Histogenesis of the Mouse Gastric Mucosa, with Special Reference to Type and Distribution of Proliferative Cells*

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Received May 12, 1984

Summary. Histogenesis of the mouse gastric mucosa and the distribution of epithelial cells capable of proliferation were studied by light microscopy, autoradiography with 3H-thymidine and electron microscopy. The formation of the gland begins on day 14 of gestation, while morphological signs of epithelial cell differentiation begin on day 15. The cell types include surface mucous, primitive chief and parietal cells during the late prenatal and first 2 weeks of postnatal development. Immature surface mucous cells and undifferentiated cells in the lower part of the foveola and the isthmus, and primitive chief cells throughout the gland become 3H-thymidine labeled. In addition, surface mucous cells in the superficial epithelium are labeled in fetuses and neonates several hours after birth. By 21 days after birth, primitive chief cells are replaced by chief and mucous neck cells. At that time, immature surface mucous and undifferentiated cells in the isthmus, and mucous neck cells in the upper part of the neck are radio-labeled and form the generative cell zone. The mucosa attains its full thickness by 6 weeks of age.

Immature parietal cells rarely incorporate 3H-thymidine during their development. It is suggested that some of the parietal cells may be derived from actively proliferating precursors, i.e., primitive chief cells and mucous neck cells in developing and adult animals, respectively.

The fine structure of four types of epithelial cells of the gastric mucosa, i.e., surface mucous cells, mucous neck cells, chief cells and parietal cells, has been extensively studied (Ito, 1967; Helander, 1981). These cells belong to the renewing population (Messier and Leblond, 1960). The majority of proliferative cells are present in the isthmus to the upper part of the neck (the generative cell zone). Surface mucous cells, which arise in this zone, migrate upward to the mucosal surface while the other three types of cells migrate downward toward the base of the gland (Hattori, 1974; Hattori and Fujita, 1976). The fine structure of the proliferative cells and the maturing process of each cell type is well known (Kataoka, 1970; Kataoka and Sakano, 1984).

Ontogenic studies on the fine structure of these cell types have been performed mainly in the rat (Helander, 1969a, b). However, only a single short report has been

* This study was supported by Grant-in-Aid for Cancer Research and Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan.
published on epithelial cell proliferation and migration in developing animals (Yeomans and Trier, 1976). A systematic study has not been carried out on the distribution and morphology of proliferative cells in the developing gastric mucosa in relation to histogenesis of the gland and development of each cell type.

MATERIALS AND METHODS

ICR mouse fetuses (at 12.5, 14, 15, 16, 17 and 18 days of gestation), young animals (0, 1, 2, 3, 7, 10 days; 2, 3, 4 and 6 weeks old) and adults (2, 2.5 and 3 months) were used for this study. The fetal age was determined after Theiler (1972) (presumed copulation = middle of the night = 0).

For electron microscopy, postnatal animals were perfused with 2.5% glutaraldehyde (cacodylate buffer, pH 7.4) from the left ventricle of the heart, and the stomach was removed thereafter. For fetuses, the stomach was removed without perfusion fixation but then immediately immersed in 2.5% glutaraldehyde. Tissue blocks were obtained from the body region of the stomach along the greater curvature. The tissue was fixed overnight with 2.5% glutaraldehyde, postfixed with 1% osmium tetroxide for 2 hrs, dehydrated by ethanol and embedded in epoxy resin. Thin sections were doubly stained with uranyl acetate and lead citrate.

For light microscopy, the stomach was fixed with Bouin’s solution and embedded in paraffin. Sections were stained with hematoxylin and eosine, or periodic acid-Schiff (PAS) reaction and hematoxylin. Thick sections of the resin-embedded material were also used for light microscopic examination. They were stained with toluidine blue, PAS and hematoxylin, or trichromatic (malachite green-toluidine blue-basic fuchsin) stain after Kurotaki (1972).

For light microscopic autoradiography, 3H-thymidine (1 μCi/g body weight for paraffin sections, or 10 μCi/g body weight for resin sections) was injected intraperitoneally into the mice. For examination of fetal mice, 300 μCi of 3H-thymidine was administered to the mother animal. The stomach was removed 1 hr after the injection, and paraffin and resin sections were made as described above. The sections were coated with Sakura NR-M2 emulsion by the dipping method. After exposure for 2 to 6 weeks, the specimen was developed with D19. Paraffin sections were stained with hematoxylin-eosin or PAS-hematoxylin, and resin sections were stained with PAS-hematoxylin or toluidine blue. PAS and hematoxylin stains were used before the autoradiographic procedure, while eosin and toluidine blue were applied afterwards.

RESULTS

The adult mouse

The mucosal surface and the foveolae of the stomach are lined with surface mucous cells. For the convenience of description, the gastric gland is divided into three parts: 1) the isthmus consisting of immature forms of surface mucous cells, parietal cells and a few undifferentiated cells; 2) the neck consisting of mucous neck cells and parietal cells; and 3) the base consisting of chief cells and some parietal cells (Plenk, 1932; Stevens and Leblond, 1953; Kataoka and Sakano, 1984). With PAS reaction, secrertory granules of the surface mucous and mucous neck cells are distinctly stained, while those of the chief cell are unstained. By trichromatic stain after Kurotaki (1972),
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secretory granules of the former two cell types are stained red, whereas the chief cell contains secretory granules of various colors, i.e., red, purple, blue and unstained.

As shown in the previous study (KATAOKA, 1970), 3H-thymidine-labeled cells are mainly found in the generative zone, i.e., the isthmus and the upper part of the neck (Fig. 1). They consist of immature surface mucous cells, a few undifferentiated cells and mucous neck cells, whose secretory granules are stained somewhat weaker by PAS reaction than the typical cell (d, arrow), and an immature parietal cell in the neck (e). PAS-hematoxylin stain. ×820. f and g. A chief cell (f, arrow) and an endocrine cell (g) are labeled at the upper part of the base. Toluidine blue stain. ×830

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As shown in the previous study (KATAOKA, 1970), 3H-thymidine-labeled cells are mainly found in the generative zone, i.e., the isthmus and the upper part of the neck (Fig. 1). They consist of immature surface mucous cells, a few undifferentiated cells and mucous neck cells, whose secretory granules are stained somewhat weaker by PAS reaction than the typical mucous neck cell. Occasionally, immature parietal cells in the neck, immature chief cells at the upper part of the base and endocrine cells are labeled.

Since the ultrastructure of the surface mucous, mucous neck, chief and parietal cells is well known (ITO, 1967; HELANDER, 1981) and ultrastructural changes in the renewing process of each cell type have been described in previous reports (KATAOKA, 1970), we only call the readers' attention here to the gradual changes in the ultrastructure of the cells along the perpendicular axis of the mucosa in the adult mouse (KATAOKA and SAKANO, 1984). Surface mucous cells mature from the isthmus to the upper part of the foveola and become abundant with the secretory granules located immediately beneath the apical cell membrane. At the mucosal surface, secretory granules are decreased in number. Mucous neck cells at the uppermost part of the neck are stained somewhat weaker with PAS reaction, and contain secretory granules denser than the typical cell type. Chief cells become larger and more mature from the upper to the lower parts of the base.

Prenatal development

On day 12.5 of gestation (day E12.5), the gastric mucosa is lined with simple epithelium (Fig. 2a). The junction between the epithelium and the underlying mesenchyme is smooth. The epithelial cells show the ultrastructural characteristics of the undiffer-
differentiated cell (Fig. 3a). The nucleus is large and contains little condensation of chromatin and prominent nucleoli. Numerous free polyribosomes are scattered throughout the cytoplasm. The rough endoplasmic reticulum is poorly developed, the Golgi complex is small, and the mitochondria are few in number. Sometimes, small granules of unknown nature are seen in the basal cytoplasm. The apical cell surface contains a few short microvilli. A single cilium is often projected from the cell apex into the gastric lumen.

On day E14, the epithelium is tall and columnar (Fig. 2b). The epithelial cell nuclei are layered, so that the epithelium looks pseudostratified. Mitotic figures are always located in the superficial position. Formation of the glandular lumen begins as an intercellular pit continuous to the gastric lumen (Fig. 3b). A single cilium is often projected into the pit.
On day E15, the intercellular pit extends to form the glandular lumen. A group of epithelial cells surrounding the glandular lumen forms a basal bulge, so that the junction between the epithelium and the underlying connective tissue is scalloped (Fig. 2c). At the center of the bulge, epithelial cells are low and face the glandular lumen. Epithelial cells are tall and face the gastric lumen between neighboring bulges. 3H-thymidine-labeled cells are diffusely distributed throughout the epithelium. Mitotic figures face the glandular lumen as well as the main gastric lumen. Epithelial cells often contain a small number of dense granules in the apical cytoplasm (Fig. 3c). Glycogen particles are often seen. Microvilli are increased in number on the apical cell surface. A single cilium is often projected into the main gastric lumen or the glandular lumen.

On day E16, a connective tissue separates each glandular tubule. The tubules elongate gradually during later prenatal and postnatal development (Fig. 2d). 3H-thymidine-labeled cells are diffusely present in the glandular epithelium throughout late prenatal development (Fig. 2e). Labeled cells in the surface epithelium are less frequent than the glandular epithelium on day E16, and gradually decrease in number during development. Most epithelial cells at the mucosal surface as well as in the gland contain dense apical granules, which increase in number with fetal development (Fig. 2d, 4a). The same cells sometimes contain small apical vesicles, which often have a moderately dense to dense core. The cytoplasmic membranous organelles, such as the rough endoplasmic reticulum, Golgi complex and mitochondria gradually develop.

Fig. 3. a. Undifferentiated epithelial cells with a single cilium projecting to the gastric lumen (arrow) and a cluster of small basal granules (Gr) on day E12.5. $\times 4,700$. b. On day E14, a cilium (arrow) is seen protruding into the intercellular pit. $\times 8,600$. c. On day E15, glandular epithelial cells contain a few dense granules in their apical cytoplasm. A cilium (arrow) is seen protruding into the glandular lumen. $\times 8,900$
Fig. 4. a. Surface epithelial and glandular cells contain dense granules in the apical cytoplasm on day E16. M a mitotic glandular cell containing dense granules and small vesicles. ×4,400. b. A very immature form of the parietal cell with characteristic microvilli at the cell apex on day E16. Accumulation of glycogen particles (Gl) is seen. L glandular lumen. ×5,300. c. An immature parietal cell with the intracellular secretory canaliculus (C) on day E18. ×6,600
with fetal age. These cells eventually become surface mucous cells at the mucosal surface, and primitive chief cells in the gastric gland. However, the fine structural distinction between the two cell types is not apparent during fetal development.

The most immature form of the parietal cell is found on day E16 in the deepest part of the gland (Fig. 4b). These cells are identified as the parietal cell only by their characteristic microvilli. On day E17, immature parietal cells project more numerous microvilli, and their mitochondria increase in number. The intracellular secretory canaliculus is seen on day E18 (Fig. 4c). Parietal cells, however, remain immature during the entire prenatal development period.

Endocrine cells, which appear in the deep part of the gland on day E16, are not dealt with in this report.

Postnatal development

Several hours after birth, numerous \(^{3}H\)-thymidine-labeled cells are present throughout the glandular epithelium. Occasionally, a few surface epithelial cells are labeled. By electron microscopy, surface mucous cells lining the mucosal surface and short foveolae were seen to contain a few secretory granules at the apical cytoplasm (Fig. 5a). Strands of the rough endoplasmic reticulum and mitochondria increased to some extent. Accumulation of glycogen particles was prominent in the supranuclear and basal cytoplasm. Mitosis of surface mucous cells is occasionally seen in the foveolar epithelium. The great majority of the glandular cells are the primitive chief cells (Fig. 5b). Dense secretory granules are increased in number in the apical cytoplasm. They also contain small apical vesicles with a dense core. Mitotic primitive chief cells are often seen. Parietal cells have more developed intracellular secretory canaliculi with numerous microvilli. Small vesicles gather near the canaliculus, and mitochondria become larger and more numerous. However, mature parietal cells can not yet be seen.

Surface mucous, primitive chief and parietal cells undergo great changes in their fine structure within 1 day after birth (Fig. 6). Surface mucous cells exhibit gradual changes in fine structure from the lower part of the foveolae to the mucosal surface, where they contain the most abundant rough endoplasmic reticulum and mitochondria. The secretory granules which evince a PAS-positive reaction are seen throughout the supranuclear and apical cytoplasm and are most numerous in the cells at the mucosal surface. Glycogen accumulation is greatly reduced. Lipid droplets are present in the cells lining the mucosal surface. Primitive chief cells are the main component of the gland, and show a gradual increase in cell size, development of the rough endoplasmic reticulum, and number and size of secretory granules from the upper toward the lower part of the gland. Secretory granules of primitive chief cells are weakly stained with PAS reaction. Parietal cells are still scarce, though some of them show a mature morphology with well-developed intracellular canaliculi, numerous tubulovesicular elements and large round mitochondria.

At 7 days after birth, secretory granules of surface mucous cells gather just beneath the apical cell membrane (Fig. 7a). Cells with the most abundant secretory granules are still located at the mucosal surface. On day 14, the isthmus region consisting of immature surface mucous cells and parietal cells is distinguishable from the foveola which does not contain parietal cells (Fig. 7b). Secretory granules of the surface mucous cell are most numerous at the upper part of the foveola as in the adult animal. However, lipid droplets, which are rarely seen in mice 21 days and older, are still present in the cells lining the mucosal surface.

From 1 to 14 days of age, primitive chief cells gradually acquire parallel strands of
Fig. 5. Surface mucous cells with accumulation of glycogen particles (GI) (a), primitive chief cells and a parietal cell (b) several hours after birth. None of the cell types shows a mature morphology. Arrows indicate small vesicles with a dense core. a: $\times6,300$, b: $\times7,000$
the rough endoplasmic reticulum, and in the lower part of the gland begin to resemble definite chief cells (Fig. 8). On Day 14, some primitive chief cells stain intensely with PAS reaction. However, at this early stage it is difficult to classify the primitive chief cells into two cell types either by PAS reaction or by fine structure. Immature and mature forms of the parietal cell increase in number. Dense granules, resembling secretory granules of the primitive chief cell, are often found in the apical cytoplasm and near the secretory canaliculi of the immature parietal cell.

$^3$H-thymidine-labeled cells are present diffusely in the lower part of the foveola,

Fig. 6. Epithelial cells in a 1 day-old mouse. a. Surface mucous cells, which contain the well-developed rough endoplasmic reticulum and numerous mitochondria. They exhibit gradual changes in cell size and number of secretory granules from the lower part of the foveolae to the mucosal surface. Li a lipid droplet. $\times 3,300$. b. Primitive chief cells show gradual changes in number and size of secretory granules as well as cell size along the longitudinal axis of the gland. $\times 1,800$. c. Primitive chief cells with strands of the rough endoplasmic reticulum and large dense secretory granules, a parietal cell with abundant tubulovesicular elements and numerous large mitochondria and an endocrine cell (E). $\times 7,000$
Fig. 7. Light micrographs of the gastric mucosa in postnatal development. 

a. On day 7, the mucosal surface and the short foveola (F) are lined with surface mucous cells, whose secretory granules attain a maximum number at the mucosal surface (arrow). The gland (G) consists of primitive chief cells and a few parietal cells. Trichromatic stain. ×740.

b. On day 14, the isthmus (I) is distinguishable between the foveola (F) and the rest of the gland (G). Secretory granules of the surface mucous cell are the most abundant at the upper part of the foveola (arrows). Trichromatic stain. ×370.

c. Mucous neck cells with PAS-positive granules (arrows) and chief cells with PAS-negative granules (arrow heads) are clearly distinguishable in a 3 week-old mouse. PAS-hematoxylin stain. ×1,600.

d. Fully developed gastric mucosa in a 6 week-old mouse with clear distinction of the foveola (F), isthmus (I), neck (N) and base (B). Trichromatic stain. ×370
the isthmus and the gland from 1 to 10 days after birth (Fig. 9a, b). On Day 14, labeled cells are somewhat decreased at the base of the gland. They belong to either the immature surface mucous cells, a few cells without evident secretory granules or the primitive chief cells (Fig. 9c). Mitotic figures of the same cell types are evidenced by both light and electron microscopy. The labeling of parietal cells is very rare.

Three weeks after birth, mucous neck cells with PAS-positive secretory granules and chief cells with PAS-negative granules can be identified in the upper and lower parts of the gland respectively, so that the neck and the base of the gland are clearly distinguishable (Fig. 7c). The mucous neck cells are small, and contain some parallel strands of rough endoplasmic reticulum, and dense secretory granules which show a tendency to adhere to each other (Fig. 10b). The chief cells contain abundant parallel strands of rough endoplasmic reticulum and dense secretory granules which are larger than mucous neck cell granules (Fig. 10c). Parietal cells greatly increase in number. ³H-thymidine-labeled cells are distributed in the isthmus and neck, and only occasionally in the base (Fig. 9d). Most originate from the immature surface mucous cells and mucous neck cells as in the case of the adult mouse. Mitotic figures observed by light and electron microscopy are of the same cell type.

Four weeks after birth, typical mucous neck cells with moderately dense secretory granules appear at the lower part of the neck. At the same time, chief cells become larger and more typical in size and ultrastructure at the lowermost part of the base.
The gland gradually elongates to some extent thereafter; mucous neck, chief and parietal cells increase in number proportionally; and the mucosa attains its full thickness by 6 weeks (Fig. 7d).

**DISCUSSION**

On the basis of the present study, the development of the mouse gastric mucosa can be classified into three stages: 1) a prenatal period extending to several hours after birth; 2) a period 1 day to 2 weeks after birth; and 3) the final period from 3 to 6 weeks of age.

The formation of the gland begins on day E14. Morphological signs of epithelial cell differentiation to surface mucous, primitive chief or parietal cells are first seen on either day E15 or E16. Thereafter, cytoplasmic membranous organelles are gradually developed in each cell type. The appearance of the intracellular secretory canaliculi in the parietal cell on day E18 coincides with the results of Pipan (1970). However, all cell types remain immature several hours after birth. Cells capable of thymidine-uptake and proliferation are present throughout the epithelium during this stage. Notwithstanding, they are gradually decreased in the superficial epithelium as the fetus ages and are rarely found in the neonate.

**Fig. 9.** a and b. Autoradiograms showing the whole thickness of the gastric mucosa of 7 (a) and 14 (d) day-old mice. ³H-thymidine-labeled cells are diffusely present in the lower part of the foveola and the gland. Hematoxylin-eosin stain. ×190. c. On day 7, labeled cells including a cell with few secretory granules in the lower part of the isthmus (arrow) and many primitive chief cells in the gland are seen. Toluidine blue stain. ×1,100. d. On day 21, most labeled cells are distributed in the isthmus and the upper part of the neck, and form the generative zone. PAS-hematoxylin stain. ×190

**Fig. 10.** a. Typical surface mucous cells at the upper part of the foveola in a 14 day-old mouse. ×6,300. b. Mucous neck cells with dense secretory granules on day 21. ×5,500. c. Chief cells with numerous parallel strands of rough endoplasmic reticulum and dense secretory granules on day 21. ×7,000. d. A typical mucous neck cell (M) and immature parietal cells (P) which contain granules like those in the mucous neck cell in an 8 week-old mouse. ×6,000
Fig. 10. Legend on the opposite page.
A single or primary cilium is known in various cell types, but their function remains obscure except for the sensory function of the elaborate cilium in the sensory cell (Wheatley, 1982). The cilium frequently protrudes from the cell apex into the main lumen of the stomach or the lumen of the developing gland in fetal mice. However, it is not seen in postnatal animals. This suggests that the cilium may play a role in early stages of gland formation.

Within postnatal day 1, the cytoplasmic organelles participating in secretory activity are rapidly developed in each cell type; the amount of rough endoplasmic reticulum and the number of secretory granules are increased in surface mucous and primitive chief cells. Some parietal cells exhibit a mature, fine structure with dilated secretory canaliculi, large round mitochondria and numerous tubulovesicular elements. Morikawa et al. (1979) reported that the development of parietal cells was accelerated by oral administration of milk in both normal neonates and premature newborn rats delivered by cesarean section. The rapid, fine structural maturation of surface mucous and primitive chief cells that are demonstrated in the present study may also be caused by the intake of milk.

The amount of rough endoplasmic reticulum and the number of mitochondria in the surface mucous cell is as abundant in the 1 day-old mouse as in the adult. Secretory granules, which are distributed throughout the supranuclear cytoplasm on postnatal day 1, are accumulated in the apical cytoplasm just beneath the apical plasmalemma, similar to the adult at day 7. On day 14, the fine structural alterations of maturing surface mucous cells along the perpendicular axis of the mucosa resemble those of the adult mouse; the immature cells proliferate in the isthmus, and maturing cells migrate upwards to the upper part of the foveola where the secretory granules are the most abundant. The origin of the lipid droplets, which are present in the cells lining the mucosal surface in the suckling mouse stomach, is unknown.

The main cell types of the developing gastric gland exhibit the typical fine structure of the protein-secreting exocrine cell. Helander (1959b) distinguished mucous neck cells and chief cells in perinatal rats. However, we do not classify the protein-secreting exocrine cells in the perinatal to 14 day-old mice into these two cell types for the following reasons: the fine structure of the cells exhibit gradual maturation from the upper to the lower part of the gland, so they can not be classified into the two cell types by their fine structure; the cells do not classify into PAS-positive and -negative populations; and the cells are actively proliferating at all levels of the gland. In this paper, the cells are tentatively called the primitive chief cells. Since mucous neck cells are thought to be the precursors of chief cells in the adult stomach (Hattori and Fujita, 1976), it is not surprising that the two populations cannot be distinguished at the time of gastric mucosa development.

Primitive chief cells acquire more and more fine structures that resemble definite chief cells in the lower part of the gland during development. At 21 days after birth, mucous neck cells and definite chief cells are distinguished by PAS as well as by their fine structures. This makes it possible to demarcate the neck and the base of the gland. Mucous neck cells are present in the neck and actively proliferate while chief cells are in the base and seldom undergo mitosis (Kataoka, 1970). Thus the generative zone, consisting of immature surface mucous and undifferentiated cells in the isthmus and mucous neck cells in the upper part of the neck, is established concomitantly with the differentiation of mucous neck and chief cells. This coincides with the period of weaning. Mucous neck and chief cells in the 3 week-old mouse resemble in fine structure these cell types at the upper part of the neck and the base of the adult.
gastric gland, respectively (Kataoka and Sakano, 1984). Typical mucous neck and chief cells appear postnatally at 4 weeks concomitantly with the elongation of the gastric gland. Similarly, Fujihata et al. (1973) found a rapid increase in the peptic activity of the developing rat gastric mucosa 20 to 30 days after birth along with the simultaneous maturation of chief cells.

The proliferative capability of parietal cells has been studied extensively. Some authors described the occasional but temporary presence of labeled parietal cells after injection of ³H-thymidine (Chen and Withers, 1975; Tamura and Fujita, 1983), while others failed to see it (Ragins et al., 1968; Kataoka, 1970; Wilems et al., 1972; Yeomans et al., 1976). In the present study, labeled immature parietal cells were rarely found in the adult mouse 1 hr after the injection of ³H-thymidine. In fact, they were seen only occasionally even in the developing gastric gland. On the other hand, immature parietal cells often contain dense granules resembling those in primitive chief cells in 2 week-old and younger mice in both the present study and in previous studies using mice (Pipan, 1970) and rats (Helander, 1969a; Morikawa et al., 1979). A few immature parietal cells containing mucous granules were found in weaned and adult animals in this and previous studies (Tamura and Fujita, 1983, Kataoka and Sakano, 1984). These results suggest that the parietal cells, which have a limited capability for proliferation, can be formed from more actively proliferating precursor cells, i.e., the primitive chief cells in the developing animal and the mucous neck cells in the adult.

Acknowledgements. We are grateful to Dr. Richard C. Miller, Department of Pathology, Radiation Effects Research Foundation, Hiroshima, Japan, for his kind assistance in preparing the manuscript.

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