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Portfolio of Ameloblasts

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Abstract-Ameloblasts are cells present only during tooth development that deposit tooth enamel, which is the hard outermost layer of the tooth forming the surface of the crown. In the developing tooth the functioning ameloblast is a tall, narrow cell, with its base attached to the cells of the stratum intermedium. The nucleus is located basally and basal cytoplasm contains abundant mitochondria. The supranuclear cytoplasm contains a large, active Golgi complex and abundant rough endoplasmic reticulum, together with microtubules, which are predominantly longitudinally arranged, and secretory vacuoles which become larger and more numerous near the upper pole. At the upper pole the cell elongates into a single large Tomes' process, and forms a fringe of smaller processes around its neck. The Tomes' process contains numerous microtubules and large numbers of secretory vacuoles. The rough endoplasmic reticulum synthesizes various proteins and glycoproteins (including amelogenin and enamelin), which form the organic matrix of enamel (pre-enamel) and are packaged by the Golgi complex into secretory vacuoles. These then move into the Tomes' process and the small neck processes, discharging their contents on to the surface. Mineralization of the matrix proteins by hydroxyapatite occurs almost instantaneously, producing small enamel crystallites and, with progressive mineralization, the enamel rods or prisms.

Ameloblasts are derived from oral epithelium tissue of ectodermal origin. Their differentiation from preameloblasts is a result of signalling from the ectomesenchymal cells of the dental papilla. The ameloblasts will only become fully functional after the first layer of dentin has been formed by odontoblasts. The cells are part of the reduced enamel epithelium after enamel maturation and then are subsequently lost during tooth eruption[1,2]

ZONES OF AMELOGENESIS

(1) Presecretory Zone

The entire layer of ameloblasts from the point of greatest convexity of the apical loop until a discrete layer of enamel was present, was classified into various regions
prior to the zone of enamel secretion.
(a) Region of Ameloblasts facing pulp,(i) posterior portion (odontogenic organ).
The apex of the ameloblast faced the the undifferentiated cells of the pulp and the base was adjacent to equally undifferentiated cells of the provisional stratum intermedium. The stellate reticulum and outer dental epithelium were also undifferentiated. The ameloblasts at this stage were organized into an apparently stratified low columnar epithelium with two or three staggered levels of nuclei. The nuclei were large, oval and elongated in the long axis of the cell. The junctions with the pulp at its apex and the provisional stratum intermedium at its base were wavy and irregular. A basement membrane separated the ameloblasts from the pulp. The term "provisional stratum intermedium" was applied to the layer of cells lying against the base of the ameloblasts. These cells were "provisional" because, first, they were continuous with the well-organized layer of stratum intermedium seen further incisally, and second, because it was often unclear as to whether a cell in this layer belonged to the ameloblasts, the stellate reticulum or to stratum intermedium itself.

The *outer dental epithelium* consisted of short flattened cells arranged as a multiple layer of cells on the labial surface of the apical loop. The cells contained a small, oval nucleus which was oriented perpendicular to the surface of the odontogenic organ. Outside the odontogenic organ were cells and extracellular connective tissue elements. Near the outer dental epithelium several layers of fibroblast-like cells formed an investing sheath similar to the dental sac.The undifferentiated mesenchymal cells of the pulp facing the ameloblasts in this region were heterogeneous in appearance.
(a) Region of Ameloblasts facing pulp,(ii) anterior portion (odontogenic organ).
There was an increased regularity of the junction between ameloblasts and provisional stratum intermedium. The cells of the provisional *stratum intermedium* were a mixture of squamous and cuboidal shapes, but the latter, containing large irregularly shaped nuclei, predominated. Outside the outer dental epithelium, small capillaries came into closer association with the odontogenic organ and disrupted the investing appearance previously shown by the cells of the dental sac. In the pulp, three changes were noted.
First, the cells adjacent to the ameloblasts became progressively organized into cuboidal, then low columnar and finally, in the region of ameloblasts facing dentin, into a single layer of differentiated columnar odontoblasts. Second, cells lying deeper in the pulp showed evidence of organization into two or three layers of flattened cells forming a subodontoblastic layer Lastly, large, thin walled capillaries came into close association with the developing subodontoblastic layer .

(b) Region of ameloblasts facing dentin
It was in this region that the ameloblasts developed all the morphological features of secretory ameloblasts except for Tomes, processes. At the apical limit of the region the appearance of the ameloblasts was more regular than in the previous region, and by the end of the apical one-third of

this region, mitotic figures were no longer seen in ameloblasts.

Half-way along this region the cells began to elongate and the nucleus as well as the mitochondria became located in the base. An apical cell web with obvious terminal bars became evident. At the incisal limit of the region the ameloblasts were fully functional in secreting the initial layer of enamel. The oval nuclei of these cells remained perpendicular to the layer of mantle dentin and were seen to lie at two staggered levels.Mitotic figures in this group of cells were seen one-third of the way into the region; after this they no longer showed division.. The thickness of the stellate reticulum was reduced to one cell layer at the incisal limit of the region. In the *pulp*, the previously differentiated odontoblasts became angled with respect to the ameloblast-dentinal junction such that the cell sloped toward the apex. Thin wall capillaries moved closer to the odontoblasts as the subodontoblastic layer was lost. The *predentin* appeared as a coarse matrix containing bundles of fibrils resembling von Korff's fibres and gradually thickened in amount and became more homogeneous near the incisal limit of the region.

(2*) Secretory Zone*

(a) Region of inner enamel secretion.

The point of initial enamel secretion was marked by the presence of large spherical dark staining bodies between the apices of adjacent ameloblasts. Gradually, the interdigitating portions of Tomes, processes were delineated by the prongs of enamel matrix and took on the characteristics of inner enamel secretion [3].The arrangement is described as the "picket-fence" and consists of processes cut at various angles as they course into the enamel. The nucleus of the ameloblast appeared to be slightly inclined incisally relative to a perpendicular line drawn to the dentino-enamel junction. In the stratum intermedium the bilayered and irregular organization of the cells disappeared, and now contained a single continuous layer of cuboidal cells with large spherical nuclei. The stellate reticulum and outer dental epithelium were now considered to collectively make up the developing papillary layer. Labial to this developing papillary layer, the elongated and attenuated squamous cells maintained their sheet-like appearance. The start of enamel secretion marked the beginning

of a distinct predentin-dentin boundary.

(b) Region of outer enamel secretion.

This region occupied a portion of the tooth from the limit of inner enamel secretion incisally to a point where Tomes, processes of outer enamel secretion disappeared. The major change in this region was in the shape and orientation of the interdigitating portion of Tomes' process. These processes became thinner and longer and were inclined at a greater angle towards the apical end of the incisor. The nuclei of the ameloblasts became markedly angled in relation to the dentinoenamel junction so that they were inclined incisally at about 45°. This angulation was more pronounced on the upper than lower incisor. The papillary layer increased in height and regularity. The thickness of the enamel and dentin layers increased progressively.

(3) Maturation Zone.

This was a very long zone which occupied the remaining incisal length of the enamel organ of the tooth. Along the length of this zone the amount of dentin increased continually until the pulp became partially occluded. The odontoblasts continued to form a stratified layer and began to show signs of regression. The thickness of enamel remained constant up to the point where it was lost by decalcification. The enamel matrix at the conclusion of outer enamel secretion was homogeneous in staining. Gradually, rod profiles began to appear and then became distinct in the region of nearly mature enamel [4] and finally faded rapidly in staining intensity and disappeared completely as it became mature enamel.

(a) Region of postsecretory transition.

For a short distance incisally, immediately after outer enamel secretion, the ameloblasts remained tall columnar, but changed their inclination and came to lie perpendicular to the surface of the enamel. The mitochondria remained in the infranuclear zone. At this stage, the stratum intermedium gradually began to lose its organization as a distinct layer. Beyond this short region, the height of the ameloblast decreased rapidly until the cell was about half its former height. Along with this shrinkage, the base of the ameloblast and the cells of the papillary layer contained intracellular dense debris[5]. In addition, cells resembling macrophages were occasionally seen in the papillary layer[6].

(b) Region of maturation proper.

After the region of postsecretory transition, the ameloblasts were modified into cells of early maturation in which changes were evident at the base and apex of the cell. Foamy vacuolization appeared at the apex of the cell and the mitochondria began to migrate towards this region. The nucleus remained basally located, but the base of the cell became irregular. This was caused by the exaggerated basal bulge and by the large intercellular spaces between the bases of adjacent ameloblasts. The papillary layer increased in height and the papillary cells showed large cytoplasm and large spherical nuclei. These cells were not oriented in any particular pattern.

(i) Portions of ameloblasts with striated border.

The ameloblasts which occupied the longest apical-incisal length of the incisor had a prominent apical striated border with heavy concentrations of mitochondria just basal to it. The large oval nuclei of the cells were basally located perpendicular to the enamel surface. The chromatin of the nucleus became coarser and more clumped in the incisal limits of this portion. The basal bulge of the ameloblast was elongated and appeared to extend

finger-like processes towards adjacent papillary cells. Large oval intercellular spaces were found between adjacent ameloblasts at their base. Concentrations of mitochondria were seen in papillary cells lying in relation to the basal projections of the ameloblasts. [7,8]

(ii) Portions of ameloblasts with unmodified apices.

Interposed between ameloblasts with striated borders were two or more portions of ameloblasts with unmodified apices. These cells showed no striated border and were separated by large, irregular intercellular spaces which ran the entire length of the lateral cell membrane except at the base and apex, where the membranes were in apposition. At the base of the cell a small blunt, cone-shaped bulge extended into the underlying papillary layer. Large intercellular darkly stained granules were often seen within these cells.

(c) Region of pigmentation.

More incisally, the ameloblasts lost their striated border and acquired dark granular accumulations, presumably the ferritin-rich pigment, in the supranuclear region approximating the position of the Golgi apparatus. Later in the pigmentation region, large dark granules also appeared in the apical and basal zones as well as in the center of the cell. Gradually, the base of the ameloblast retracted its extensive interdigitation with the papillary layer, and as this happened, the basal intercellular spaces disappeared. The papillary layer remained prominent up to the point where the large dark granules were accumulating in the ameloblasts and it was here that this layer showed the first signs of atrophy.

(d) Region of reduced ameloblasts.

As the ameloblasts decreased in height, the nuclei decreased in size, became spherical and more closely packed. When the cell became cuboidal in shape, the dark staining granules were either replaced by or were transformed into yellowish brown granules which accumulated within the cytoplasm. As the cells flattened, they gradually tipped in an apical direction so that they came to lie almost parallel to the enamel surface. In the papillary layer, large capillaries were the first components to disappear during atrophy. Concomitantly, the layer shrunk in height. In the region of ameloblast modulation the enamel organ consisted of a layer of columnar ameloblasts and a well-developed papillary layer . The ameloblasts were 40 to 60 ,um tall and about 5 ,um in diameter. Their distal surfaces faced enamel, which was lost in the course of demineralization and isolation of the enamel organ except in the apical one third of the region, where remaining matrix proteins were stained to a varying extent.The border between the ameloblasts and the papillary layer was undulated, with the concavities located opposite capillary loops. Everywhere in the region macrophages were seen extending into the intercellular spaces between the ameloblasts. In the ameloblasts, the elliptical nucleus with one or two prominent nucleoli was placed in the proximal half of the cell and occupied one third to one fourth of the total cell length. Giant ameloblasts with several nuclei were regularly observed, especially in the incisal part of the region. In cross sections of such ameloblasts up to 13 nuclei were counted. Incisally from about the middle of the region of ameloblast modulation pigment granules gradually accumulated in the ameloblasts. The granules first appeared supranuclearly in close apposition to the Golgi apparatus. As they increased in number they spread to most of the cytoplasm, even accumulating lateral and proximal to the nucleus. Near the end of the region, the cells could be characterized as moderate or heavily pigmented ameloblasts.

Ruffle-ended ameloblasts (RA)

In areas with ruffle-ended ameloblasts the slender cells exhibited rather even lateral cell surfaces limiting intercellular spaces of varying size. Lateral cell contacts were sparse except in their apical 4-6 pm, where a terminal bar was located and no intercellular spaces could be discerned. Proximally the lateral interameloblast spaces seemed to communicate freely with those of the papillary layer. The apical cytoplasm had a characteristic foamy vacuolization, predominantly toward the cell body; and longitudinal striation could sometimes be seen. In the electron microscope this latter specialization appeared as a ruffled border. Proximal to the ruffled border a heavy concentration of mitochondria was found. Several dark bodies were evenly distributed in the supranuclear region, while a few light bodies of vacuoles were located mainly juxtanuclearly. The infranuclear region was short, and formed a basal bulge or process which extended into the papillary layer. The cytoplasm contained a few dark bodies and a welldefined concentration of mitochondria.

Smooth-ended ameloblasts (SA)

In areas with smooth-ended ameloblasts the lateral cell surfaces were highly irregular giving the cell borders, and sometimes the nucleus, an undulated appearance. This was due to the presence of many cytoplasmic bridges connecting neighbouring ameloblasts. The intercellular spaces, which were very wide, could be followed right up to the distal cell membrane towards the enamel, but were not found at the proximal end, where a terminal bar like structure was seen towards the intercellular spaces of the papillary layer. The infranuclearcytoplasm extended laterally in the region of the terminal bars, thus creating apparently band-like structure. The apical end of the cells was unspecialized, and the mitochondria evenly distributed in the distal half of the cells. In the central lightly stained region a considerable number of light bodies or vacuole was located. The cytoplasmic content of the infranuclear region did not differ from that of the corresponding part of ruffle-ended ameloblasts. Transition between ruffle-ended and smooth-ended ameloblast was rather long - 75 cum to 100 um - and was characterized by a decrease in the height of the ruffled border until it completely disappeared.

Transition between smooth-ended and ruffle-ended ameloblasts.

In contrast this transition was very abrupt. A ruffled border zone was developed within a distance of one or two cells from smooth-ended ameloblasts and the lateral and proximal intercellular spaces communicated again. The apical cell specialization close to the transition border often had a dense appearance, and ameloblasts here were defined as smooth- to ruffle-ended ameloblasts (S-RA). More incisally, in the area of ruffle-ended ameloblasts, the ruffled border zone became open and vacuolized.[9]

FUNCTION

Ameloblasts are cells which secrete the enamel proteins enamelin and amelogenin which will later mineralize to form enamel, the hardest substance in the human body.[10] Ameloblasts control ionic and organic compositions of enamel. It is theorized that a circadian clock probably regulates enamel production on a daily cycle by the ameloblasts. [11,12] Ameloblasts adjust their secretory and resorptive activities to maintain favorable conditions for biomineralization.[13]

PATHOPHYSIOLOGY

These cells are sensitive to their environment. One common example is illustrated by the neonatal line, a pronounced incremental line of Retzius found in the primary teeth and in the larger cusps of the permanent first molars, showing a disruption in enamel production when the person is born.[14]

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