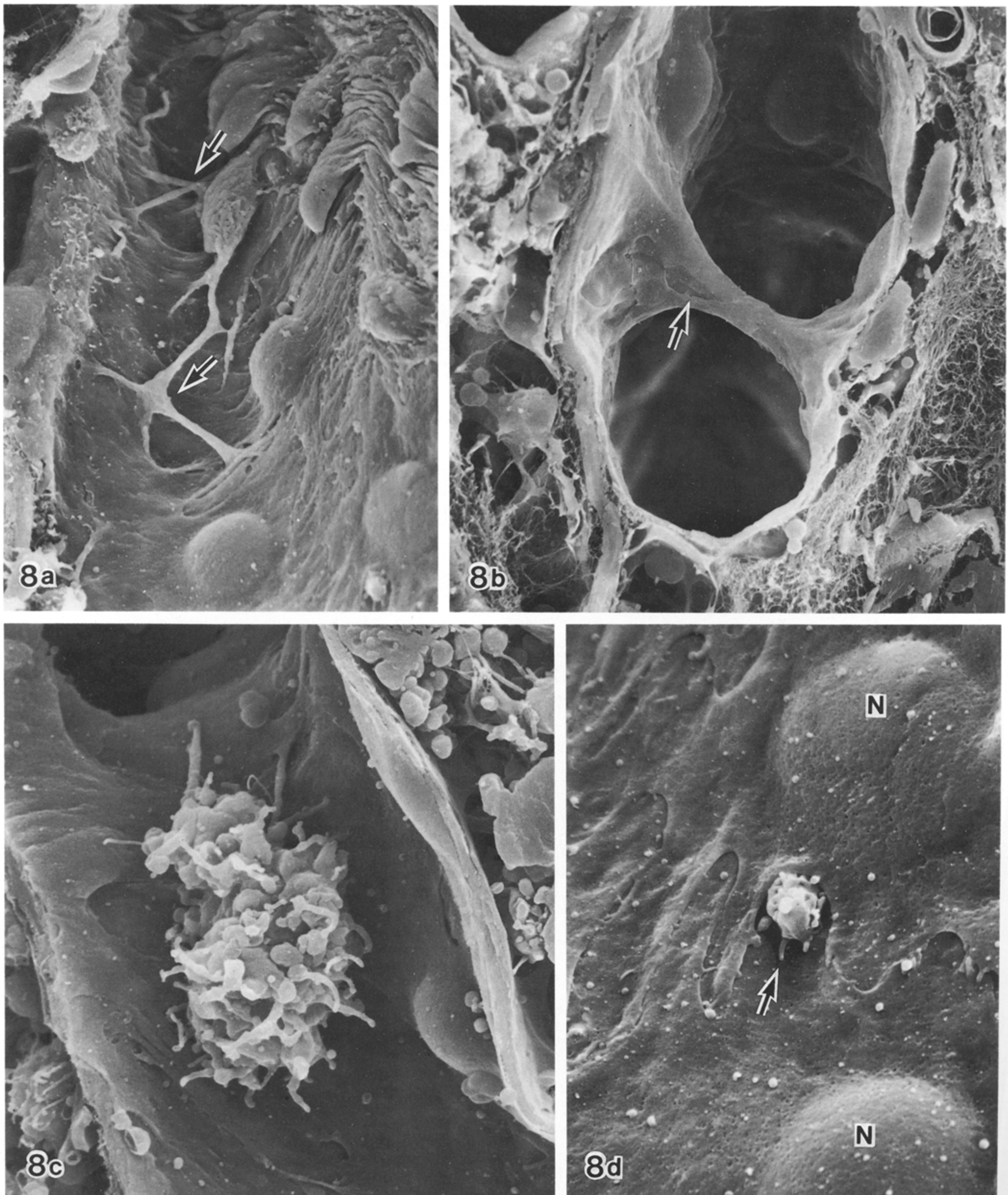

Fig. 8a–d. SEM images of lacteals in the lamina propria. **a** Central lacteal near the tip of a villus. Thread-like processes of endothelial cells span the lumen (*arrows*). ×2300. **b** Lacteal lumen near the base of a villus shows a thick trabecula with undulating pattern of endothelial cell boundaries (*arrow*). ×2200. **c** Macrophage-like cell in a central lacteal. ×3700. **d** Detailed view of lacteal endothelium. Note the undulating pattern of interdigitating endothelial cells and round elevations corresponding to nuclei (*N*). Pseudopod (*arrow*) of a free cell protruding into the lumen between endothelial cells. ×5400

possessed a thick trabecula formed by the processes of some endothelial cells (Fig. 8b).

Free cells occasionally occurred in the lacteals. Macrophages were found to adhere to the endothelium (Fig. 8c). Cytoplasmic processes of free cells protruded into the lacteal lumen through the spaces between the endothelial cells (Fig. 8d).

The blood vessels were composed of flat endothelial cells, which formed neither luminal processes nor trabeculae. No high endothelial venules could be found that would represent the principal sites of lymphocyte passage from the blood.

Discussion

1. General architecture

The present study clearly demonstrates that the lamina propria of the rat jejunal mucosa is a typical reticular tissue, since this tissue is supported by reticular fibers and three-dimensional cellular networks containing numerous infiltrating free cells. Collagen fibrils in the lamina propria did not form thick bundles that would correspond to collagen fibers. However, the architecture of the lamina propria differed in various regions of the jejunal mucosa. The intravillous lamina propria showed a closer resemblance to other lymphoid tissues than did the intercryptal lamina propria. It is noteworthy to mention that the fibroblast processes of the reticular framework in the intravillous lamina propria ensheathed blood and lymph vessels tightly, reminiscent of the reticulum cells that surround blood vessels in lymph nodes (Anderson and Anderson 1975). At the bases of the villi and around the crypts, the cellular reticulum became more discontinuous, being accompanied by increasing amounts of collagen, and the free cells were more loosely dispersed.

2. Superficial portion of the lamina propria

The flattened cells immediately beneath the epithelium formed a two-dimensional meshwork, while the network of ordinary fibroblasts in the deeper layer showed a three-dimensional pattern. These two types of cellular meshes were clearly separated from each other. The flattened cells probably corresponded to the fibroblast-like cells described by Pitha (1968) in his TEM study. He reported that the cells could be distinguished from the ordinary fibroblasts by their very low electron density and numerous intracellular filaments. He described the fibroblast-like cells as not being restricted to the subepithelial region, but rather found at random around the crypts. However, the present SEM study demonstrated that the fibroblast-like cells formed a single distinct layer of network even in the cryptal region, tightly surrounding the crypts, like the myoepithelial cells of excretory glands.

The fibroblast-like cells probably protect the blood capillaries in the intestinal villi by covering them with their fine processes, for the adepithelial side of these capillaries lacks this coverage by pericytes. Recently, Desaki et al. (1984) investigated the fibroblast-like cells by use of SEM and TEM, and discussed their possible functions, such as contractile and vitamin A-uptake ability. However, the present SEM study could not provide any further information on these assumptions.

Previous TEM studies have reported that the basal lamina of the intestinal epithelium displays occasional gaps penetrated by lymphocytes or basal processes of the epithelial cells (Palay and Karlin 1959; Donnellan 1965; Toner and Ferguson 1971). Fat particles were often found passing through the gaps after feeding with corn oil (Rubin 1966). Low and McClugage (1984; McClugage and Low 1984) demonstrated by use of SEM that these gaps corresponded to round pores in the epithelial basal lamina, and that these pores were more numerous in the Peyer's patches than in the intestinal villi. Komuro (1985) observed the pores in the intestinal basal lamina by SEM and TEM. His findings on the frequency and size of the pores are largely in agreement with our observations.

We presume that the pores are formed by the cells or cellular processes that pass across the basal lamina and that the pores are repaired in a certain period after the passage of the cells. These assumptions are supported by several findings of the present study, such as the variation in size of the pores, occurrence of free cells in various stages of presumed passage, and centrifugal deviation and deformation of flattened cells around the pores.

3. Reticular framework and free cells

The spongy frameworks of the anastomosing fibroblasts in the lamina propria appeared similar to those of some other lymphoid tissues, such as the medullary cords of lymph nodes (Luk et al. 1973; Miyoshi and Shingu 1983) and splenic cords (Fujita 1974; Fujita 1978). Processes of the cells that construct these meshworks were short and broad, or "wing-like", as described by Fujita and Kashimura (1983). However, the fibroblast processes in the lamina propria showed a characteristic fenestration, which was not found in lymph nodes (Luk et al. 1973, Figs. 11, 12) or in splenic cords (Fujita 1974, Fig. 15).

The subepithelial macrophages probably trap and process the luminar antigens with the cytoplasmic processes projected into the pores in the basal lamina. Owen et al. (1981) reported that macrophages in Peyer's patches showed such behavior during phagocytosis of parasites. Furthermore, the macrophages may present antigens to the lymphoid cells in the lamina propria by close contact with them. Such an intimate relationship between these two cell types was also observed in the intestinal lamina propria by Deane (1964) with the TEM, in the spleen by Fujita (1974) with the SEM, and in the lymph node sinus by Farr and DeBruyn (1975) with the TEM.

Most lymphocytes in the blood are small lymphocytes, displaying a spherical shape with surface microvilli. However, the lymphoid cells in the lamina propria rarely showed such an appearance. They resembled the mitogen-stimulated lymphoblasts observed with the SEM by Newell et al. (1978), with regard to their irregular shape and various microprojections. This finding is consistent with the results of previous studies in which the intestinal mucosa was not populated by small lymphocytes, but by T- and B-immunoblasts which enter from the circulating blood (Gowans and Knight 1964).

4. Vessels in the lamina propria

Papp et al. (1962), in a TEM study, described the frequent occurrence of irregular luminal protrusions of lacteal en-

dothelium. Cord-like structures traversing the lacteal lumen were reported in an SEM study by Nakamura and Murakami (1981). In addition to these findings, the present study demonstrated that the cords of endothelial cell processes branched or crossed each other in a manner reminiscent of the reticulum cells that support the lymph sinus. By this analogy, one is reminded of the postulation by Petersen (1931) that the lymph sinus is equivalent to the lymphatic vessel. Although the biological significance of these structures is not clear, the thick trabeculae, at least, probably prevent the lacteal lumen from collapsing.

The macrophages probably migrate across the lacteal endothelium via the intercellular pathway. Previous TEM studies reported that cell junctions of the lacteal endothelium were loosened at some sites (Palay and Karlin 1959).

In the present study, the lamina propria of the jejunal mucosa exhibited many of the morphological characteristics common to lymphoid tissues: a network of reticular fibers as a supporting tissue, distribution of numerous macrophages, and dense infiltration of lymphoid cells. In particular, the intravillous lamina propria possessed a well-organized cellular framework like that in the splenic cords or in the pulp of the lymph nodes. These findings are consistent with the previous assumption that the lamina propria, especially that in the villi, plays an important role in the defense mechanism of the digestive tract against the luminal antigens.

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