A CONCISE OVERVIEW OF DENTAL ONTOGENY

Teeth make up a significant portion of the fossil record. Dental studies provide researchers with many angles of information such as evolution, life history and diet. To understand dental morphology, the ontogeny of the dentition needs to be understood. In this paper a concise overview of dental development from the earliest stages to eruption will be presented with the aim of better understanding dental morphology. The focus shall be on the modern human dentition, because most embryological studies concern humans. Further focus is on molars, because cusp formation can best be discussed in multicuspid teeth.

Compared to other organs, the dentition is unusual in development (Kraus & Jordan 1965, 158). In humans, the embryological period is defined as the first eight weeks after fertilisation and is characterised by the establishment of basic shape and germ cell tissues (from which all other tissues are formed) and differentiation of systems and organ. After this, in the fetal stage, maturation of these systems and organs takes place. The deciduous dentition starts differentiation from stem cells on post-ovulatory day 55 in humans (Ten Cate 1998, 95). However, when the last permanent molar erupts at age 17 or above, the roots are not even fully formed (Ten Cate 1998, 313).

Earliest embryological development is concerned with the establishment of the three germ cell tissues (ectoderm, mesoderm and endoderm) in the shape of a three layered disc. From these three tissues all other tissues will develop, including the dentition. In the third week after fertilisation the axes of the body are established, after which folding of the three tissues results in a basic three dimensional shape, described as a tube-in-a-tube. The first tube is formed when neural crest cells rise upwards and finally inwards to form the neural tube (the developing spinal cord). Then the dietary tract is also folded into existence, with a connection to the umbilical cord. Finally, the ectoderm folds around both tubes and all other embryonic tissues, so that the outside of the embryo is created and the yolk sac is created. Both ends of the tube-in-a-tube fold towards each other. The top end becomes the head, the bottom end is the tail fold*. To complete the overview: by week 4 the limb buds are visible.

As is to be expected, the embryological development of the head (brain, cranial bones, eyes, mouth, etc.) is very complex. However, the establishment of the pre-dental tissues depends on the cranial development and so will be described briefly.

During the third to fifth week the cranial end develops sets of internal and external bulges: rhombomeres that become part of the brain, somatomeres that give rise to muscles in the cranial region, somites that will develop into the spine and associated muscles and skin, and six pharyngeal arches. In fish these arches are named branchial arches and support the gills, but in mammals the arches have evolved into the jaws, hyoid, thyroid cartilage and bones of the middle ear. Also, cranial muscles arise from the pharyngeal arches. The first pharyngeal arch contributes to the maxilla and forms a cartilagineous model around which germ cells concentrate and in week 7 start ossification. In both upper and lower jaw secondary bone growth takes place: the alveolar bone in which the teeth will be set. By week 10 the basic shape of the jaws is established and by week 20 only some cartilage in the mandibular joint remains to be ossified. The last remaining cartilage enables growth until complete ossification by the end of teenage. The maxilla originally is separated into a left and right side, on each side of the embryological mouth opening. The maxillary processes grow towards each other and start fusing in the midline.

The dentition develops from the odontogenic epithelial band, which grows into the mesenchyme of the jaws. By 4.5 weeks, during facial development, the odontogenic epithelial band is already present. Both mesenchyme and epithelium contribute to separate parts of a tooth. Oral epithelium is derived from ectoderm (although research suggests an endodermal origin for oral epithelium in amphibians, which mei extend to mammals too) and will give rise to the enamel (Feduccia *et al.* 1991). Dentine grows from mesenchyme, which originates from neural crest cells, which in turn originates from the ectoderm. This means that teeth develop through interaction of two germ tissue types. Hillson (2005, 155) notes about

	Mineralisation start	*Enamel complete*	*Root complete (years)*	*Emergence into oral cavity*
di_1	18 weeks in utero (w.i.u.)	2.5m	1.5	6m
di_2	18 w.i.u.	3m	1.5	7m
dc	20 w.i.u	9m	3.25	16m
dm_1	12-15.5 w.i.u	5.5m	2.25	12m
dm_2	12.5-18 w.i.u	10m	3	20m
I_1	3-4m	3.6/3.3y*	9.2/8.1	7.3/6.7y
I_2	3-4m	4.0/3.7y	9.9/8.8	8.1/7.3y
C	4-5m	4.8/4.1y	13.5/11.4	10.9/9.2y
P_1	1.75-2y	5.6/5.0y	13.3/11.9	11.2/9.9y
P_2	2.25-2.5y	6.3/5.9y	14.0/12.8	11.9/10.6y
M_1	At birth	2.7/2.6y	10.0/9.2	7.8/7.2y
M_2	2.5-3y	6.7/6.3y	14.8/13.8	12.5/11.8y
M_3	8-10y	13.3/12.8y	18.5/18.3	17.4/17.7y

Table 1. Timing of key events of the human mandibular dentition. w.i.u: weeks in utero, m: months, y: years. (Source: Sadler 2010, 312-313)
**Male/Female*

enamel that it "*is unique amongst mammal tissues. It is almost entirely inorganic and is acellular – effectively dead even in living organisms. By dry weight fresh enamel contains 96% inorganic material, less than 1% organic material, and the rest water*". Dentine, by contrast, is 18% collagen in fibres. Between these fibres mineral is deposited (mainly apatite, 72% of total dry weight).

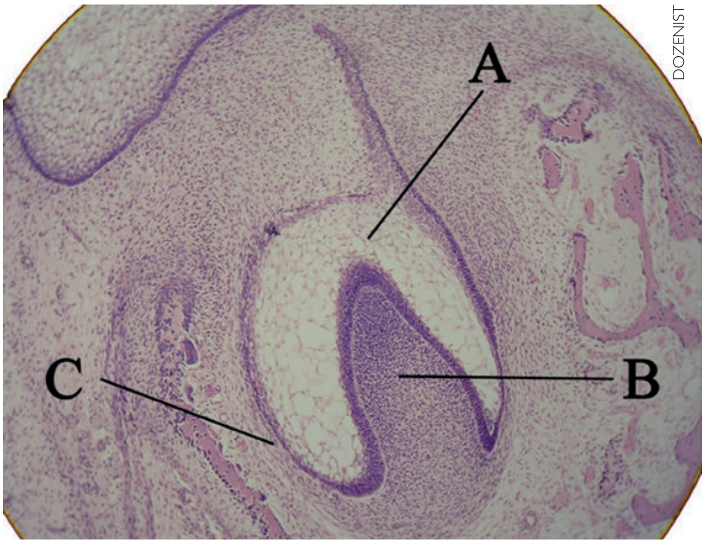
HOW TO GROW A TOOTH

At day 42 to 48 the odontogenic epithelium grows into the mesenchyme and by day 55 to 56 it develops buds at the future positions of the deciduous teeth. This process starts anteriorly and then progresses posteriorly, as do all other dental developments (Kavanagh *et al.* 2007). Each single permanent incisor, canine and premolar bud develops from one deciduous tooth bud. Besides timing, developmental processes of the deciduous and permanent dentition are the same. An obvious difference is that growth of the permanent teeth causes the deciduous teeth to be shed. Also, the permanent molars are slightly different: their buds only develop when growth of the mandibular body has progressed far enough in posterior direction. Here follows a description of these processes.

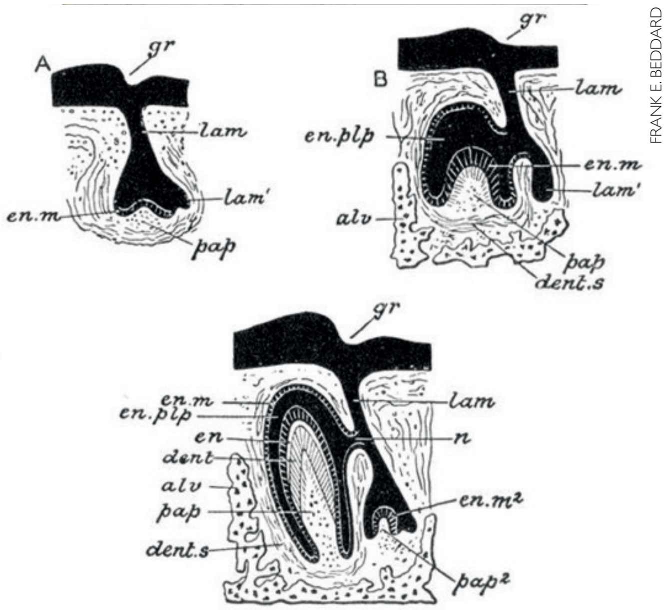
After the buds are formed in the aptly named bud stage, the underside (i.e. in the case of the mandible) becomes indented like a cap and rests on a condensation of mesenchymal cells called the dental papilla (the cap stage, see figure 1). Surrounding and containing dental cap and dental organ is the dental follicle. These three structures together form the tooth germ.

During the bell stage the dental cap cells bordering the dental papilla differentiate into the inner dental epithelium. At this stage the whole tooth germ slightly resembles a water balloon with a division in the middle: the dental cap is dense and exerts pressure on its outsides, while the dental papilla also exerts pressure on the division (i.e. inner dental epithelium) because it is contained by the follicle (Ten Cate 1998, 87). The pressure from growth on both sides on the inner dental epithelium keeps each other in balance and is not responsible for the shaping of cusps. Rather, different parts of the inner dental epithelium grow at different speeds which causes formation of cusps. This is also because the dental follicle is smaller in cross-section than the inner dental epithelium, so that folding is inevitable (Butler 1956, 39).

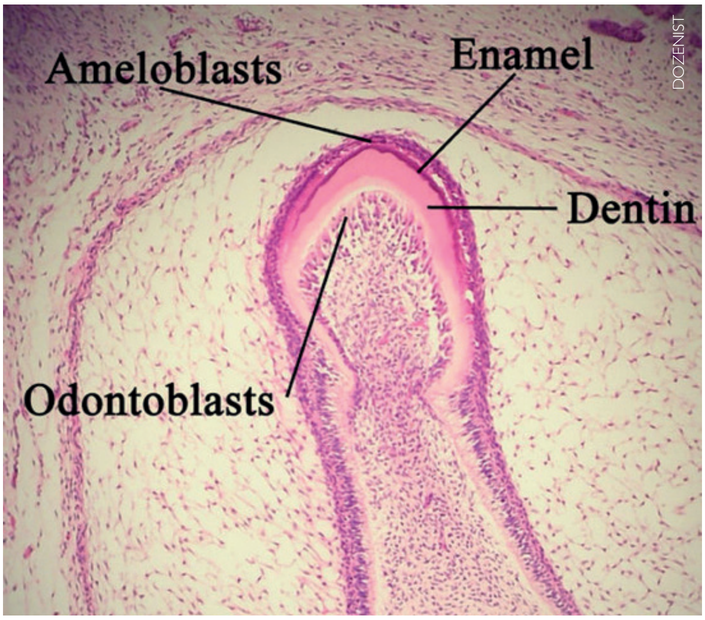
Directly next to the inner dental epithelium a concentration of epithelial cells forms the enamel knot: a temporary structure but essential in the formation of cusps. This is because it expresses



Section of tooth bud. A: dental cap. B: papilla. C: dental follicle. The broad purple band between dental cap and papilla is the inner dental epithelium



Sections showing stages of dental development. A: Cap stage. B: Early bell stage. Below: late bell stage showing deposition of enamel and dentine. Also note the developing permanent tooth bud on the right side of the deciduous bud. Relevant abbreviations: pap - dental papilla, en.plp - dental cap, dent.s - dental follicle, en - enamel, dent - dentine, alv - alveolar bone



Section of cusp tip during early mineralisation showing enamel and dentine deposition

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many different gene products (proteins) that induce the inner dental epithelium to fold, which creates the cusps. The first enamel knot induces the first cusp to begin folding (in human mandibles this is the mesiobuccal cusp, or protoconid). Each other cusp is induced by its own enamel knot, by definition only in teeth with multiple cusps, like human premolars and molars. The enamel knot is responsible for cusp formation because it induces the underlying inner epithelial cells to stop cell division and thus growth at that site ceases, while other parts of the inner dental epithelium continue growth. As noted above, the different growth speeds within the inner dental epithelium are responsible for cusp formation: the cells that have stopped cell division start differentiating into ameloblasts (enamel-depositing cells). Underneath these differentiating ameloblasts, cells of the dental papilla start differentiating into odontoblasts (dentine-depositing cells). Dentine and enamel deposition starts at a cusp tip, so that at this site the enamel-dentine junction (EDJ) is permanent (figure 2). Deposition of enamel proceeds upwards and deposition of dentine towards the roots, and the process also continues down the slope of each cusp. While the tips have started mineralisation the bases of the cusps are still growing and the distance between cusps still increases. As each cusp starts mineralisation from its own growth centre, the various growth centres meet in between of the cusps. Finally, the whole EDJ is permanently established (it is never reworked, only altered by tooth wear and cavities). Enamel deposition continues to complete the crown and mainly follows the shape established at the EDJ but can contribute to crown morphology in varying degree (depending on species). Dentine deposition continues for even longer to complete the roots. Part of the dental papilla becomes trapped in a chamber within the tooth and becomes the pulp which carries blood vessels and nerves from the root canal. On the outside of the roots cementum is deposited and mesenchyme grows soft tissue around the roots which holds the root in the tooth socket and also cushions bite force (i.e. the periodontal ligament). Before the roots have been fully formed, the tooth starts erupting into the oral cavity.

The permanent dentition follows the same developmental processes as the deciduous dentition. The tooth buds of the permanent dentition form during the third month of pregnancy. After this, the buds remain dormant until they start progressing to the next stages several years after birth (see table 1). While the permanent tooth grows in size, the roots of the deciduous tooth at that site is resorbed and pushed up because of the pressure until it is finally shed so that the permanent tooth has space to erupt (Sadler 2010, 289). In some individuals eruption and root completion of M3 takes place as late as early to mid-twenties.

CONCLUSION

Studying dental ontogeny is important in understanding dental morphology because it shows that crown morphology arises from (and is clearer on) the EDJ. Enamel deposition is a separate process and controlled by separate genes. In animals with thin enamel this distinction makes little difference, while in animals with thicker enamel (such as certain primates) enamel deposition can alter and contribute to the morphology at the EDJ (Skinner *et al.* 2010). Also, cusp formation is dictated by the enamel knot, which expresses the same genes for each molar and each separate cusp, while the resultant morphology differs between molars and cusps (e.g. Jernvall 2000, Jernvall & Jung 2000, Jernvall & Thesleff 2000). From an evolutionary perspective this is important because this has implications for homology and homoplasy of dental traits. This requires even deeper understanding of the genes that control cusp formation, which is best discussed separately.

ACKNOWLEDGMENTS

The preparation for this text was done as part of the MSc Palaeoanthropology and Palaeolithic Archaeology, University College London. My thanks to the *Cranium* editors for allowing me to do this text in English.

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FURTHER INFORMATION, IMAGES AND DESCRIPTION ON EMBRYONIC FOLDING

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http://www.embryology.ch/anglais/iperiodembry/popupperiod/video/stade06_12ca.html

http://www.ultratwistersgym.com/Resources/Folding/5.1.jpg

SAMENVATTING

De embryologie van het gebit is bijzonder, omdat dit over een lange periode plaatsvindt. Al in de eerste paar weken na bevruchting begint het melkgebit met ontwikkelen, terwijl de wortels van de laatste permanente kies nog bezig zijn met vormen als deze kies in de mond doorbreekt rond het zeventiende jaar. Tanden ontwikkelen door een interactie tussen twee van drie embryonale basisweefsels ("kiembladen"). Knobbelvorming vindt plaats door differentiële groei van cellen in de contactlaag tussen die twee basisweefsels. Cellen aan de top van een knobbel stoppen met celdeling en transformeren in emaille-afzettende en dentine-afzettende cellen. Het proces van mineralisatie verspreidt zich vervolgens weg van de knobbeltop in alle richtingen. In het geval van tanden met meerdere knobbels (molaren en premolaren, in tegenstelling tot snij- en hoektanden) begint elke knobbel onafhankelijk te mineraliseren. Nadat over de gehele contactlaag emaille erboven en dentine eronder is afgezet, gaat mineralisatie door om de emaillekroon te voltooien en om de wortels te vormen. Hierna, zoals gezegd, breken de tanden door het tandvlees al voor de wortels compleet zijn. Zodra de permanente tanden ontwikkelen, worden de wortels van het melkgebit hierdoor geresorbeerd en omhoog geduwd.