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Evolution and Development of the Supporting Structures of Teeth

Authors:

1. Dr. Dhirendra Singh, Professor**,** Department of Periodontics & Oral Implantology, Kalinga Institute of Dental Sciences, KIIT Deemed to be University, Bhubaneswar

2. Dr. Subhalaxmi, PGT, Department of Periodontics & Oral Implantology, Kalinga Institute of Dental Sciences, KIIT Deemed to be University, Bhubaneswar.

3. Dr. Md. Jalaluddin, Professor**,** Department of Periodontics & Oral Implantology, Kalinga Institute of Dental Sciences, KIIT Deemed to be University, Bhubaneswar

Corresponding Author:

Dr. Dhirendra Kumar Singh, Professor**,** Department of Periodontics & Oral Implantology, Kalinga Institute of Dental Sciences, KIIT Deemed to be University, Bhubaneswar.

Mobile No. 8895910320

Email ID: dr.dhirendra27@gmail.com

Abstract:

The supporting structures of teeth are collectively called "periodontium" and can be defined as tissues supporting and investing the tooth, consist of the tooth's root cementum, periodontal ligament, alveolar bone, and gingiva. The widespread occurrence of periodontal diseases and the realization that lost tissues can be repaired and, perhaps, regenerated has generated considerable interest in the factors and cells regulating their formation and maintenance. It is important to understand that each of the periodontal components has its very specialized structure and that these structural characteristics directly define function. Indeed, proper functioning of the periodontium is only achieved through structural integrity and interaction between its components. The present review paper is an initiative to collect comprehensive knowledge on the development of the periodontium and its other supporting structures which will help students and researchers of periodontology in understanding the topic.

Key Words: Periodontium, Gingiva, Periodontal ligament, Alveolar bone, Cementum

INTRODUCTION:

Evolution: It is defined as a developmental process in which an organ or organism becomes more and more complex by differentiation of its parts.[1]

Periodontium is a CT organ covered by epithelium that attaches teeth to bone of jaws and provides continually adapting apparatus for support of teeth during function [2]. It consists of 2 mineralized tissues and 2 fibrous tissues.

The socketed attachment of teeth is one of the most important modifications that took place around 200 million years ago when the earliest mammals were evolving from their reptilian predecessors. This method of attachment also occurred in primitive birds which evolved from reptilian ancestors. Present-day reptilian members of crocodile order demonstrate Thecodont gomphosis which differs in many aspects from mammalian gomphosis[3].

The evolution of mammalian periodontium is based on changing and developing the relationship between tooth and bone of the jaw or more specifically between dentin and bone.

Primitive bone and dentin were both present in the earliest vertebrates, Archodus and Palaeodus from the early Ordovician of Russia 400 million years ago. Although the primitive form of bone was present these earliest vertebrates were jawless and it seems that primitive tooth-like structures preceded jaws in development. An early example of the combination of jaws and teeth is to be found in Acanthodil which are members of Gnathostomata.

I. TYPES OF VERTEBRATE TOOTH ATTACHMENT

A. FIBROUS ATTACHMENT

Seen in sharks, rays, skate, and other members of Elasmobranch class. In this method of attachment, teeth are attached to the skeleton by a union of their basal portions with fibrous tissue covering the cartilaginous jaws. The teeth are composed of tubular dentin with a thin covering layer of vitro dentin. At their base, they have a mass of irregular calcified tissue in which are embedded fibers from the fibrous layers covering the jaws. This basal portion is a continuation of tubular dentin but contains few tubules. The odontoblast layer is continuous on its inner aspect. Teeth erupt from an area of development on the inner aspect of each jaw known as thecal fold [4]. Several dentitions develop successively within the thecal fold. The eruption occurs by the gradual movement of fibrous tissue to which the teeth are attached. So teeth develop on the inner aspect of each jaw and are brought to the functional position at each jaw margin.

Cartilage was believed to be a more primitive tissue than bone. It was thought that the presence of cartilaginous skeleton in the present-day Elasmobranchii was an example of retention of a more primitive type of skeleton by these fish.

B. ANKYLOSIS

In the earliest vertebrates, a calcified union existed between tubercles of primitive dentin and bone of the underlying skeleton. A similar form of rigid attachment is seen in most fish, amphibians, and reptiles. This type of attachment is known as ankylosis. In some, a layer of fibrous tissue intervenes e.g. Python. Her tubules of orthodontic mingle with layers of bone of attachment, which in turn are directly linked by calcification to the bone of the jaw. The weaker part of this attachment lies between the bone of attachment and the jawbone. Accidental loss of tooth results in a saucer-shaped depression on margins of the jawbone where the bone of attachment existed. A succession of teeth erupt. Consequently, the bony attachment must be formed at the base of each tooth. This type of calcified ankylosis is found in many members of Teleostei where an outer row of ankylosed teeth surrounds the inner row of hinged teeth.

Acrodont ankylosis is a term used to describe the position of a tooth that is perched on top of the bone to which it is attached [5]. This is seen in Eel and some amphibians. The tooth is attached by its base to a small cylindrical pedicel of bone which is in turn attached by calcification to the bone of the jaw.

In Haddock inner surface of the bone of attachment is recessed to take a projection from the base of the tooth, which is therefore half perched upon and half situated within the bone of attachment.

In pleurodont ankylosis lower part of each tooth is situated entirely within the cylindrical bone of attachment e.g. Mackerel.[6]

The fibrous tissue between the tooth and pedicel appears to be an uncalcified dentin matrix.

C. HINGED ATTACHMENT

An uncalcified fibrous hinge is seen between tooth and bone of attachment.[7]

In the Angler it is in the form of a simple strip of fibrous tissue extending from the distal surface of the tooth to the bone of attachment. In the Pike, the posterior fibrous hinge is supplemented by a more centrally placed uncalcified trabeculae of osteopontin.

The Hake posterior part of the hinge consists of a combination of uncalcified dentin and fibrous tissue.

Hinged attachment is an adaptive modification which along with the recurved form of tooth greatly assists the swallowing of a slippery prey in these animals.

D. GOMPHOSIS

Gomphosis is the only form of tooth attachment present in mammals.[8] Great variations exist in the size and position of the socket but the suspensory function of PDL where biting or masticatory forces are transmitted to the bony walls of the socket is a common factor in every case.

The socketed attachment has been described in some fish. In reptiles members of the crocodilian exhibit a form of socketed attachment of their polyphyodont dentitions. In this case remodeling of the bone of the socket does not take place to suit each successional tooth. The sockets once formed persist and as each successional tooth erupts it is attached by fibrous tissue to the walls of the socket.

Miller (1967) observed that in reptiles a channel is formed by the outer and inner plates of bone in each jaw within which the polyphyodont dentition developed. Subdivision of this channel to form individual sockets started near the front of each jaw and progressed backward but in the most posterior part of each jaw, the groove remained undivided.

The bone lining of each socket did not show evidence of additional layers of bone to attach fibers that support the tooth in the socket nor was it adapted closely to the root of the tooth. But the proliferation of cementum reduced the space between the cylindrical tooth and tubular socket.

In the posterior part of the jaw where individual sockets were not present apposition of cementum produced roots that were oblong in crosssection as they lay within the groove formed by outer and inner plates of bone. This specialized attachment is known as Thecodont gomphosis

There are different ideas concerning the evolution of the attachment apparatus.

Teeth were originally firmly attached to the jaw bone by an underlying area of bone known as bone of attachment.

The fibrous membrane which developed between the tooth and bone of attachment is regarded as the earliest development of periodontal ligament, the bone of attachment later developing into the alveolar process.

The different relationships between teeth and bone of attachment as seen in Haddock and Mackerel are believed to represent the process whereby tooth gradually developed a root portion, which remained within the bone of attachment. Further differentiation of crown from root portion was accompanied by a redistribution of dental tissues. The development of a dental follicle or sac around the tooth germ and the appearance of cementum are believed to be transitional stages between pleurodont ankylosis and gomphosis in the course of evolution of this higher method of attachment.

Hinged attachment is not regarded as occupying any place in the sequence of changes leading to Gomphosis. It is regarded as a specialized form of ankylosis to suit a particular need in fish.

Hertwig (1874 and 1879) believed that bone of attachment is homologous with the cementum. Periodontal membrane developed as a fibrous ligament between the bone of attachment and basal bone and the fibrous membrane observed between the bone of attachment and tooth in the ankylosed and hinged teeth of fish disappeared later.

II. EVOLUTION OF THE TISSUES OF TOOTH ATTACHMENT

A. BONES OF THE JAWS

1. Bone is the principal component of the skeleton in most vertebrates. In the earlier forms bones formed protective outer covering (exoskeleton). Later bones formed rigid central supports for the limbs and internal organs (endoskeleton). The bones of the jaws and vault of the cranium are derived from the exoskeleton.

2. Bone is regarded as a primitive tissue associated with the withdrawn of vertebrate history (Romer, 1964).[9] Small fragments of dental calcification have been identified as belonging to fossil vertebrates from the early Ordovician geological strata in Russia. Histological investigation of these calcified fragments of exoskeleton showed a coarse-fibered type of bone without any osteocyte lacunae. This is called spin**.** True bone appears in the fossil record 50 million years later. This bone was mainly developed within the exoskeleton. In laser fossils, cancellated endochondral bone and calcified cartilage made their appearance. The internal cartilaginous skeleton was gradually replaced by bone, there was a concomitant reduction in the exoskeleton.

Tarlo (1964) concluded that bone initially functioned as a storehouse of phosphates. Later it fulfilled a protective function and finally succeeded to the mechanical role of a supporting skeletal framework.

3. **Contribution of Cartilage**

The earliest occurrence of bone precedes that of cartilage in the fossil record. Romer (1942) and Tarlo (1964) insist that bone has evolved separately from cartilage. Romero assumed that cartilage as a biologic adaptation accomplishes the embryonic development of an internal skeleton. He does not consider the persistence of cartilage in the embryonic stage of development as evidence of an earlier stage in evolution.

4. **History of Development**

Currey (1962) found dinosaur bone has more physiological specialization than living reptiles and it was similar in structure to that of recent mammals. Modeling resorption was observed in one species. Many of these modifications later disappeared from reptiles but some formed basis for further development among the Mammalia.

B. THE EVOLUTION OF DENTIN

1. Dentin is the most superficial of the calcified mesodermal tissues and was in the earliest stages of its evolution, always related to the exoskeleton. [10]

2. **Earliest appearance**

Tubular dentin evolved as the outer layer of the carapace of the earliest vertebrates over 400 million years ago. The tubular appearance of the earliest dentin is similar to tubular orthodentin of the present day.

3. **Varieties of Dentin**

Tubular orthodentin is the most primitive type of dentin to be found. Osteodentin and vasodentin are modifications resulting from alteration in dentin forming mesoderm.

Plicidentin is a complex infolding of walls of a single central pulp cavity. The dentin is identical in structure to tubular orthodentin.[11]

4. **History of development**

Extensive modification of dentin tubercles upon the surface layer of fragmented carapace led to the appearance of teeth.

C. DENTAL FOLLICLE

1. The developmental origins of PDL are closely associated with the earliest appearance of dental follicles.

The existence of follicle and PDL provides protection against harmful forces, which is lacking in teeth attached by a calcified form of ankylosis.

2. **Earliest appearance**

The earliest appearance of a follicle in present-day vertebrates is difficult to determine.

3. **History of Development**

It is believed that bone of attachment in fish having teeth with hinged attachment is developed from mesodermal tissue at the base of the dental papilla. The mesodermal tissue is stimulated to differentiate by the enamel organ.

The principal difference between the calcified tissue at the base of ankylosed teeth hinge attachment in bony fish and the cementum surrounding the roots of gomphosed teeth is one of the arrangements.

The dental follicle is formed by spreading upwards of the tissue from the base of the dental papilla.

D. EVOLUTION OF CEMENTUM

1. Cementum is the least specialized of the calcified tooth tissues. It is an integral part of the attached apparatus in the gomphosed teeth.
2. **Earliest appearance**

Cementum is present throughout the mammalian

Although normally present on the roots of teeth, it is also found on the crown of the teeth of persistent growth and continuous eruption e.g. Horse and other ungulates.

An herbivore's teeth of semipersistent growth, cover the enamel of the crown and so provides attachment for fibers of PDL since the roots of these teeth do not make their appearance until a much later stage in tooth development.

3. **Variation**

Cellular and Acellular forms of cementum occur in most species of Mammalia. The type of cementum formed may be related to that some surfaces of the root exposed to tension while others are exposed to pressure during function. Cellular cementum is deposited when a greater bulk of cementum is required to be formed rapidly.

4. **History of Development**

A distinct layer of cementum cannot be observed in those teeth attached by ankylosis. Cementum made its appearance with the advent of PDL to the outer calcified surface of dentin.

E. EVOLUTION OF ALVEOLAR BONE

1. Alveolar bone first appears around developing tooth germs to form the protective crypts [12]. During teeth eruption, crypts are modified to form sockets or alveoli. Alveolar bone is indistinguishable from basal bone histologically and biochemically.

2. **Earliest appearance**

Alveolar bone is present in very few fish and it is a prominent part in the jaws of reptilian particularly in members of crocodilian. Because of its a vascularity, it is not vital and so resorption does not occur with loss of teeth and regeneration does not occur with the eruption of the successor.

3. **Variations**

In carnivore and insectivore because of the stationary position of teeth, do not require adaption of alveolar bone.

In the Rodents and Herbivora active eruption occurs throughout the life of the tooth. It is accomplished by continuous activity of alveolar bone. This is particularly seen in the case of molars of elephants.

When alveolar bone develops entirely out with basal bone a thin balloon-like structure known as the Alveolar bulb develops e.g.: Maxillary molars in a Pig. Bone surrounding sockets is very thick in canine tusks of wild Boar and warthog.

Baume (1956, 1961) proposed tooth and investing bone form a “developmental entity”, Thomas (1934) insisted that tooth and alveolar bone were distinct developmentally but he believed that the presence of teeth influences the growth of bone.

4. **History of development**

Many similarities exist between mammalian alveolar bone and bone of attachment of ankylosed or hinged teeth in fish, amphibians, and reptiles. The labial plate of alveolar bone is first to develop and Jacob Hagen (1965) used the term “labial pleurodontism” for this.

F. EVOLUTION OF PERIODONTAL LIGAMENT

Alveolar bone is closely adapted to the root surface but everywhere it is separated from it by a layer of CT containing BV, nerves, and lymphatics [13]. If fibers separate then it can be referred to as membrane but the majority of fibers are connecting the two surfaces. So more correctly it is rendered as ligament (separating 2 surfaces is the function of a membrane).

The first function of PDL is attaching the tooth to the alveolus. The second function is receiving and transmitting forces of mastication.

2. Earliest appearance

PDL is present throughout the mammalian and occurs in a simpler form in those fish and reptiles, which have gomphosed teeth.

The presence of a fibrous ligament between the base of tooth and bone of attachment in certain ankylosed teeth like Eel is cited as an early example of PDL.

3. Variations

PDL varies widely from species to species with degrees of active eruption during the functional period. The distribution and orientation of periodontal fibers are not uniform. The most prominent variation is seen in the ligament of continuously growing teeth such as rodent incisors. Continuous changes in PDL take place in the intermediate plexus to accommodate the continuous growth and eruption.

4. History of Development

Attachment of teeth by gomphosis is said to be evolved 120 million years before the appearance of the earliest mammals. Many Jurassic birds which lived 85 million years before mammals appeared possessed gomphosed dentitions.

III. PROCESSES ASSOCIATED WITH EVOLUTION OF MAMMALIAN PERIODONTUM

A. ROOT DEVELOPMENT

In the more primitive forms of tooth attachment, the teeth were simply attached by their basal surfaces to the underlying tissues. Bone gradually developed around the base of the tooth. This process continued until there was sufficient bone for attachment of the tooth.

A key element in the evolution of a root is the epithelial root sheath of Hertwig, which determines the surface contour of root dentin. The root portions of the earliest gomphosed teeth were simply cylindrical extensions of the crown portion. There was no narrowing of root at apical foramen and it was a funnel-shaped apex. It is seen in the thecodont gomphosis. Later tapered roots and divided roots were developed.

The anchorage of a tooth whose root is other than a simple continuation of the wider part of the crown implies a more advanced type of attachment than Thecodont gomphosis.

B. ERUPTION

The earliest teeth and placoid scales developed on or just below the epithelium. So no great movement is required for them to reach a functional position.

In elasmobranches, eruption involves movement across a surface to a position of optimal function i.e. movement over the surface of the jaw to a position on the margin.

In the case of hinged and ankylosed teeth of bony fish, development starts below the surface. Eruption proceeds as the tooth lengthens. The teeth of polyphyodont dentition of reptiles erupt from infra-bony crypts into the sockets of their predecessors.

Dental lamina which is present lingual to each developing tooth first moves on the buccal direction to line up with the long axis of the preformed socket, on part of its successor.

In most mammals, pre-functional and functional eruptions are seen. The functional eruption is great in rodent incisor because of its continued growth. It is of sight importance in dentition particularly when attrition is severe.

Ankylosed teeth were stationary in their functional position and it is uncertain whether the earliest gomphosed teeth in reptiles were also stationary or were constantly erupting. Therefore, the eruption is of great importance when considering the evolution of mammalian periodontium.

C. ROOT RESORPTION

Resorption of unwanted tooth substance is observed in bony fish and crocodilians. Shedding of teeth from a polyphyodont dentition is possible by resorption of earlier dentition so that the succeeding tooth can erupt.

D. BONE RECONSTRUCTION

In Crocodilians, teeth are simple and uniform. There is no extensive bone reconstruction. So greater demands are placed upon the fibrous attaching tissue and so it is not an effective mechanism. In mammals, bone reconstruction permits the development of the diversity of sizes, shapes, and multirooted teeth. Bone formation coupled with modeling resorption is the sensitive mechanism that permitted the evolution of well-organized PDL.

E. OCCLUSION

The dentitions in opposing jaws of Fish, Amphibia, and Reptiles do not usually occlude. They fit in with each other or interdigitate. Occlusion is associated with the evolution of mammalian periodontium and more complex temporomandibular articulation.

F. MASTICATION

Crushing fish shells may be regarded as a simple form of mastication. Dentitions of fish, Amphibians, and Reptiles which are recurved and hinged teeth assist in swallowing.

The preparation of food for digestion by mammalian dentition is because of the evolution of occlusion and attachment by gomphosis.

Periodontium exerts a cushioning effect to prevent accidental fracture of calcified dental tissues. It also has proprioceptive innervation and so prevents exertion of excessive forces by masticatory musculature.

DEVELOPMENT OF PERIODONTIUM:

The majority of periodontal tissues develop along with the formation of roots of teeth and teeth eruption. They have an origin from dental follicles derived from the neural crest.

A. DEVELOPMENT OF DENTAL FOLLICLE

Numerous studies were focused on the earliest stages of tooth bud development with emphasis on the interaction between enamel organs and dental papilla. Less attention is given to the role of gene activation and growth factor regulation in the development of periodontium.

Following the development of neural tube invagination of overlying ectoderm neural crest cells migrate from the neural tube to invade developing branchial arches. In exciting from neural tube neural crest cells lose their epitheloid nature and assume a mesenchymal phenotype capable of directed cell migration. In organ cultures of developing dental arches, it is proved that neural crest cells formed dental ectomesenchyme.

Failure of migration of neural crest mesenchymal cells to appropriate sites during development may lead to anodontia, micrognathia, etc. Neutral crest ectomesenchymal cells interact with early oral epithelium to form tooth primordial. Subsets of cranial neural crest cells give rise to chondrocytes, osteoblasts, PDL fibroblasts, cementoblasts, and odontoblasts.

The dental papilla and dental follicle, the non-ectodermal components of tooth buds are formed by the concentration of neural crest ectomesenchymal cells. Schroeder, Moxham, and Grant described the development, histology, and fate of dental follicles in forming the tissues of the periodontium. It has been suggested that the interaction between cell surface syndecan and tenascin, an extracellular matrix adhesion molecule reduces migration and promotes aggregation of ectomesenchymal cells to form the dental papilla and dental follicle.

Dental papilla gives rise to odontoblasts and pulp while dental follicle gives rise to cementum, PDL, and alveolar bone. Anatomically dental follicle consists of dental follicle proper, a well-defined band of cells juxtaposed to the dental papilla and the convex outer surface of the enamel organ and perifollicular mesenchyme, a loosely defined population of cells bordering the developing bony trabeculae surrounding the tooth bud [14]. A poorly populated zone of loose CT separates these layers.

The developmental potential of dental follicles was studied in numerous tooth transplantation experiments.

Hoffman demonstrated that cementum and PDL originated from transplanted tooth buds but he was less certain about the origin of surrounding bone[15]. He speculated that bone cells might be induced in host cells by the epithelial components of tooth bud. Tencate et al studied the fate of transplanted tooth buds labeled with tritiated thymidine. Cementoblasts and PDL fibroblasts in developing tooth were clearly labeled indicating their origin from the transplanted tooth bud. Since osteoblasts were only weakly labeled their origin was less certain.

When tooth buds are transplanted to sites that are unable to form mineralized tissue like the anterior chamber of the eye, root formation with cementum and alveolar bone formation were noted. These studies concluded that tooth bud developed as a biological unit capable of giving rise to all components of the mature tooth.

Yoshikawa and Kollar demonstrated that dental papilla and dental follicle had similar developmental potentials and could be substituted for one another on reconstituting a fully developed tooth. Migrating fibroblasts from perifollicular mesenchyme may proliferate and contribute to the pool of PDL fibroblasts. Mesenchyme and perivascular cells may also give rise to osteoblasts of alveolar bone.

B. DEVELOPMENT OF PERIODONTAL LIGAMENT

The development of PDL begins with root formation before tooth eruption. The continuous proliferation of inner and outer enamel epithelial forms the cervical loop of the tooth bud. This sheath of epithelial cells grows apically to form Hertwig epithelial root sheath between the dental papilla and dental follicle. Hertwig sheath separates dental papilla from dental follicle cells at this stage. Dental follicle cells located between the alveolar bone and Hertwig’s root sheath consist of 2 populations of cells: dental follicle proper cells which form a continuous intact surface all along with the outer sheath cells and the 2nd group of perifollicular mesenchyme cells which are stellate shaped and randomly oriented. Cementoblasts originate primarily from the cells of the dental follicle proper.

Perifollicular mesenchyme cells contain short collagen fibers located close to the cell's surface. As root formation continues they gain polarity, increased cellular volume, and synthetic activity. They become elongate and contain rougher ER, mitochondria, and active Golgi complex. They actively synthesize and deposit collagen fibrils and glycoproteins in the developing PDL.

The developing PDL, as well as mature PDL, contains undifferentiated stem cells that retain the potential to differentiate into osteoblasts, cementoblasts, and fibroblasts.

Stemcells occupy perivascular sites in the PDL and adjacent endosteal spaces, whether or not osteoblasts, cementoblasts, and fibroblasts originate from a common ancestor or a specific line of progenitor cells remains to be clarified.

There are some concepts concerned with stem cells from which fibroblasts, osteoblasts, cementoblasts, and osteoclasts are derived.

1. Fibroblasts: Two theories concerning their origin have been advanced. The first is that they originate from emigrating blood-borne cells and the second that they arise locally from cells in CT particularly those associated with blood vessels.
2. Osteoblasts and cementoblasts: are derived from undifferentiated CT cells / undifferentiated mesenchymal cells. The undifferentiated cells synthesize DNA and undergo mitosis after which some of the daughter cells differentiate (osteoprogenitor cells) into osteoblasts.
3. Osteoclasts and Cementoclasts: they are formed by the fusion of mononucleated cells. Undifferentiated cells are precursors of osteoclasts. Scott claims that osteoblasts and osteoclasts are derived from different morphologically distinct perivascular cells.

Cellular components: Fibroblasts are the most abundant cells in PDL and are responsible for the metabolism of extracellular matrix components. PDL is known to have a heterogeneous population of fibroblasts. A subpopulation of osteoblast-like fibroblasts rich in alkaline phosphatase has been identified in PDL. These cells can give to bone cells and cementoblasts.

i) COLLAGEN FIBER FORMATION

The development of major collagen bundles, the principal fibers of PDL is closely correlated to root formation. The formation of ligament fibers does not differ from fiber formation in other CTs.

Collagen fibers are composed largely of the unique protein collagen. The collagen macromolecules are assembled to form fibrils. The diameter of fibrils increases with age. Collagen fibrils are gathered together in bundles. They are called fibers. The fibers are gathered to form bundles.

Fibroblast arrangement depends on the development of stress in the environment.[16.] Fiber bundles originate at the surface of newly formed root dentin in close relation to elongated and highly polarized fibroblasts. These nascent fiber bundles or fringe fibers are tightly packed by the action of cementoblasts during the initial development of acellular cementum. During tooth eruption PDL matures, the fringe fibers merge across the width of the ligament to form principal fiber bundles. In the middle of the PDL collagen fiber bundles are less tightly packed.

Majority of principle fibers course in coronal direction from the cementum to the bone-forming oblique fiber group. The causative factors bringing oblique orientation of principal fibers are still not clear. Oblique orientation is attributed to axial load bone by functional tooth (Bhaskar and Brodie) and the resistance of overlying tissues as the tooth erupts (Orban). Thomas assumed it is concomitant with the onset of tooth eruption. There is general agreement that the appearance of fibers oriented in an oblique direction first occurs in the region of CEJ probably at the onset of tooth eruption and progresses apically.

There is very little information on the development of other fiber groups. Ordinarily complete organization of fiber groups is not achieved until the tooth reaches clinical occlusion with its antagonist.

As development continues principal fibers are established as continuous structures embedded as Sharpey's fibers in bone and cementum. Sloban and crater reviewed different fiber groups. They are dentogingival, alveolar crest, transseptal, inter radicular, horizontal, oblique, and apical fiber bundles.

Oblique fibers occupy 2/3rd of the ligament and they absorb intensive forces generated during mastication.

To attach a tooth to its alveolus, fibers must be embedded in mineralized bone and cementum. A nonfibrillar matrix appears to 'cement' terminus of Sharpey's fibers in newly formed cementum and bone and fully developed specimens on a reversal line deep within bone or cementum. Osteopontin is a significant component of the matrix of the reversal line. The mature PDL can be subdivided into 3 regions.

a. A bone-related region, rich in cells and blood vessels.

b. Cementum-related region characterized by dense well ordered collagen bundles.

c. A middle zone containing fewer cells and thinner collagen fibrils.

ii) OXYTALAN FIBER FORMATION

The largest and most numerous oxytalan fibers are found in the trans septal region. Smaller fibers are present in the middle and apical 3rd of the ligament.[17] They are first found in relation to forming periodontium adjacent to the external dental epithelium. As teeth develop they proliferate lateral to Hertwig sheath as it progresses apically. When this sheath fragments they become embedded in newly formed cementum. As the vascular system becomes established in periodontium they extend from adventitia to become attached to teeth.

iii) INTERMEDIATE PLEXUS

Fiber bundles develop in relation to bone and cementum. They meet and interdigitate in the middle of forming ligament and this union generated the concept of intermediate plexus.[18] This concept is useful to explain the changes which occur in PDL to accommodate rapid vertical eruption, mesial drift, and occlusal attrition. However, its presence is disputed. Some argue that it is an artifact arising out of the plane of section and may be attributed to that collagen fibers do not course only in one bundle but may move from one bundle to the other.

C. DEVELOPMENT OF CEMENTUM

Cementoblast differentiation and cementogenesis are closely related to root formation.[19] the most apical portion of the developing root contains an intact epithelial root sheath located between preodontoblasts of the dental papilla and dental follicle proper. Internal basal lamina separates root sheath cells from preodontoblasts while external basal lamina separates them from cells of dental follicle proper. Elongated fibroblast-like dental follicle proper cells are oriented parallel to the external basal lamina, which forms a continuous intact surface all along root sheath. Dental follicle proper cells appear to invade intercellular spaces of root sheath. These cells are identified as precementoblasts and they can synthesize matrix components. The unidirectional migration of precementoblasts towards the predentin surface appears to contribute to the breakup of root sheath and formation of Sharpey's fibers.

Upon contact with the predentin surface, elongated precementoblasts differentiate into cementoblasts. First formed cementum is acellular seen in coronal 2/3rd of tooth root differs from cellular cementum which is seen in apical 1/3rd depending on presence or absence of cementocytes in cementum.

Following a brief period of cementogenesis, cementoblasts detach from the newly formed cementum surface and join the fibroblast population in the periodontal ligament.

D. DEVELOPMENT OF ALVEOLAR BONE

Maxilla and mandible consist of alveolar bone proper and basal bone. The major changes in alveolar processes begin to occur with the development of roots of teeth and tooth eruption. As roots of teeth develop the alveolar processes increase in height. Some cells in dental follicles differentiate into osteoblasts and form alveolar bone proper.[20]

The formation of alveolar bone proper is closely related to the formation of PDL and cementum during root formation. Remodeling of bone is necessary for tooth eruption.

E. DEVELOPMENT OF GINGIVA

Gingival is composed of gingival epithelium and CT.

Gingival epithelium shows regional morphological variations that are a reflection of tissue adaptation to tooth and alveolar bone.[21] they include oral gingival epithelium, oral sulcular epithelium, and JE. Gingival evolves as the crown enters the oral cavity by breaking through the oral epithelium.

During tooth eruption, REE fuses with oral epithelium and transforms JE.

The rate of turnover of JE (4-6 days) is faster than sulcular epithelium. The oral gingival epithelium has the slowest rate of proliferation of all the 3 regions (9-12 days).

Gingival CT fibroblasts originate from perifollicular mesenchyme. Gingival collagen turnover more rapidly than that of skin and bone but slower than that of PDL.

The collagen matrix of gingival CT is well organized into fiber bundles. It is made up of transseptal, circular, semicircular, transgingival, and intergingival fibers. They secure the teeth against rotation and prevent mesial drift.

F. DEVELOPMENT OF BLOOD SUPPLY

Arterial vessels of PDL are derived from 3 sources,

1. In PDL from apical vessels that supply dental pulp.
2. From intra-alveolar vessels.
3. From gingival vessels. They form anastomosis in the marginal periodontium.

Arteries entering the ligament increase in number towards posterior teeth and to be the greatest number in gingival 3rd of the ligament.

In the developing tooth, rich capillary plexus is found in a relationship with the investing layer. Vascular osteogenic tissue is also found in association with forming alveolar bone.[22] it is most likely associated with osteogenesis. High capillary density in relation to the dental organ is linked with formative function.

G. NERVE SUPPLY OF PERIODONTUM

Nerves which are usually associated with blood vessels pass through foramina in alveolar bone including apical foramen to enter the PDL. The fibers break up and were found to end in small rounded bodies.[23] No fibers were traced entering cementum but nerve loops were described close to cementum surface.

H. DEVELOPMENT OF EPITHELIAL ATTACHMENT

When ameloblasts finish the formation of the enamel matrix, they leave a thin membrane on the surface of the enamel, the primary enamel cuticle. Then ameloblasts shorten and the epithelial enamel organ is reduced to a few layers of cuboid cells called reduced enamel epithelium.[24] during the eruption, the tip of the tooth approaches oral mucosa, and REE and oral epithelium meet and fuse. Epithelium that covers the tip of the crown degenerates in its center and the tooth erupts into the oral cavity. Once the tip of the crown has emerged, REE is termed primary attachment epithelium.

A process of transformation then takes place whereby REE gradually becomes junctional epithelium. The final conversion of REE to JE may not occur until 3-4 years after the tooth has erupted[25].

CONCLUSION:

The origin of the tooth's supporting apparatus from the dental follicle has important clinical applications. When a tooth is avulsed every effort is made to preserve all the soft tissues still adherent to the root surface of an avulsed tooth before its reimplantation. When this course is followed, regeneration of the tooth's original supporting apparatus is more likely to occur.

When part of the attachment apparatus is lost because of periodontal disease, it is difficult to replace lost tissue due to the specific origin of the tooth's supporting tissue[26, 27].

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