Histology and Function of the Dental Gubernacular Cord

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INTRODUCTION

The term dental lamina has been given to a specialized band of oral epithelium lying on the facing margins of the primary jaws from which the epithelial portions of the teeth develop. The lamina proliferates into the underlying mesenchyme or becomes enfolded by mesenchymal tissue from below and accompanies the upward growth of the alveolar process with the result that it comes to lie lingual to the primary teeth after their eruption. During this period a second epithelial lamina is given off from the primary lamina and results in the formation of a permanent tooth germ. At first, this lies within the same follicle as the deciduous tooth crown. Alveolar bone surrounds both, but does not close over them.

As the root of the primary tooth begins to develop and it starts to erupt, it leaves the permanent tooth germ behind, enclosed within alveolar bone which has developed around and between it and the deciduous tooth. The permanent tooth is still connected to the dental lamina through the strand of cells that resulted in its own formation. This strand of epithelium, like the original dental lamina, is enfolded within collagenous tissue which is connected above with the submucous connective tissue and below with that of the tooth follicle. The cord (gubernacular cord) formed of the two tissues is enclosed by alveolar bone as it develops, so that a canal (gubernacular canal) through the bone results. The canal opens on the surface of the jaw lingual to each primary tooth.

These small holes attracted the attention of anatomists long ago, e.g., Albinus, Fox and Hunter.[1] They demonstrated that the holes led to the tooth germs lying within the bone of the jaws. It has been suggested by Scott[2] that the slicing of tissues for microscopic examination probably caused these minute canals and their contents to be overlooked. Reference to them disappeared from the literature until 1923 when Tomes[3] wrote of the cords, "It is a structure once thought important, but now known to be a mere bundle of fibrous tissue which is called the gubernaculum from the notion entertained by the old anatomists that it is concerned in directing or effecting the eruption of the teeth."

It was the purpose of the present investigation to: 1) confirm the anatomical connections between the dental lamina and the developing tooth; 2) to make a histological study of the structure of the normal gubernacular cord, the relationships among the tissues composing it and their possible functions; and 3) to determine the effect of experimental removal of the cord upon the patency of the gubernacular canal and the eruption of the teeth.

MATERIALS AND METHODS

The lingual alveolar plates of the mandibles of nine commercially bred 8-9-week-old Yorkshire-Hampshire pigs

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were removed by dissection to expose the connections between the remnants of the dental lamina and the developing teeth. Frontal and horizontal histological sections were made of the lower premolar area of three pigs to show the normal histology and relations of the gubernacular cord at early crown stage, bell stage[4]. Three 7-8-week-old mongrel dog littermates were sacrificed to demonstrate the normal histology of the cord at late crown stage, Schour's shell stage.

In order to ascertain the effect of cord obliteration, the gubernacular cords to the lower premolar on one side were surgically removed in three additional dogs with a No. 700 dental bur in a dental handpiece under sodium nembutal anesthesia following reflection of the lingual mucosa. The contralateral side served as the control. The experimental animals were sacrificed after two, six, and twelve weeks and observations were made of the tissues filling the former gubernacular canals. Preliminary observations were also noted regarding the timing and direction of eruption of teeth whose gubernacular cords had been removed.

To assist in locating the former canal in radiographs and in determining the timing and directions of tooth eruption in the absence of the cord, metallic pins were tapped into the gubernacular canals of five dogs after the cord had been removed. These dogs were x-rayed weekly.

Specimens were fixed in ten per cent buffered formalin, decalcified in formic acid sodium citrate solution, embedded in celloidin or paraffin, sectioned at fifteen microns and stained with hematoxylin and eosin.

Findings

Gross Dissection

The gross dissection of the lower jaw in pigs revealed a continuous horizontal collagenous band of connective tissue lying on the surface of the bone of the alveolar crest lingual to the deciduous posterior teeth. It lay on the superior surface of the mandible in the region of the diastema. This was interpreted as the collagenous remnants associated with the original horizontal epithelial dental lamina. It was tightly bound to the periosteum and extended completely around the jaw to end anterior to the mandibular foramen on each side. Extensions from this horizontal band were found at locations where permanent teeth were destined to be formed and each lay in its own individual canal except those for the permanent molars. These occupied a single canal in the ramus. Dissection of the contents of the canal in this region revealed three separate cords for the permanent molars. Each cord to a molar originated from the horizontal lamina anterior to the ramus and ran posteriorly in the common canal in the ramus before turning slightly inferiorly to end at the forming molar. All other gubernacular cords passed more vertically to each respective forming tooth. Thus gross dissection of the gubernacular cord in this study confirms the observations of the early workers.

Histology

During early crown formation the developing permanent teeth were connected to the oral mucous membrane by the gubernacular cords. Histologically, the cord was composed of a centrally placed epithelial lamina surrounded by collagenous connective tissue. The epithelium of the cord extended from the submucosa above the bony canal opening and terminated in the canal above the tooth germ in a cluster of cells which formed an enlargement at its end (Figs. 1 and 2). When viewed in horizontal cross section, the cord epithelium was seen to consist of a ribbon or lamina two or three cells thick and sixty to seventy

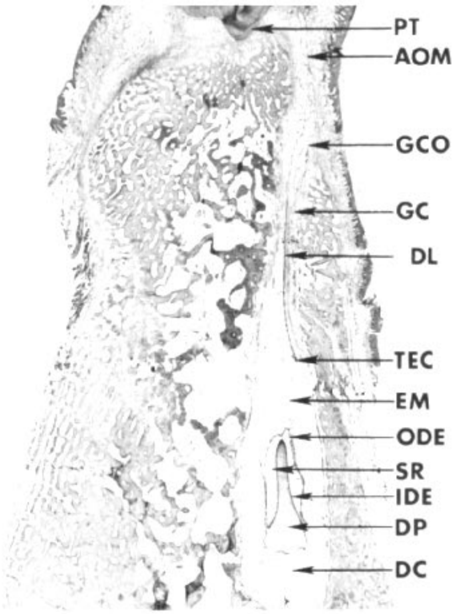

Fig. 1 Frontal section through developing second permanent mandibular premolar tooth in the pig, demonstrating the gubernacular cord at early crown formation. X25

AOM Attached Oral Mucosa
DC Dental Crypt
DP Dental Papilla
EM Epithelial Membrane
GC Gubernacular Canal
GCO Gubernacular Canal Opening
IDE Inner Dental Epithelium
ODE Outer Dental Epithelium
PT Primary Tooth
DL Dental Lamina, epith. of gubernacular cord
SR Stellate Reticulum
TEC Terminal End Cluster

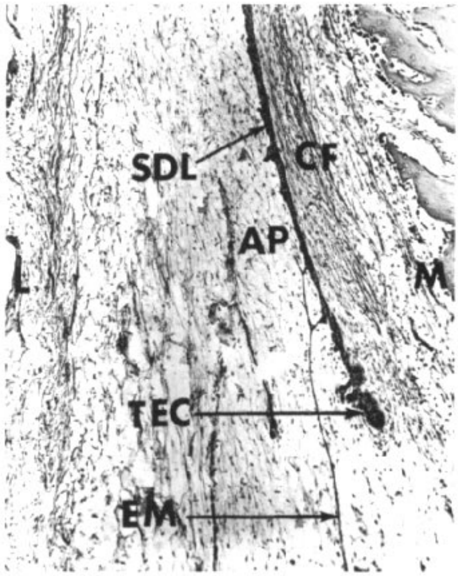

Fig. 2 Frontal section through the second permanent mandibular premolar gubernacular cord in the pig, demonstrating the apex of epithelial cone and the terminal end cluster of epithelial cells of the secondary dental lamina. X85

AP Apex of Membrane Cone
CF Collagen Fibers
EM Epithelial Membrane
M Medial
SDL Secondary Dental Lamina
TEC Terminal End Cluster

cells wide (Fig. 3). Viewed in frontal section, the odontogenic epithelium of each developing tooth was attached to the side of this lamina near its termination by means of a cone-shaped epithelial membrane which was but one cell thick (Figs. 2 and 4). The apex of the cone was attached to the epithelial lamina of the cord and the periphery of the cone's base was attached to the outer dental epithelium of the developing tooth (Fig. 4). The cone was filled with stellate-shaped cells resembling those of the stellate reticulum, but were more densely packed. Small, longitudinally directed blood vessels were also seen in this tissue which resembled primitive enamel pulp.

Connective tissues around the epithelium of the gubernacular cord were continuous superiorly with the subcutaneous connective tissue of the oral mucosa and inferiorly with the connective tissue of the dental sac surrounding the developing tooth. In the area of the cord these connective tissues were organized into an inner and an outer layer (Figs. 3 and 5). The inner layer was immediately adjacent to the epithelial lamina while the outer layer was adjacent to the bony wall of the gubernacular canal. Collagen fibers of the inner layer exhibited greater organ-

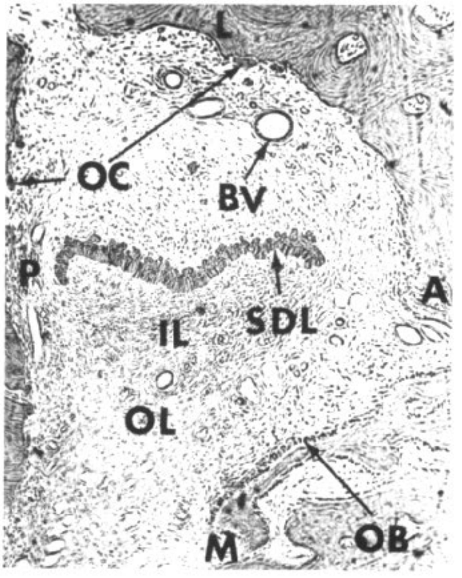

Fig. 3 Horizontal section through the second permanent mandibular premolar gubernacular cord in the pig, demonstrating epithelium and associated connective tissue. X85

A Anterior
BV Blood Vessels
IL Inner Layer
L Lateral
M Medial
OB Osteoblasts
OC Osteoclasts
OL Outer Layer
P Posterior
SDL Secondary Dental Lamina, the epithelial lamina of the gubernacular cord.

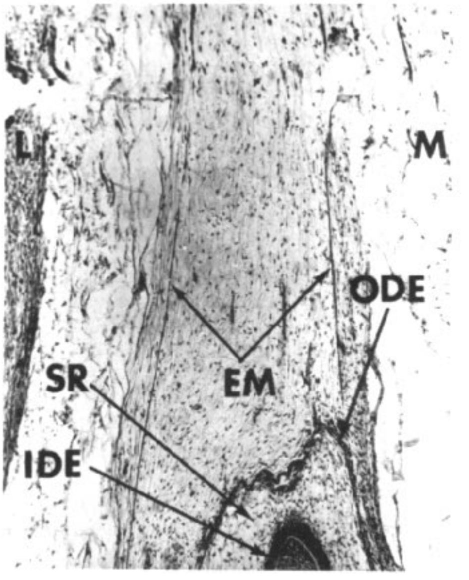

Fig. 4 Frontal section through the second permanent mandibular premolar gubernacular cord in the pig, demonstrating the epithelial membrane cone. X85

EM Epithelial Membrane
IDE Inner Dental Epithelium
L Lateral
M Medial
ODE Outer Dental Epithelium
SR Stellate Reticulum

ization and, in general, ran parallel to the long axis of the epithelial lamina. They were of greater density on the medial aspect of the lamina than on the lateral. Only small capillaries were found in the inner layer. In the outer layer the density of collagen fibers was reduced and the collagen fiber orientation was less organized.

The collagen fibers of the connective tissue adjacent to the epithelial membrane were oriented parallel to the epithelium (Fig. 4). They were more densely packed nearer the epithelium than in the outer layer of the connective tissue near the bone. This collagen aggregation and orientation was similar to that observed around the gubernacular cord epithelium and like that ordinarily seen in the connective tissue of the dental sac.

Throughout the length of the posterolateral aspect of the bony gubernacular canal, many osteoclasts were seen while many osteoblasts were observed along the entire extent of its anteromedial aspect (Figs. 3 and 5). Several larger arteries and veins were observed running parallel to the long axis of the gubernacular canal in the outer layer of connective tissue. The distribution of osteoclasts and osteoblasts along the bony border of the tooth crypt was similar to that observed in the gubernacular canal, i.e., osteoclasts were ob-

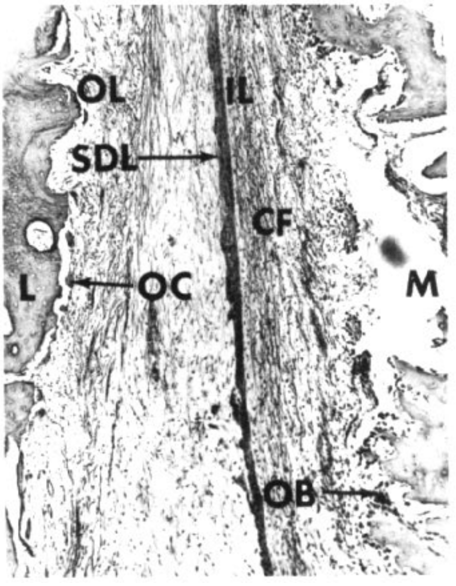

Fig. 5 Frontal section through the second permanent mandibular premolar gubernacular cord in the pig, demonstrating osteoblasts, osteoclasts, and connective tissue organization around the secondary dental lamina. X85

CF Collagen Fibers
IL Inner Layer
L Lateral
M Medial
OB Osteoblasts
OC Osteoclasts
OL Outer Layer
SDL Secondary Dental Lamina, epith. lamina of gubernacular cord.

served along the posterolateral border while osteoblasts lined the anteromedial border. Spicules of bone opposite the apex of the tooth revealed osteoclasts along their superior surfaces and osteoblasts lining their inferior surfaces.

At the late crown formation stage both coronal enamel and dentin were being formed. Functional ameloblasts were found at the enamel surface, even at the cusp tip, and odontoblasts lined the pulp surface of the dentin. Root formation was just starting, and there was some evidence of bone resorption at the border of the crypt above the tooth. However, the epithelium of the gubernacular cord had become fenestrated, and its cells were dispersed in the connective tissue of the cord as centrally located clusters reminiscent of the epithelial rests of Malassez in the periodontal ligament. The clusters were one to three cell layers thick and were found scattered along the length of the cord.

With the fenestration of the epithelium the connective tissue surrounding the disintegrating lamina exhibited an altered collagen fiber arrangement from that observed at the stage of early crown formation. Collagenous fibers near the epithelial remnants were more loosely arranged and no longer as definitely oriented in the direction of the long axis of the canal. The fibers on the lingual side remained densely packed and oriented in the long axis of the gubernacular cord. Osteoblasts lined the medial aspect of only the upper portion of the gubernacular canal while a few osteoclasts were found along its lateral aspect, especially in the inferior portions of the gubernacular canal and near the tip of the tooth cusp. Neither osteoblasts nor osteoclasts were observed at the sides of the crypt at the level of the developing tooth.

Microscopic examination of serial sections of healed jaws after the removal of the gubernacular cord showed no identifiable epithelial cells remaining in the former canal area. The canal was completely occluded by the formation of cancellous bone except at its former orifice near the oral mucosa where a small amount of connective tissue remained (Fig. 6). When comparing the areas of new bone formation in the former canal with the bone adjacent to the canal in the control, it was found that, at this stage of healing, there were more intertrabecular spaces filled with connective tissue and smaller trabeculae where the gubernacular cord had been removed. Osteoblasts lined all of the trabecular spaces, however, indicating the formation of new bone. The cancellous bone which filled the lower third of the gubernacular canal was more dense than the new bone in the remainder of the canal and was comparable to the denser lamellated bone of the adjacent tooth crypt.

Preliminary observations of radiographs indicated that, despite the occlusion of the canal, the teeth had moved in active eruption although at a slower rate and in an altered course so that they erupted medial (lingual) to their usual position. Serial sections of several specimens indicated that the erupting tooth was not in contact with the metal pin which had been inserted into the canal in some of the cases. It is not known whether the teeth ever had been in contact with the pins. Further experimentation without the use of pins, which may have deflected the erupting tooth, may help to clarify the degree of eruptive retardation and the manner in which its course was altered.

Fig. 6 Frontal section through the developing second permanent mandibular premolar tooth in the dog, demonstrating the occlusion of the canal with bone. X25

Discussion

The site of development of a given tooth depends, in large part, upon the genetic patterns of growth inherent in the epithelium of the dental lamina. The dental lamina is established around the jaw from one side to the other, possibly under the inductive influence of neural crest mesenchyme which has migrated into the jaw[5]. It contains, in the human, ten secondary areas which will develop extensions forming the enamel organs of the primary teeth.[4,6]

The position and growth of the original horizontal lamina would seem to position these teeth anteroposteriorly. Whether additional growth of the lamina occurs between areas of tooth initiation is not known. The actual position within the jaw would also depend upon the direction and amount of growth in the extensions of the lamina to the primary teeth and in the lamina of the gubernacular cords to the permanent teeth. These extensions would position the developmental sites of the primary teeth in the mesenchyme which occupies the bony trough of the jaw. Subsequent laminar extensions from the lingual side of the developing lamina of the primary tooth determine the sites of permanent tooth development.

It is not certain whether the developing permanent tooth, which becomes enclosed by bone except for the gubernacular cord, changes its position vertically within the jaw during its development prior to eruption or whether the upward growth of surrounding tissues is responsible for a changed relationship with the oral mucosa. Orban's view[7] was that the developing tooth does not sink deeper into the jaw, but rather that the growth in height of the alveolar process above the tooth produces that illusion. Serial x-ray measurements between tooth points and the lower border of the mandible support this view.[8]

With respect to the horizontal plane, it has been suggested that the developing tooth migrates through the bone prior to active eruption. Sicher[6,9] has stated that the maxillary teeth begin their development in a relatively small area below the orbit and that individual teeth move prior to active eruption anteriorly, laterally, and/or posteriorly with the growth of the jaws. Brash,[10] using madder-fed pigs, demonstrated what he interpreted to be a migration of the tooth germ during growth and development. The histological evidence for migration of the developing tooth itself in the present study, in addition to clear evidence that the gubernacular cord to the developing tooth was changing position, suggests this view. Resorption on one side of the canal and crypt with apposition of the opposite side of each indicated movement of the cord and developing tooth in a posterolateral direction at least during the functional stage of the cord and before its fenestration. With demonstrable movement of the cord and also the developing tooth itself, one may suggest that the movement of the cord and tooth may be due to the changed position of the mucosal-periosteal attachment during growth, perhaps through growth of the alveolar process.

Scott[11] suggested that "each tooth is related to a definite region of the growing mouth cavity in virtue of the attachment of the follicle to the oral mucous membrane either directly or through a gubernacular cord". He also found the upper end of the cord tightly adherent to the mucoperiosteum and suggested that this attachment moves with the growth of the jaws resulting in migration of the developing tooth in the direction of growth. Symons and Scott[12] have made similar suggestions.

The tooth erupts through the gubernacular canal which has been shown in this study to be maintained patent by the presence of the cord.[1,2,13,14,15,16] Therefore, the direction of the canal would seem to be an important factor in the direction of eruption and thus in the placement of the tooth in the mouth.

It should be noted that, from initiation through active eruption, the developing tooth is surrounded by connective tissue of the dental sac. This connective tissue is continuous with that surrounding the epithelium of the gubernacular cord, and the collagen in both the crypt and around the cord appears to be under the organizational influence of the epithelium.

Disintegration of the lamina of the gubernacular cord and loss of the connective tissue organization around it just before active eruption of the tooth would argue against the cord having an active part in the eruption process. Removal of the cord did not prevent eruption and therefore the eruptive process, *per se*, does not appear to reside in the gubernacular cord, or at least in its epithelial component.

Summary and Conclusions

1. Dissections of pig jaws in this study confirmed previous observations that gubernacular cords connect developing unerupted teeth with the oral mucosa and alveolar crest.
2. Histological examination of sections of the cord at the early crown stage showed a central strand of epithelium surrounded by connective tissue resembling that of the primitive den-

tal sac. A cone-shaped epithelial membrane was found to be the actual connection between the epithelium of the cord and that of the developing tooth.

Connective tissue collagen was seen concentrated near both the epithelium of the cord and the epithelial membrane and running in the long axis of the cord. When, in later development, the epithelium of the cord became fenestrated, the collagen aggregation and orientation was lost.

3. When the gubernacular cord was surgically removed, the canal filled with bone. This suggested that the cord and possibly the epithelium alone was responsible for the maintenance of the bony gubernacular canal.
4. Since removal of the gubernacular cord did not prevent eruptive movement of the tooth, the essential mechanism of tooth eruption does not appear to reside in the cord, or at least in its epithelial constituents. It does, however, seem to function in maintaining the patency of the canal through which the tooth erupts. Evidence of osteoclastic and osteoblastic activity along the posterolateral and anteromedial sides, respectively, of the gubernacular canal and the bony crypt suggests that the cord also functions to maintain the spatial relation between the developing tooth and the jaw as the jaw grows backward and laterally.

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