Histol Histopath (1986) 1: 355-362

Histology and Histopathology

Duodenal microanatomy of the domestic cat (*Felis catus*)

Robert W. Henry[1] and F.K. Al-Bagdadi[2]

[1]Department of Animal Science, College of Veterinary Medicine, The University of Tennessee, Knoxville, TN, 37901-1071, USA

[2]Department of Veterinary Anatomy and Fine Structure, School of Veterinary Medicine, Lousiana State University and Agricultural and Mechanical College, Baton Rouge, LA, 70803-8408, USA

Summary. Duodenal samples were taken from similar locations in six cats, processed, stained, and examined via light microscope. There were no prominent circular folds (plicae circulares) or stratum compactum (lamina subglandularis). The 1072 pm x 201 pm villi were covered by 46 pm high columnar epitheliocytes proximally which decreased in height (41 pm) distally and displayed a 1.1 - 1.7 pm striated border. Globular leukocytes, mononuclear cells, and twenty-eight goblet cells (exocrinocytus calciformis) per villus were seen. The intestinal gland (crypt of Lieberkuhn) epithelium was 20 pm tall and had a less distinct striated border. The 515 pm simple straight tubular intestinal gland layer displayed distal branching. Many mitotic figures, 12 goblet cells per gland, and occasional columnar to triangular cells with red cytoplasmic granules were seen. The thickness of the lamina propria mucosa (glandular portion) decreased from proximal to distal (563-465 pm). The lamina muscularis mucosa had two layers and decreased in thickness distally (71-28 pm). The proximal muscularis mucosa was penetrated by the ducts of submucosal (Brunner's, duodenal) glands. The tela submucosa decreased in thickness distally (593-192 pm) and contained submucosal glands with 11.5 - 75 pm lumina for the first 1.5 - 2.5 cm. However, submucosal glands could be found to a distance of 8 cm. The glandular epithelium ranged from 7.5 - 22.5 pm in height. Only one type of secretory cell was observed, with both mucous and serous properties. The tunica muscularis ranged from 190-1425 pm (median thickness of 557 pm) and had two layers.

Key words: Duodenum - Cat (Feline) - Light microscopy - Submucosal (Brunner's) glands

Offprint requests to: R.W. Henry DVM, Ph D, P.O. Box 1071, College of Veterinary Medicine, University of Tennessee, Knoxville, TN 37901-1071, USA

Introduction

Studies on the cat duodenum are incomplete and results are variable. Hence, information is often taught by extrapolation from other species. This paper updates the microscopic anatomy of the cat duodenum. Available information is limited (Elias, 1947; Titkemeyer and Calhoun, 1955; Moe, 1963: Banks, 1986; Dellman and Brown, 1981; Smith et al., 1981). Titkemeyer and Calhoun (1955) carried out a comparative study of domestic animal small intestines in which ten evenly spaced samples, throughout the length, were taken. Consequently, little information is reported on the duodenum in their work. Moe (1963) did a quantitative study on the occurrence of goblet cells. Two veterinary histology texts (Banks, 1986; Dellman and Brown, 1981) make few comments on the feline species. Banks (1986) reports the presence of a stratum compactum in carnivors. Moe (1963) indicates Brunner's glands to be confined to the upper 2-3 cm of the duodenum. More recently, scanning and transmission electron microscopy have added to the literature (Moe, 1960; Papp et al., 1963; Pratt and Napolitano, 1969; Hutchison et al., 1980; Smith et al., 1981). They report on the fine structure of submucosal glands and villi and on the occurrence of enterochromaffin cells. In this study, we generally use the terminology of the Nomina Histologica 2nd Ed. and Nomina Anatomica Veterinaria 3rd Ed.

Materials and methods

Six adult cats weighing 7 - 9 pounds were anesthetized with intramuscular ketamine (10 mg/lb) and xylazine (.75 mg/lb). The duodenum was exposed through a ventral midline incision. The duodenum was freed by incising proximal to the pylorus, distal to the attachment of the duodenocolic fold (ligament) at the duodenojejunal flexure, and the entire length of the mesoduodenum. The tubular

mass with the pancreas attached was removed and gently flushed with saline. It was immersed in 0.07 mol/L 10% phosphate-buffered formalin for fixation and the lumen flushed with this mixture. The distal end was ligated and the lumen was gently filled with and stored in 10% phosphate-buffered formalin for three weeks. Beginning 5 mm distal to the pylorus, 5 mm thick specimens of tissue were cut every centimeter and labeled for paraffin processing and sectioning. This report deals with the most proximal pieces (P, P_{1-3}); one piece (M) was cut 8 cm caudal to the pylorus and two pieces (D,E) from the last 1.5 cm of the duodenum (ascending portion) (Fig. 1).

Sections were prepared and processed for routine light microscopy in paraffin. Specimens were stained with hematoxylin and eosin (H and E) for morphological interpretation. Masson's trichrome and periodic acid-Schiff reagent were utilized for further differentiation. Three slides from each sampled area were evaluated using a calibrated ocular micrometer on Zeiss or Olympus light microscopes or a Zeiss MOP 3 digital image analyzer video plan. Recordings were randomly made at the 12, 4, and 8 o'clock positions.

Results

The duodenum was covered by a serosal layer (mesoduodenum) attached to the dorsal body wall. The median length of the duodenum was 16.4 cm (15.5 - 18 cm). The pancreas lay closely apposed in the mesoduodenum, extending from the cranial flexure of the duodenum to midway around the caudal flexure.

The three classical tunics (mucosal, muscular, and serosal) and the tela submucosa were seen (Figs. 2-4) but no circular folds (plicae circulares, valves of Kerckring) observed. The *tunica mucosa* had two areas; villar and intestinal glandular (Figs. 2-4). The tunica mucosa surface was modified by 83 (45-114) finger to leaf-shaped villi which were 1072 µm (625-1771) high by 207 µm (101-400) wide. The *epithelial mucosa* covered the villi (Fig. 5) and decreased in median height from 46 µm (28-59 µm) proximally (P, P_{1-3}) to 40 µm (29-52) distally (M, E, D). The apex of the epitheliocytes was covered by a 1.1 - 1.7 µm thick striated border composed of microvilli and a glycocalyx. The pale oval nucleus with clumped chromatin was located at the junction of the middle and basal thirds of the cell. An average of 28 (7 - 65) goblet cells (exocrinocytus calciformis) per villus were present among the epitheliocytes, as were occasional intraepithelial globular leukocytes and small mononuclear cells with pale-stained cytoplasm. The goblet cells had apical microvilli and decreased in number from proximal (31) to distal (27). The median number of indentations in the epithelial layer (Figs. 2 - 5) of the villus was 19 (7 - 40).

The epithelial mucosa of the intestinal glands (crypts of Lieberkuhn, crypt) was 20 µm (13 - 29) tall with a less distinct striated border. The majority of the cells were nondifferentiated columnar cells which had round pale-stained nuclei with prominent nucleoli in the basal third of the cell (Fig. 7). Many mitotic figures were seen in the nondifferentiated columnar cells. On average, 12 (6 - 22) goblet cells (exocrinocytus calciformis) were seen per gland. These cells were filled with mucoid material and had a basally compressed nucleus. Often a fine, red, granular material was observed around the mucoid material and the nucleus. Occasional columnar to triangular cells were seen with round basally located nuclei. Their cytoplasm, especially basally, was full of red granules (Figure 8). The glands were simple straight tubular; but occasional distal branching was observed. The median thickness of the gland layer was 515 µm.

The *lamina propia mucosa* had two areas: (1) within the villus (core) and (2) the intestinal gland zone (between the base of the villi and the lamina muscularis muscosa). The propria was composed of a loose connective tissue network which supported the epithelium of the villi and the intestinal glands while forming the core of the villus. An extensive arteriole, capillary and venule network was seen, both in the villus and in the intestinal gland area.

Delicate strands of smooth muscle coursed through the intestinal gland propria and nearly the length of the villar propria. A central lymph vessel, many nerve fibers and cellular profiles (plasma cells, leukocytes, fibrocytes, eosinophiles, lymphocytes, globular leukocytes and macrophages) were observed in the villar propria (Figs. 2, 3).

The lamina propria mucosa of the intestinal gland region contained similar elements plus the submucosal gland ducts coursing to empty into the lumen near the bases of the villi. The median thickness of the lamina propria of the intestinal gland zone decreased from proximal to distal (P - 495 µm, P_1 - 563 µm, P_2 - 566 µm, P_3 - 560 µm, M - 520 µm, E - 461 µm, and D - 465 µm) with a range of 310 - 800 µm proximally and 245 - 725 µm distally. A small amount (0 - 10 µm) of loose connective tissue infiltrated with plasma cells and lymphocytes could separate the intestinal glands from the lamina muscularis mucosa.

The *lamina muscularis mucosa* (Figs. 6, 7) decreased in median thickness distally (71 - 28 µm). It was formed by two distinct layers which decreased in thickness distally. The proximal median thickness of the inner circular muscle layer (P, P_{1-3}) was 14 µm (5 - 25), which decreased to a median thickness of 9 µm (5 - 20) distally (M, E, D). The median thickness of the outer longitudinal layer was 44 µm (10 - 105) proximally (P, P_{1-3}) and 23 µm (10 - 45) distally (M, E, D). The lamina muscularis mucosa was penetrated (interrupted) by the submucosal gland ducts, blood and lymph vessels and nerves.

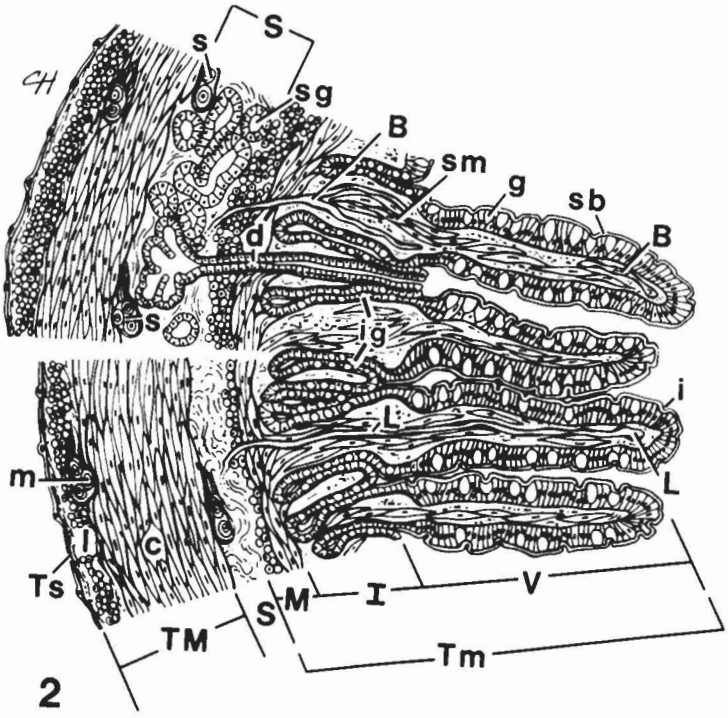
The *tela submucosa* decreased in median thickness distally (593 - 192 µm) with a range of 90 - 1250 µm proximally (P, P_{1-3}) and 62.5 - 600 µm distally (M, E, D) (Figs. 2 - 4). It contained submucosal (Brunner's, duodenal) glands for the first 1.5 cm. Two cats had glands for 2.5 cm while one cat had a few glands as far distal as M section (8 cm distal to the pylorus). The height of the submucosal gland epithelium ranged from 7.5 - 22.5 µm, while the width of the lumina of the glands ranged from 11.5 - 75 µm. Tubular, acinar and alveolar profiles were observed. The epithelium consisted of simple columnar epitheliocytes which had round, medium-stained, basally located nuclei with prominent nucleoli, and clumped chromatin. The cytoplasm was filled with mucous-like material and occasional

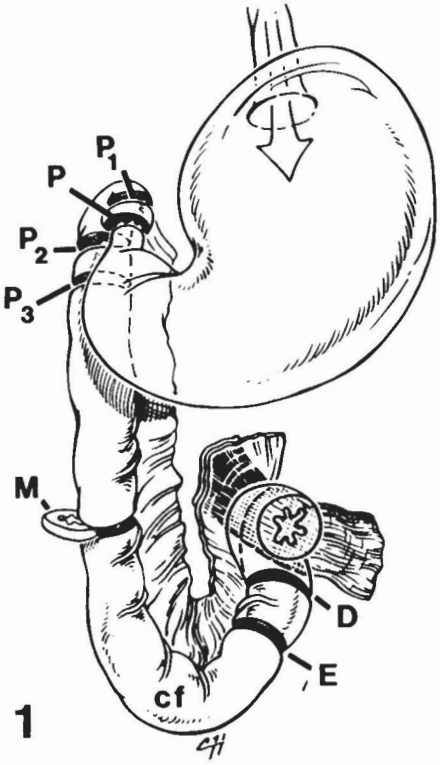
eosinophilic material was seen, along with other filamentous type material. No serous demilunes were observed (Fig. 9).

The connective tissue stroma consisted of dense irregular collagen and elastic fibers which also surrounded the proximally located submucosal glands. Blood and lymph vessels, nerve fibers, submucosal (Meissner's, parasympathetic) nerve plexuses, as well as lymphatic infiltration and nodules were found throughout the length of the submucosa.

The *tunica muscularis* increased in thickness from proximal to distal (527 - 645 µm), had a median thickness of 557 µm (190-1425) and two layers (Figures 2, 6). Between the thinner outer longitudinal layer (109 µm average) and the thicker inner circular layer (448 µm average), there was a scant layer of loose connective tissue with numerous myenteric (Auerbach's, parasympathetic) nerve plexuses.

The *tunica serosa* of simple squamous epithelium (mesothelium) with an underlying loose connective tissue (tela subserosa) layer. At the mesenteric border, the tela subserosa continued deeper through the outer longitudinal muscle layer of the tunica muscularis to become continuous with the loose connective tissue which lay between the two layers of the tunica muscularis.





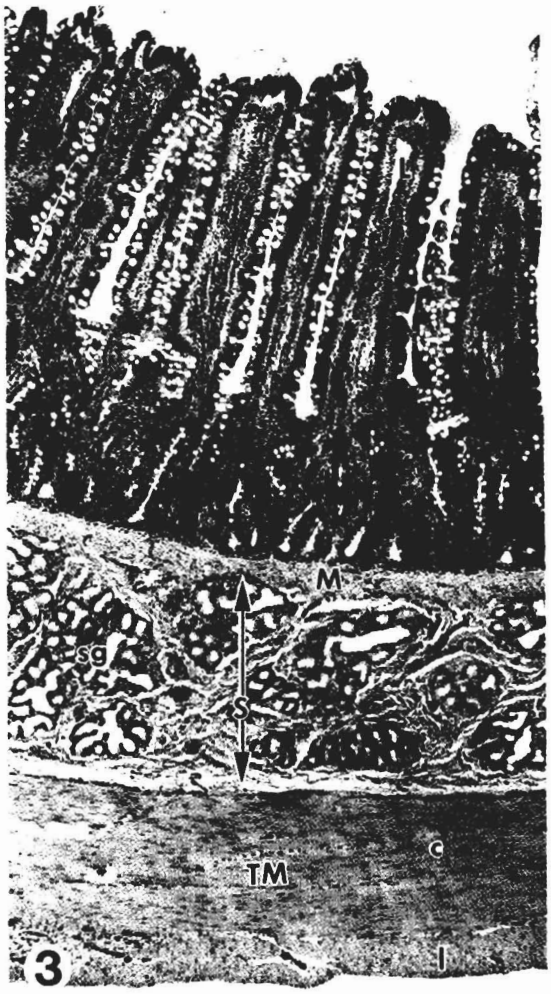
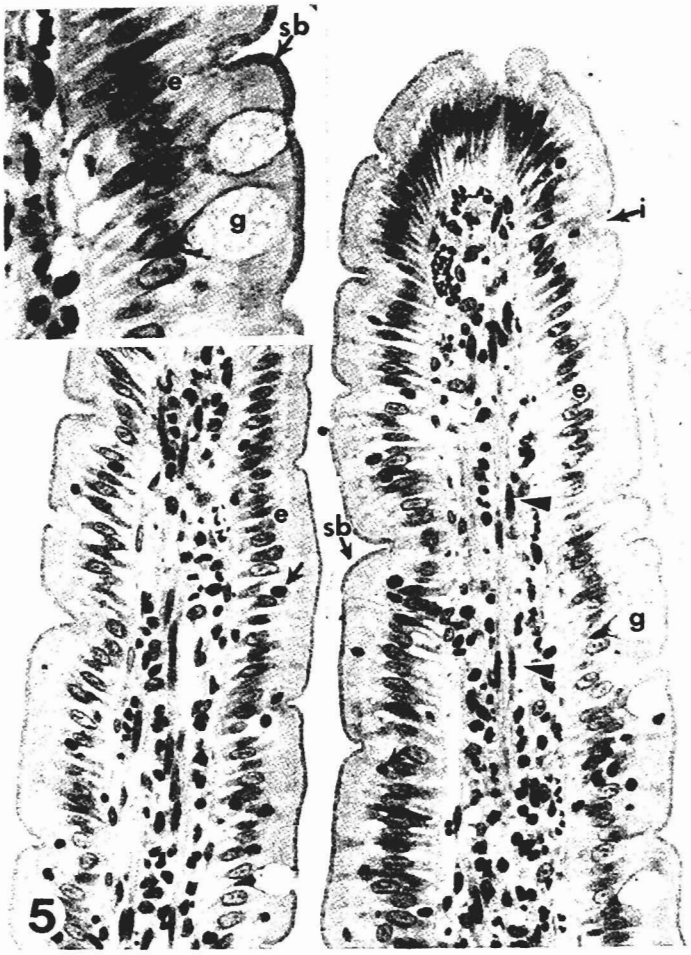
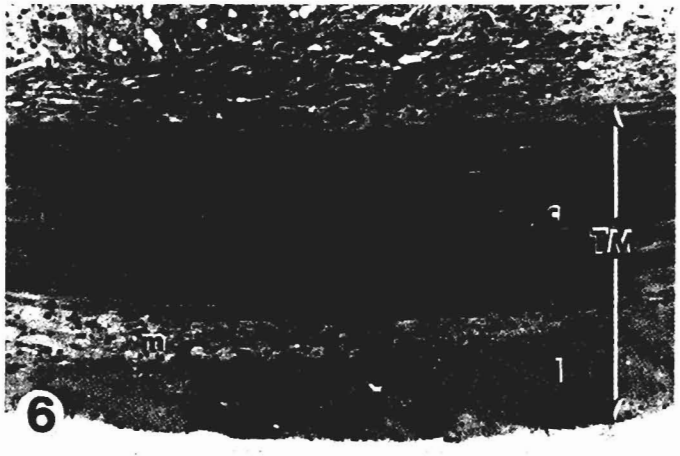


Fig. 1. Ventral view of the stomach and duodenum, illustrating the reported sample areas P, P_{1-3}, M, E, D. P-most proximal, D-most distal sample (at duodenojejunal flexure), cf-caudal duodenal flexure.

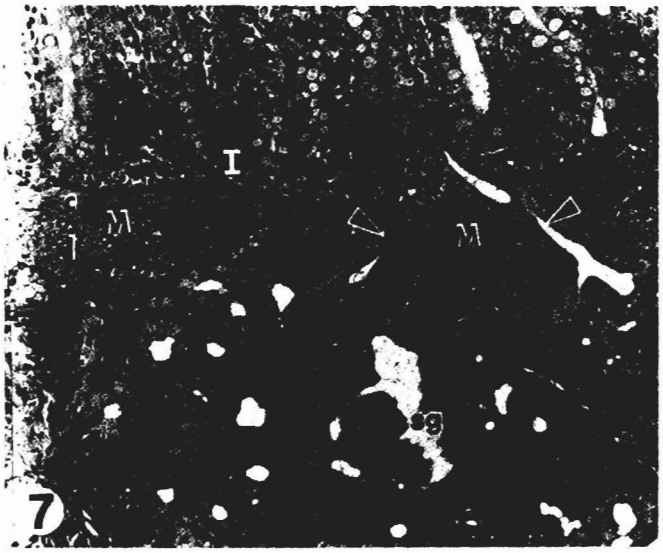
4



5



6



7

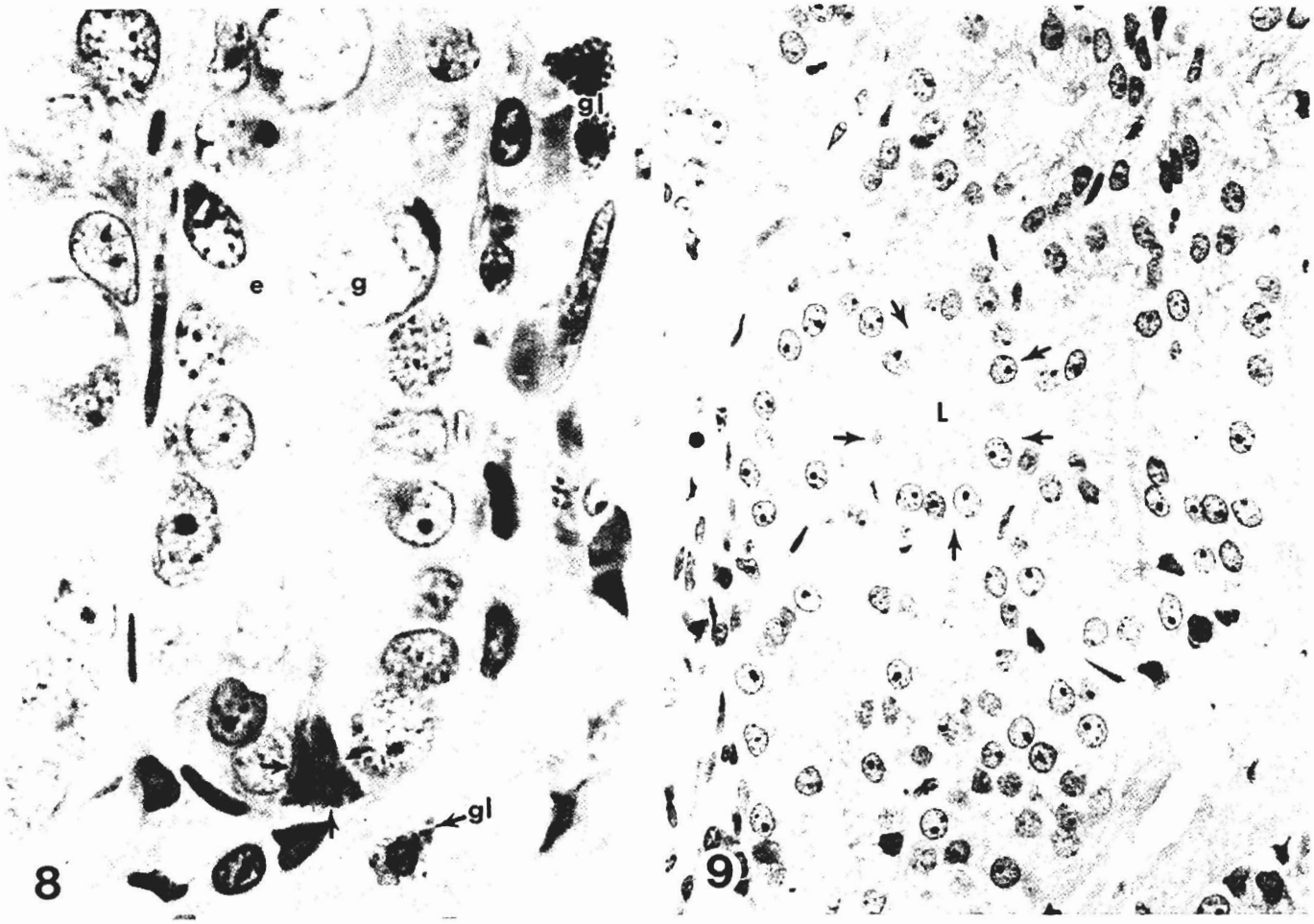


Table 1. Average data for each reported sample area

Sample Area	—	P	P_1	P_2	P_3	M	E	D	Median[1]	Range[2]
# of cats with Submucosal glands		6	6	3	1	1	0	0		
Epithelial mucosa thickness*		46	46	46	46	42	39	40	44	28-59
# of villi per section		67	73	82	84	88	99	95	83	45-114
Goblet cells per villus		31	29	26	26	27	27	27	28	7-65
Intestinal gland thickness*		495	563	566	560	520	461	465	515	320-800
Lamina muscularis mucosa thickness*		71	55	48	47	37	26	28	45	15-105
(inner layer)*		15	13	14	12	9	6	10	11	5-25
(outer layer)*		56	42	35	35	28	19	18	33	10-100
Tela submucosa thickness*		593	375	216	214	180	180	192	289	62.5-1250
Tunica muscularis thickness*		527	454	535	527	528	550	645	557	190-1425
(inner layer)*		405	351	423	434	435	465	550	448	135-1225
(outer layer)*		122	103	113	93	93	85	95	109	25-200

*in micrometers
1. Median value of P, P_1, P_2, P_3, M, E, D.
2. Range of P, P_1, P_2, P_3, M, E, D.

Fig. 2. Illustration of proximal (top portion) and distal (bottom portion) duodenum. Proximally (top portion), the tela submucosa (S) is thicker due to the presence of submucosal glands (sg). Distally (bottom portion), the thinner tela submucosa (S) has no submucosal glands and a thicker tunica muscularis (TM) [inner circular (c) and outer longitudinal (l) layers]. Tm-tunica mucosa, V-villus, I-intestinal gland zone, ig-intestinal glands, i-indentation of villar mucosa, L-central lymph vessel, B-blood vessels, g-goblet cell, sb-striated border, sm-smooth muscle strands, M-muscularis mucosa (inner circular and outer longitudinal layers), d-submucosal gland duct, s-submucosal nerve plexuses, m-myenteric plexus, Ts-tunica serosa.

Fig. 3. Cross-section of proximal (P_1) duodenum (1½ cm distal to the pylorus). Note the increased width of the tela submucosa (S) with numerous submucosal glands (sg). Note the tunica muscularis (TM) with inner circular (c) and outer longitudinal (l) layers and the distinct muscularis mucosa (M). ig-intestianl glands, L-central lymph vessel. H.E. 55 x

Fig. 4. Cross-section of the mid (M section) duodenum. Note the reduction of the tela submucosa (S) and that it contains no submucosal glands. M-muscularis mucosa, TM-tunica muscularis, ig-intestinal glands. H.E. 55 x

Fig. 5. Longitudinal section of two villi, showing indentations (i) in the mucosa and smooth muscle strands (arrowheads) in the lamina propria. Scattered mononuclear cells (arrows) are seen in the villar mucosa among the tall columnar epitheliocytes (e) and the goblet cells (g). The epithelium of the mucosa is covered with a striated border (sb). H. E. 260 x

Fig. 6. Cross-section of the proximal duodenum (P_2), showing the thick tunica muscularis (TM) with an inner circular (c) and an outer longitudinal (l). Fibrous connective tissue and myenteric nerve plexuses (m) are found between the two muscle layers. S-tela submucosa. H. E. 80 x

Fig. 7. Cross-section of duodenum (P section), showing distinct inner circular (c) and outer longitudinal (l) layers of the muscularis mucosa (M). The ducts (arrowheads) of the submucosal glands (sg) are penetrating M. I-intestinal glands. H. E. 140 x

Fig. 8. Cross-sectin of duodenum (P section), showing basal cells of intestinal glands (longitudinal section). e-epitheliocyte, g-goblet cell, arrows-triangular cell with red granules, gl-globular leukocytes. H.E. 530 x

Fig. 9. Submucosal gland (P section), showing the round basally-located nuclei with prominent nucleoli and filamentous cytoplasm. L-lumen of acinus (surrounded by arrows). H. E. 1300 x

Discussion

Compared to body length, the cat duodenum is relatively long (16.4 cm mèdian). This is similar to the length of 14-16 cm reported by Crouch (1969). Comparatively, the human duodenum is only 25 cm in length (Moog, 1981). No permanent circular folds (plicae circulares) are seen, as reported by Banks (1986).

The tunica mucosa has the two classical areas: villar and underlying intestinal gland region .The median height of the villi was 1072 µm, being taller than the 963 µm reported by Titkemeyer and Calhoun (1955). This difference could be shrinkage artifact. The villar epithelial mucosa (columnar epitheliocytes) median height was taller proximally (47 µm) and decreased in height (41 µm) distally. This height is greater than the 16 µm reported by Titkemeyer and Calhoun (1955). The 1.1 - 1.7 µm thick striated border is somewhat thicker than that reported for the chick, rat and mouse (Granger and Baker, 1950; Dalton, 1951; Palay and Karlin, 1959; Overton and Sharp, 1964; Ito, 1965; Pratt and Napolitano, 1969). Intraepithelial globular leukocytes were common in most villi and were seen in multiple numbers. Dellman (1981) demonstrated their presence in the cat mucosa. The small intraepithelial mononuclear cells could be inflamatory cells or dying cells which are being sloughed. The 7 - 40 indentations in the epithelial mucosa of the villus were probably caused by contraction of the villar smooth muscle strands. Hutchison et al. (1980), using SEM, described deep ridges which seemed to be similar to the indentations seen on histological section. Indentation seems to be a more appropriate term than ridge. The 28 (median number) goblet cells (exocrinocytus calciformis) per villus decreased slightly (31-27) from proximal to distal. This is similar to the findings of Moe (1963) who found a decrease in the absolute number of goblet cells in the first 20 cm of the small intestine of cats, but an overall increase in number from there to the end of the tract.

The epithelial mucosa of the intestinal glands measured 20 µm and had a less distinct striated border, which is similar to the findings of Moe (1960). The majority of the cells were nondifferentiated epitheliocytes with many mitotic figures. On average, 12 goblet cells per gland were found. The occasional columnar to triangular cell with red granules may be an enterochromaffin [endocrinocytus gastrointestinalis (Argentaffin, APUD, Type I)] or other endocrine cell. Smith et al. (1981) showed isolated enterochromaffin cells to be present in the intestinal glands of the cat, via immunocytochemical studies using region specific motilin antisera. Trier (1963) described a similar cell (enterochromaffin), the apex of which did not reach the lumen and had irregular-shaped cytoplasmic granules at the base of human inestinal glands; Cheng (1969) demonstrated these cells in Man, mouse and rat. Dellman and Brown (1981) reported the presence of enterochromaffin cells in the intestinal glands of the cat. Vassallo et al. (1969) observed endocrine cells which were non enterochromaffin and stained violet to red. These cells resembled Paneth cells of other species, except that Paneth granules are basally-located, rather than apical. Paneth cells (exocrinocytes with acidophilic granules) have not been reported in the cat. Wolter (1986) has described three phases of granule production by the same cell type in Brunner's glands of the rat. Thus, the same mucous-producing cell has mucous, serous or endocrine properties, depending on

the stage of production. Hence, these may be immature goblet cells. The general architecture of the glands was simple straight tubular; however, distal branching was observed. Dellman and Brown (1981) reported only simple tubular glands.

The lamina propria of the villus has a loose connective tissue network which supports the central lymph vessel and a vascular and nerve fiber bed. Papp et al. (1962) demonstrated a triad-arrangement of lymph vessel, unmyelinated nerve fibers and smooth muscle strands; a 10 - 12 μm diameter lacteal; and endothelial cells with no basement membrane. Plasma cells, leukocytes, fibrocytes and lymphocytes were the most common cells. The propria of the intestinal glands was thickest proximally (563 μm) and thinned distally (465 μm), with a range of 320 - 800 μm. Moe (1963) found the glands to vary from 400 - 700 μm. The ducts of the submucosal glands coursed through this area to empty into the lumen between the bases of the villi. Leeson and Leeson (1967) found the submucosal gland ducts of the rabbit to empty into the base of the intestinal glands. A scant (0 - 10 μm) layer of loose connective tissue separated the intestinal glands from the lamina muscularis mucosa. This was not a well-defined lamina (stratum compactum), as reported by Banks (1986) in carnivors. Titkemeyer and Calhoun (1955) reported "a special connective tissue layer" in this region only in the dog.

The lamina muscularis mucosa had a thin (5 - 25 μm), but distinct, inner circular layer and a substantial (10 - 105 μm) outer longitudinal layer, of which the individual and the combined thicknesses decreased distally (71 - 28 μm). Titkemeyer and Calhoun (1955) and Dellman and Brown (1981) reported the lamina to be very thin (15 μm) and incomplete.

The increased proximal thickness in the tela submucosa is from the thick encircling layer of submucosal glands. The few thicker areas (600 μm) in the distal regions were due to heavy lymphatic infiltration and nodules. The first 1.5 cm of the submucosa contained the submucosal glands in all cats sampled. Half of the cats had glands 2.5 cm distal to the pylorus and one cat to M point. Titkemeyer and Calhoun (1955) reported submucosal glands only in the initial segment of the small intestine, Moe (1963) in the first 2 - 3 cm, while Sloss (1954) to a distance of 53 cm in the pig. The epithelium of the submucosal glands was neither mucous nor serous but the cytoplasm appeared as a mixture of the two. The cytoplasm appeared to be filled with small mucous particles but also contained eosinophilic material and filamentous structures. Moe (1960) described these cells in the cat as having alpha-cytomembranes which were attached to dense granules. Although typical of serous type secretion, they also had large mucoid type secretory granules. Therefore, he described these cells as neither typical serous nor mucous but a hybrid of the two. No serous demilunes were observed, as Leeson and Leeson (1967) reported in the rabbit. The epithelial height of these glands ranged from 7.5 - 22.5 μm, which is higher than the 10 μm reported by Titkemeyer and Calhoun (1955). The submucosal gland lumina ranged from 11.5 - 75 μm. Tubular, acinar and alveolar end pieces were seen. This description is similar to the tubuloalveolar or acinar of Elias (1947) and Moe (1960). The duct epithelium was of a similar height and cytoplasmic architecture to the gland. Moe (1960) reported occasional enterochromaffin and goblet cells in the submucosal glands. Lymph infiltration and nodules, as well as submucosal (Meissner's) nerve plexuses, were found at random.

The tunica muscularis (557 μm thick) increased in width distally (527 - 645 μm). It had two distinct layers with a small amount of loose connective tissue and myenteric (Auerbach's) nerve plexuses between them. This thickness was similar to the 555 μm recorded by Titkemeyer and Calhoun (1955). However, the third reported muscle layer (inner oblique) was not observed. Wood (1980) has classified the neurons of these plexuses as S/type 1 and A H/type 2.

The tunica serosa is a layer of mesothelium, attached to the underlying longitudinal muscle by delicate loose connective tissue (tela subserosa).

Acknowledgements. We gratefully acknowledge our secretarial staff J. Stringfield and M. West, who so graciously typed this manuscript. Also to our staff a special thanks for their fine attention to details: D. Bernander, P. Ellis, and L. Cherpow. Thanks are extended to Dr. Dianne Wallace; the College of Veterinary Medicihe of The University of Tennessee, Knoxville, TN; and the School of Veterinary Medicine of Louisiana State University and Agricultural and Mechanical College, Baton Rouge, LA for funding.

References

Banks W.J. (1986). Applied Veterinary Histology. 2nd ed. Williams & Wilkins. Baltimore. pp 405-409.

Cheng H., Merzel J. and Leblond C. (1969). Renewal of Paneth cells in the small intestine of the mouse. J. Anat. 126, 507-526.

Crouch J.E. (1969). Introduction to the celom and viscera. In: Text-Atlas of Cat Anatomy. Lea & Febiger. Philadelphia. pp 126-128.

Dalton A.J. (1951). Electron micrography of epithelial cells of the gastrointestinal tract and pancreas. Am. J. Anat. 89, 109-131.

Dellmann H.D. and Brown E. (1981). Textbook of Veterinary Histology. 2nd ed. Lea & Febiger. Philadelphia. pp 227, 237-246.

Elias H. (1947). Duodenal glands in domestic animals. Am. J. Vet. Res. 8, 311-313.

Granger B. and Baker R. (1950). Electron microscope investigation of the striated border of intestinal epithelium. Anat. Rec. 107, 423-441.

Hutchison W.M., Pittilo R., Ball S. and Siim J. (1980). Scanning electron microscopy of the cat small intestine and mucosal alteration observed during Toxoplasma gondii infection. Ann. Trop. Med. Par. 74, 427-436.

International Committee on Veterinary Anatomical Nomenclature. (1983). Nomina Anatomica Veterinaria with Nomina Histologica. World Association of Veterinary Anatomists. Vienna. 3rd Ed.

Ito S. (1965). Enteric surface coat on intestinal microvilli. J. Cell Biol. 27, 475-491.

Leeson C.R. and Leeson T. (1967). The fine structure of Brunner's glands in the rabbit. Anat. Rec. 159, 409-419.

Moe H. (1960). The ultrastructure of Brunner's glands of the cat. J. Ultra. Res. 4, 58-72.

Moe H. (1963). A quantitative study of the occurence of goblet cells in the small intestine of the cat. Ann. N.Y. Acad. Sci. 106, 518-544.

Moog F. (1981). The lining of the small intestine. Scientific American 245, 154-176.

Murray M., Miller H. and Jarrett W. (1968). The globule leukocyte and its derivation from the subepithelial mast cell. Lab. Invest. 19, 222-234.

Overton J. and Shoup J. (1964). Fine structure of cell surface specialization in the maturing duodenal mucosa of the chick. J. Cell Biol. 21, 75-84.

Palay S.L and Karlin L. (1959). An electron microscopic study of the intestinal villus. J. Biophysic. and Biochem. Cytol. 5, 363-372.

Papp M., Rohlich P., Ruszynak I. and Toro I. (1962). An electron microscopic study of the central lacteal in the intestinal villus of the cat. Zeits. Zellforsh. 57, 475-486.

Pratt S.A. and Napolitano L. (1969). Osmium binding to the surface coat of intestinal microvilli in the cat under various conditions. Anat. Rec. 165, 197-210.

Sloss M.W. (1954). The microscopic anatomy of the digestive tract of *Sus scrofa domestica*. Am. J. Vet. Res. 15, 578-593.

Smith P.H., Davis, B. Seino Y. and Yanaihara N. (1981). Localization of motilin-containing cells in the intestinal tract of mammals: A further comparison using region-specific motilin antisera. Gen. Comp. Endocrin. 44, 288-291.

Titkemeyer C.W. and Calhoun M. (1955). A comparative study of the structure of the small instestines of domestic aniamls. Am. J. Vet. Res. 16, 152-157.

Trier J.S. (1963). Studies on small intestine crypt epithelium. J. Cell Biol. 18, 599-620.

Vassallo G., Solcia E. and Capella C. (1969). Light and electron microscopic identification of several types of endocrine cells in the gastrointestinal mucosa of the cat. Z. Zellfrosh. 98, 333-356.

Wood J.D. (1980). Intracellular study of effects of morphine on electrical activity of myenteric neurons in cat small intestine. Gastroenter. 79, 1222-1230.

Wolter H.J. (1986). Endocrine cells do not exist in rat Brunner's glands. An electron microscopic study. Brain Res. 367, 141-150.

Accepted March 31, 1986