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Postnatal Tooth Development in Cattle

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INTEREST in the teeth of cattle dates from the latter half of the nineteenth century when disputes as to the age of veal carcasses were settled by the state of eruption and amount of wear of the incisor teeth.[5] Recently, additional attention has been drawn to the teeth of cattle by the recognition of the role played by fluorides in the mottling of the teeth. Many studies have been done to classify and analyze the effect which dietary fluorides have on the teeth.[4] It is also recognized that other systemic factors may influence the quality of the dental structures. However, these studies are hampered by a paucity of knowledge concerning the details of tooth development in cattle, and especially the exact chronology of enamel development. Without an exact knowledge of the chronology of tooth development, it is not possible to make an accurate correlation between the systemic ailment and its effects on the teeth. Except for Garlick's study in 1954,[3] few controlled studies have been conducted relative to the development of teeth of cattle.

PURPOSE

The primary purpose of this study was to examine and describe the development, eruption, and resorption of the teeth in cattle, with special emphasis on the *chronology of enamel and dentin development in the mandibular incisor and canine teeth.* It was hoped thereby to provide a baseline of reference for future studies in tooth ring analysis, *i.e.,* effects of various systemic factors such as fluorosis, nutritional deficiencies, and infectious diseases upon tooth development in cattle.

A secondary, but important, purpose of this study was to determine whether tooth development was strongly influenced by genetic differences. Several breeds of dairy and beef cattle were examined radiographically to determine whether the different breeds have significantly different chronological schedules. If they had, this might be due to genetic difference. If, however, the schedules were similar, it must be concluded that tooth development probably follows a fixed schedule and is not likely to vary in different genetic strains.

This study presents the chronology of crown and root formation for the four permanent teeth in the anterior portion of the mandibles of 869 purebred dairy and beef cattle. The chronology of lower premolar and molar development is also presented. The chronology of tooth development was found to be similar in the four dairy and three beef breeds of cattle studied. None showed any consistent precociousness or retardation of any one of the developmental processes. Interestingly, no consistent differences were found in the chronology of tooth development between the bulls and the cows.

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A Review of Tooth Development

ENAMEL AND DENTIN FORMATION

The fundamental stages of anterior tooth development in cattle are essentially the same as have been described in human teeth.[8] The life cycle of a human deciduous incisor is shown (fig. 1). Schour and Massler have divided tooth development into the following stages:

1) *Growth*
   a) Initiation of cells from the oral epithelium to form tooth buds.
   b) Proliferation of tooth bud cells to form the cap stage of development
   c) Histodifferentiation of cells into pre-enamel and pre-dentin forming cells.
   d) Morphodifferentiation and alignment of cells to outline the size and shape of the future tooth.
   e) Apposition of enamel and dentin matrix by ameloblasts and dentinoblasts.
2) *Calcification* of the enamel and dentin matrix.
3) *Eruption** of the tooth toward and into the oral cavity.
4) *Attrition* or abrasive wear of the teeth.
5) *Resorption* of the deciduous root and *exfolia tion* of the tooth.
6) Repetition of the above cycle in each perma nent tooth (except resorption and exfoliation).

The enamel which forms the outer cap of the crown is derived from ectodermal cells which line the oral cavity. The underlying mesoderm differentiates into the dental pulp which, in turn, forms the central core of dentin.

o) *Initiation.*—The life cycle of a tooth begins *in utero* with a thickening of the oral epithelium. The cells multiply and form a tooth bud (A of fig. 1).

6) *Proliferation.*—Unequal growth of the tooth bud leads to the cap stage (B in fig. 1). Changes then take place in the inner and outer layers of epithelium and in the cells between. When these occur, this epithelial structure is known as the "enamel organ" and is composed of an outer and inner enamel epithelium with an enclosed stellate reticulum. At the same time, the cells of the mesenchyme which are enclosed by the epithelial cap condense to form the dentin-forming organ or " dental papilla." The mesodermal cells around and outside the enamel organ condense to form the dental sac which will contribute cells for the development of the periodontal membrane.

c) *Histodifferentiation.*—The cells of the enamel- and dentin-forming organs undergo marked histologic changes and become specialized to form the enamel and dentin matrix (the bell stage of the tooth germ, C in fig. 1). The layer of inner epi thelial cells of the enamel organ differentiate just prior to amelogenesis into tall enamel-forming cells, the ameloblasts. As soon as this occurs, the subjacent mesenchymal cells of the dental papilla differentiate into odontoblasts, the dentin-producing cells. The stratum intermedium is a layer of cells that forms from the stellate reticulum next to the inner enamel epithelium. They apparently are part of the enamel-forming mechanism.

When the crown of the tooth is completed, the inner and outer enamel epithelium proliferate at the margins of the bell-shaped enamel organ and give rise to Hertwig's epithelial sheath. This grows downward to outline the dentino-cemental junction and the future root (E in fig. 1).

d) Morphodifferentiation.—As the formative cells differentiate, they align themselves along the future dentino-enamel and dentino-eemental junc tion and thus establish the size and shape of the future crown and root just before beginning the deposition of enamel and dentin matrix. Thus *the final size and shape of the tooth are already determined before deposition of enamel and den tin commences.*

e) Apposition.—This is a regular and rhythmic deposition of the extracellular material by the enamel- and dentin-forming cells.

* Eruption refers to the physiologic tooth movements through the jaw bone and after emergence into the oral cavity.

A B C D E F G H I

Fig. 2 – Mixed anterior dentition (teeth occluding with maxillary pad.)

GROWTH

A B C

Initiation Proliferation Histodifferentiation

Bud stage Cap stage Bell stage

CALCIFICATION

D

Apposition

ERUPTION

E F

Intra-osseous into oral cavity

ATTRITION

G H

Fig. 1 Life cycle of the hman incisor tooth (Orban 4th Ed)

Amelogenesis is a two-phase system consisting of a deposition of the enamel matrix followed by a maturation or calcification of this organic matrix. The enamel matrix is formed of enamel rods and interprismatic substance. However, the chemical and physical properties for the newly deposited matrix differ from mature enamel. When newly deposited, the enamel matrix is composed of approximately 25 to 30 per cent mineral salts, while the rest is organic material and water. The mature, fully calcified enamel contains 96 per cent mineral salts and only 4 per cent organic constituents and water.

The process of enamel formation is accomplished by ameloblasts depositing a globule of organic matrix one upon the other to form a tall enamel prism which extends from the dentino-enamel junction to the periphery of the crown. Each prism is built up rhythmically and regularly, globule by globule, in daily increments until the ameloblast reaches the tooth periphery. The daily increments are distinguished in the mature enamel by cross-striations (incremental lines of Eetzius).

When the enamel prism is completed, it contains calcium salts in only 30 per cent concentration. Final calcification of the enamel matrix begins at the incisal or cuspal tip when the full width of the enamel has been formed and proceeds in planes at right angles to the long axis of the tooth.

Dentinogenesis.—Dentin is formed by cells differentiated from the mesodermal tissue, in contrast to enamel which is formed by cells of ectodermal origin. Dentin formation begins with a deposition of fibrils and matrix at the dentino-enamel junction. Coincident with the formation of these fibrils is the appearance of irregularly spiraling Korff's fibers which originate in the pulp and merge with the fibrils at the dentino-enamel junction. At the same time as the Korff 's fibers appear, the spindle-shaped mesenchymal cells closest to the dentino-enamel junction differentiate into tall columnar cells, the odontoblasts. The odontoblasts then form a row of tall columnar cells opposite the tall columnar ameloblasts (C and D in fig. 1). These dentin-forming cells develop processes which extend toward the ameloblasts. As the odontoblasts migrate pulpally, forming as they go incremental layers of dentin matrix (pre-dentin), the protoplasmic extensions of the odontoblasts are left behind within the dentin matrix (the dentinal tubules).

It has been established by numerous studies that, while the ameloblasts and dentin-forming cells deposit matrix, they are extremely sensitive to systemic upsets, toxins, and stress. These systemic disturbances affect the activity of these cells and, in turn, the quality and quantity of matrix deposited. Such defects are permanent and not repairable, so that a history of the health of the animal is inscribed permanently within the structure of the enamel and dentin. These effects can be seen grossly as hypoplastie or hypocalcified defects in enamel (as mottled enamel in fluorosis or hypoplastic defects in the enamel caused by calcium deficiencies or fevers) or as microscopic defects in histologie sections of the tooth such as the neonatal line in the enamel and dentin of the deciduous teeth. Analysis of these lines is termed "tooth ring analysis." This study attempts to delineate, accurately, the exact date at which each level of enamel and dentin is deposited and is therefore a fundamental requirement before tooth ring analysis can be attempted in cattle. It will permit the assessment of the role played by such stress factors as pregnancy, lactation, nutritional deficiencies, and acute infections upon tooth development.

Eruption.—The teeth of cattle, like those of human beings, move from their site or origin within the bone crypt toward their place in the dental arch (E to H in fig. 1). This process of the tooth migration is termed eruption and is a distinct and unique phase in the development of teeth. As will be demonstrated, eruption begins in cattle only after all the, crown is formed and one third or more of the root is developed (fig. 13). In man, eruption begins within the jaw bone with the formation of the root.[5]

The eruption of teeth occurs in two stages; the prefunctional eruptive phase and the functional phase. The prefunctional phase refers to the tooth movement within the jaws and ends when the teeth occlude with their antagonist in the opposing jaw. The antagonist may be the opposite teeth or the gum pad, as is the case with the lower anterior teeth of cattle. The prefunctional phase of eruptive tooth movement is very complicated. It takes place by three types of movement, incisal toward the occlusal plane, rotatory around a spiral, and lateral toward the midline of the mandible.

Eruption continues even after the teeth are in 'occlusion (functioning phase)." The rate of migration is slow and compensates for the loss of vertical height of the tooth from wear."

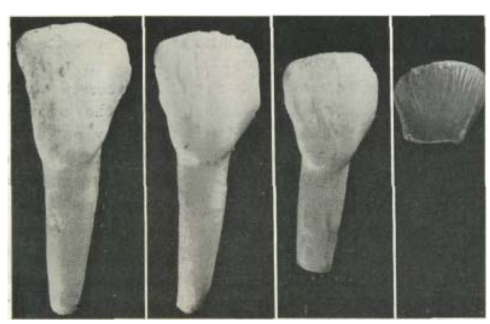


Fig. 3—Anatomy of the three permanent incisors and deciduous canine teeth at different levels of development (dissected from the mandible of a 30-month-old animal). Notice the decreasing size of the crown from the first to the third incisor.

Attrition —This refers to the normal wear of .the enamel and exposed dentin which takes place on the occlusal surfaces of the molars and premolars and on .the lingual surface at the incisal tip of the lower anterior teeth. It also takes place on the approximal surface of the teeth. There is a constant slow eruption of the teeth to compensate for the loss of height of the crown caused by wear, to maintain masticatory efficiency. Protection of the pulpal tissue is assured by the continuous deposition of secondary dentin which always takes place in advance of the wearing away process.

The rate of attrition in man is related to his diet, the coarser diets eaten by primitive, societies causing a greater amount of wear. Similarly, in cattle, different diets cause different rates of wear. It should be remembered that the mandibular premolars and molars occlude against their equivalent opponents in the maxilla, while the mandibular incisors and canine teeth occlude against the comparatively soft upper gum pad (fig.: :g). These differences in occlusion are reflected not only in ,the rates of .wear of the teeth but also by their morphologic characteristics. The molars and premolars have crowns which are long in comparison with their roots, while the incisor crowns are shorter than their roots.

Root Resorption and Shedding.—At birth, the jaws are far too small to support the large permanent teeth, and so the young animal has small deciduous teeth to fit its smaller jaws. When the jaws become larger, the deciduous teeth are shed and replaced in an orderly fashion by the erupting permanent teeth.

Shedding of the deciduous teeth is accomplished by resorption of the root. Associated with this process are osteoclast cells derived from the surrounding connective tissues. In their presence, the cementum and dentin and the surrounding bone are removed by resorption. The destruction usually begins at the apex of the deciduous teeth and proceeds gradually toward the crown. Eesorption of bone also takes place around and in advance of the erupting permanent tooth.

Methods

INTRA-ORAL RADIOGRAPHS or INCISOR TEETH IN CATTLE

It became obvious that the data required for an accurate study of the chronology of different stages in tooth development could be obtained only through dental radiographs in large numbers of healthy animals whose exact birth dates were known. Fortunately, a method of quickly obtaining accurate intra-oral x rays of the anterior teeth of living cattle had been perfected by Christofferson and Weiss in 1958.[7] The reader is referred to their paper for the details whereby radiographs of the anterior teeth can be obtained quickly and easily in living animals.

ANALYSIS OF RADIOGRAPHS

All the radiographs for the cattle studied were arranged in sequence according to age, by days. Examination was made over a light box with the aid of a magnifying lens (x5). The deciduous and permanent teeth visible on the radiographs were then analyzed as follows:

A) The deciduous teeth
   1) The amount of root formation at each age period
   2) The amount of root resorption

No material was available to determine the beginning of crown formation *in utero.*

B) The permanent teeth
   1) The beginning and completion of crown formation
   2) The development of the root
   3) The time of intra-osseous eruption
   4) The age at which the tooth emerges into the oral cavity

This last assessment was possible because the level of the incisal edge in relation to the gum margin could be determined in the radiograph.

TABLE 1—Number and Classes of Cattle Studied Radiographically

Breeds*	Birth to 1 year	1 Year to 2 years	2 Tears to 3 years	3 Years to 4 years	4 Years to 5 years	Totals for each class
DAIRY						
Holstein-Friesian	62	124	90	76	18	365
Guernsev	4	33	S3	IS	1	76
Jersev	ir.	9	5	3	1	33
Brown Swiss	i	1	-	1	1	I4
Ayrshire	2	5	0	0	0	7
All Dairy	**84**	**172**	**125**	**98**	**16**	**495**
BEEF						
Hereford	104	68	47	30	9	258
Aberdeen Angus	38	37	18	5	2	100
Shorthorn	8	1	5	1	1	16
All Beef	**150**	**106**	**70**	**36**	**12**	**374**
All Cows	168	262	176	120	22	748
All Bulls	54	14	17	14	6	105
All Steers	12	2	2	0	0	16
Totals for each age group	**234**	**278**	**195**	**134**	**28**	**869**

* Cattle were selected for optimal nutritional status and accuracy of birth date.

It was confirmed by examination of intra-oral color transparencies.

The developmental processes occurred almost simultaneously for each of a pair of incisors, so that they were treated as one. When this was not so, the more advanced tooth was recorded. A difference among members of a pair was most often encountered in the process of eruption.

After the average age and range had been derived for each of the developmental processes in days, the data were regrouped in months to determine the range and average age in months (table 3). The range was finally computed as 1.5 standard deviations of this mean, which included more than 80 per cent of the animals examined and allowed for omission of less than 20 per cent of the very precocious or retarded animals. This was done for each breed separately and, from these, an average and standard deviation for each of the breeds was established (see section on comparison of breeds).

COLOR PHOTOGRAPHS

In addition to the radiographs obtained *in vivo,* a large series of color transparencies of these teeth in living cattle were made immediately after the radiographs were taken. A specially constructed camera with an electronic flash was used. This produced excellent 35-mm. color transparencies for study of the teeth and soft tissues (fig 2).

DISSECTIONS

To supplement the information obtained in the living animals by radiographs and photographs, a number of dried and preserved specimens were dissected to expose the incisor, canine, and molar teeth for the study of three dimensional relationships (fig. 3 and 4).

HISTOLOGOIC SECTIONS

Finally, a number of histologic ground and decalcified sections were prepared from selected formalin-fixed specimens. These were studied microscopically to determine more exactly the structural and anatomic relationships of bovine dental tissues and to compare them with the teeth of man (fig. 5 and 6). However, a more detailed analysis and description of the dental and periodontal tissues was left for a subsequent report.

Materials

A total of 869 selected purebred dairy and beef cattle were studied radiographically (table 1). The animals were selected from farms where it would be certain to find optimal nutritional levels and management—and, most important of all, where exact birth dates of the animals would be known.

The beef cattle came from breeding farms and were living under more favored condtions than the usual range animal. Most of the bulls were young and came from beef herds. Most of the dairy bulls were from a large stud farm in Illinois.

Findings

ANATOMIC CONSIDERATIONS

Dental Formulas.—Cattle possess 20 deciduous teeth: three pairs of incisors and one pair of canine teeth in the anterior area of the mandible (none in the maxillae), and three pair of premolars in the posterior areas of the mandibles and maxillae. These are replaced by permanent teeth. The permanent molars do not have deciduous predecessors. The dental formulas are:

Deciduous teeth: $(i^{0}_{3} - c^{0}_{1} - p^{3}_{3}) \text{ X } 2 = 20$

Permanent: $(I^{0}_{3} - C^{0}_{1} - P^{3}_{3} - M^{3}_{3}) \text{ X } 2 = 32$

The Anterior Teeth.- — Many contemporary veterinary authors refer to the fourth anterior tooth of cattle erroneously as a

TABLE *2*—Chronology of Root Formation and Resorption in Deciduous Incisor and Canine Teeth

	Deciduous			
Root formation	First incisor (months)	Second incisor (months)	Third incisor (months)	Canine tooth (months)
Root formation completed	6.0 ± 1	6.0± 1	6.0 ± 1	7.0 ± 1
Root resorption begins	6.4 ± *1*	8.3 ± 2	18.0 ± 3	25.0 ± 3
Resorption advanced*	16.2 ± 1	24.4 ± 1	31.0 ± 1	36. 0± 1
Exfoliation	23.0 ± 1	30.0=t 1	35. 7 ±2	42. .0 ± 2
Duration of root resorption	16.6	21.7	17.7	17.0

* One third or more of root resorbed.

fourth incisor.[12] This is based on its incisor form and position in the arch. However, studies by Loomis [8] have established that this is a true canine tooth which, since the Oligocene epoch, has slowly changed its canine form and migrated anteriorly to become aligned beside the third incisor. The term "fourth incisor" is incorrect since the Eutheria (placental animals) have only three pairs of incisors and one pair of canine teeth. The evolutionary history of this tooth to its present incisor form and position in cattle is quite clearly shown in paleontologic records.

The calf is usually born with most of its deciduous teeth already partially erupted and visible, to different degrees, within the mouth (fig. 8 and 20). This enables it to partake of a mixed diet of milk and hay shortly after birth. The human child, in contrast, is without any teeth for six months.

The deciduous teeth are replaced consecutively by their permanent successors until the last pair is exfoliated toward the end of the third year. Occasionally a deciduous tooth is retained and, when this occurs, a radiograph will usually show that the permanent successor failed to form.

Occlusion.—The incisor and canine teeth erupt to occlude against the upper gum pad (fig. 6).

Attrition.—The lingual surfaces at the incisal one third of these teeth become abraded early. The enamel is worn away and the underlying dentin is exposed. This takes place at an acute angle to the long axis of the tooth and reflects the curvature of the upper gum pad (fig. 5 and 6). It has been assumed that this abrasive wear is related to the breed of animal and the character of the food ingested.[1] However, the precise mechanism as to how this takes place is still unknown and, in view of its importance to the feeding of these animals, should be investigated in more detail.

Gingivae.—The appearance of the mucosa investing the teeth and covering the supporting bone is similar to that of man. There is a narrow band of free gingiva below which is the pink immovable attached gingiva (fig. 2). The attached gingiva is separated by a distinct muco-gingival junction from the less keratinized, more richly vascular and loosely attached, alveolar mucosa. The latter is reflected onto the inner surface of the lower lip as the muscular mucosa (fig. 2).

Although the external appearance of the gingival tissues are similar to human gingiva, microscopic examination of histologic sections showed that the attached gingiva of cattle is firmly adherent by fasiculi of collagenous fibers to the cementum of the teeth rather than the alveolar bone as in man. A broad mass of connective tissue firmly secures the attached gingiva to the tooth cementum well above the level of the crest of the alveolar bone (fig. 5).

It is commonly thought that the gingivae gradually recede to expose the roots as animals age. This is certainly true in many cases, but not always. Exposure of the roots may occur due to continuous eruption of the teeth. Figure 2 shows the mixed dentition of a 2-year-old animal with the roots of the second deciduous incisor exposed. Comparison with figures 9 and 14 suggests that this eruption occurred because the deciduous anterior teeth would have been below the level of the occlusal plane of the permanent anterior tooth and would become functionless.

Gingivitis is of common occurrence at the time of tooth eruption and appears similar to the eruption gingivitis described in children.[9] Quite often, traumatic gingivitis is observed, caused by fragments of trapped vegetation.

Incisor Tooth Form.—The first permanent incisor has the largest crown and the longest root. The crowns have been likened to shovels, whose proximal surfaces are flared. The second and third incisors are successively smaller (fig. 3). The canine tooth is incisor in form and often appears to be larger than the third incisor. This

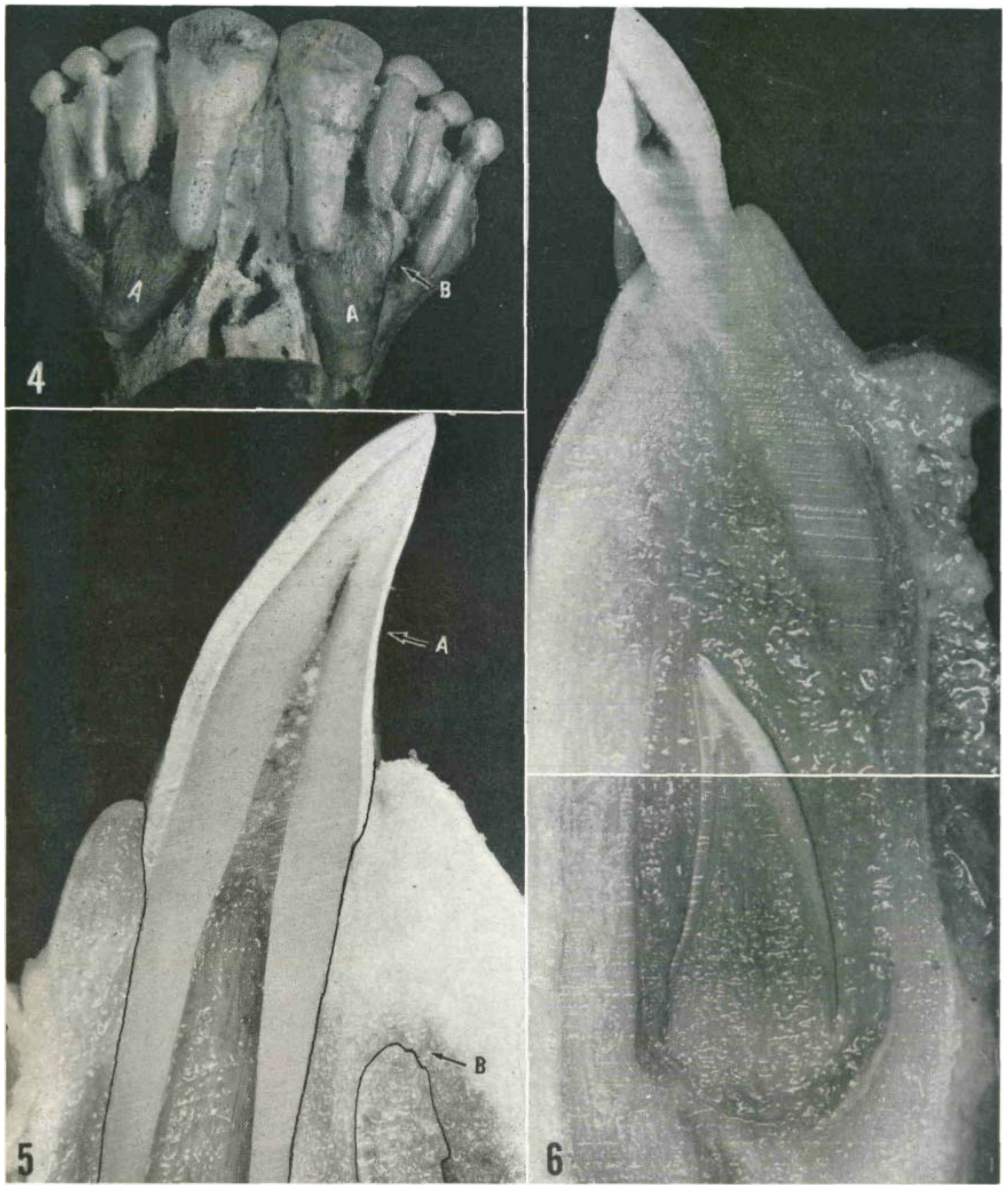


Plate I

Fig. 4—Mandible from *a.* 22-month-old animal dissected to show the relation between the erupted deciduous teeth and the developing permanent tooth germs. The root of the permanent first incisor is still incomplete. The second permanent incisor (A) lies lingual to the root of the first, while the third permanent incisor tooth germ (B) can be partly seen lingual to the crown of the second incisor.

Fig. 5—A buccolingual section through the mandible showing a recently erupted first permanent incisor. Notice the width of the labial enamel and the thin lingual enamel (A), also the low level of the crest of the alveolar bone (B). The marginal gingivae are attached to the cementum, instead of the bone, by dense collagenous fibers. The parallel markings on the dentin are from saw cuts.

Fig. 6—A labiolingual section showing the relation of the developing permanent incisor to the lingual apical surface of the deciduous predecessor.

TABLE 3—Chronology of Development of Permanent Incisor and Canine Teeth

	Permanent			
Development	First incisor (months)	Second incisor (months)	Third incisor (months)	Canine tooth (months)
Crown formation begins	6.0	12.2 ±1	20.0 ±1	27.5 ±2.5
Crown formation completed	12.3 ± 1	18.6 ±1	24.0 ± 1	33.4 ± 2
Intra-osseus eruption begins	18.2 ± 1	24.7 ± 1	30.3 ± 2	38.0 ± 2
Emergence into oral cavity	23.0 ± 1	30.0 ± 1	35.7 ± 2	42.0 ±2
Root formation completed	28.0 ± 1	35.0 ± 2	43.5 ± 2	52.0 ± 2
Duration of crown formation	6.3	6.4	4.0	5.9
Duration of intra-osseus eruption	4.8	5.3	5.4	4.0
Duration of root formation	15.7	16.4	19.5	18.6

is equally true for the deciduous and permanent incisors.

When the teeth first appear in the oral cavity, the enamel is marked by several vertical striations which become polished and erased by age and wear.[1] These vertical striations are so large that it is unlikely that they reflect the corrugated contour of the dentino-enamel junction as stated by Garlick.[3]

Enamel and Dentin.—A longitudinal section through the crown shows that the enamel cap is thick and even on the labial surface, but much thinner on the lingual surface (fig. 5). The enamel is thinnest at the incisal one third of the tooth which probably accounts for the rapid exposure of the dentin in this area once the tooth has started to function.

The dentin extends practically the whole length of the tooth. In the crown it is covered by a cap of enamel, and in the root it is protected by a thin layer of cementum. The cementum usually overlays a small portion of the cervical border of the enamel. The cementum is the specialized tissue which embeds the fibers of the periodontal ligament and thus secures the tooth within its bony socket.

The central cavity of the dentin is filled with a sensitive soft tissue, the pulp. In the young animal, the pulp is large and vascular, but as the tooth becomes abraded, the odontoblasts that line the pulpal wall are stimulated to deposit secondary dentin until, in the older animal, the pulp of the tooth is nearly filled in.

The Attachment Apparatus.—The incisor and canine teeth in cattle have a somewhat different attachment apparatus than those in man. When the tooth has reached its functional level, only the apical two thirds of the tooth lies within bone, while the cervical third is supported by collagenous fibers which run between the cementum and the gingivae (fig. 5). The periodontal membrane is wide and there is no dense lamina dura of bone as is found in all human teeth and in the premolar-molar region of these same cattle (fig. 16 and 17). The bone of the labial aspect of the alveolar process is thinner than the lingual bone.

The loose arrangement of the attachment apparatus may explain why the tooth is quite mobile in the living animal. It would appear that this is another example of adaption to function. The wide and loose periodontium may serve to cushion the effect of the incisal edge striking the premaxillary pad during mastication.

Relation of Permanent Tooth Germ to Deciduous Incisor and Canine Teeth.—As in man, the tooth germs of the permanent incisor and canine teeth are derived from the lingual aspect of the enamel organ of the corresponding deciduous tooth. The permanent incisor and canine tooth germs, therefore, come to lie in the region of the

TABLE 4—Chronology of Development of Permanent Uandibular Premolar and Molar Teeth

	Permanent					
Development	First premolar (months)	Second premolar (months)	Third premolar (months)	First molar (months)	Second molar (months)	Third molar (months)
Crown formation begins	12-13	9-10	11-12	In utero	1	9-10
Crown formation completed	22-23	16-20	24-30	2-3	12-13	23-24
Root formation completed	36-40	36-40	36-40	1.3	24-25	38

deciduous root apex and lingual to it (fig. 6 and 16).

The large developing permanent incisors are crowded within the small, still growing jaw. They cannot align themselves correctly within this space and, therefore, become staggered and rotated. The second permanent incisor lies lingual to the root of the first, while the third incisor tooth germ can be seen just behind the crown of the developing second incisor (fig. 4). When the teeth first emerge they are unevenly placed, but they soon become correctly aligned by the moulding action of the muscular tongue and lips. This has been adequately described in children.[10] The mechanism in cattle is probably similiar.

Chronology of Incisor and Canine Tooth Development

DECIDUOUS ANTERIOR TEETH

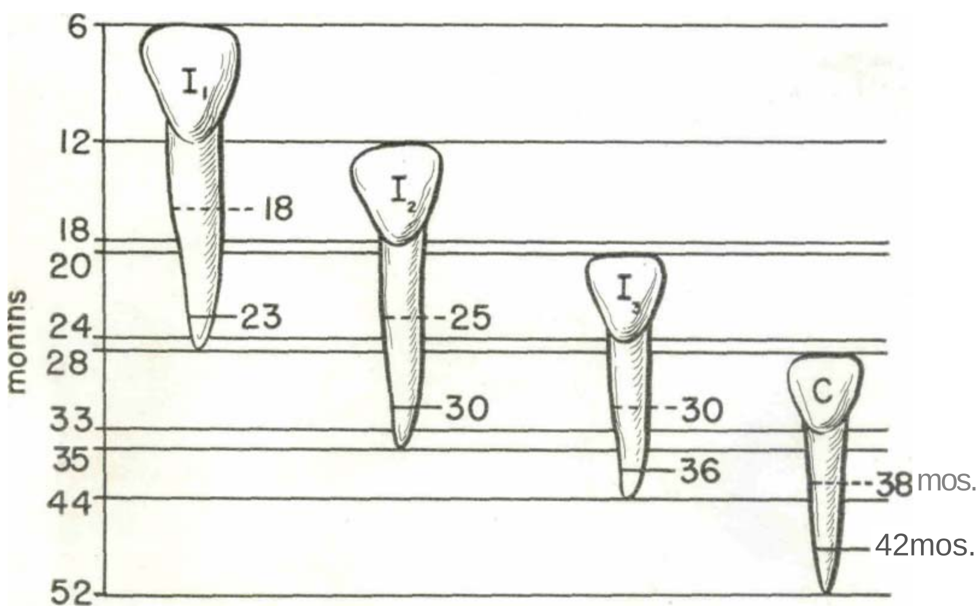
Initiation.—Garlick[3] has indicated that initiation of proliferation of epithelial cells from the oral epithelium takes place sometime during the second month of intrauterine life. However, his study was not a chronologic one and additional work on the chronology of tooth development in utero is needed.

Beginning Crown Formation.—The advanced stage of the deciduous incisor tooth development at birth indicates the deposition of enamel and dentin matrix begins approximately during the fourth to fifth month *in utero* and possibly earlier.

Completion of Crown.—The crowns of the deciduous incisors are probably completely formed two to three months after the beginning of enamel formation—that is, at seven to nine months *in utero* from the first to the fourth incisor.

Eruption.—Emergence of the teeth into the oral cavity takes place at birth and shortly afterward (table 6). The first, second, and third deciduous incisors may have a quarter or more of their crowns exposed in the oral cavity at birth. The

DEVELOPMENT OF PERMANENT ANTERIORS



--------- **INTRA-OSSEOUS ERUPTION BEGINS**

—----- **EMERGENCE INTO ORAL CAVITY**

Fig. 7—A composite drawing showing the chronologic sequence in the development of the three permanent incisor and the canine teeth showing the beginning and completion of crown formation, level of root formation at beginning of intra-osseous eruption and age of emergence into the oral cavity.

canine teeth will appear when the animal is approximately 2 weeks old.

Root Formation.—At the time of the emergence, the anterior teeth have from one half to two thirds of their roots formed (table 5). Completion of the roots takes place approximately 6 months of *age* for the first three incisors and one month later for the canine teeth (table 2).

Resorption.—Resorption of the first deciduous incisor starts soon after the root has formed and is coincident with the appearance of the first permanent incisor follicle at 6 months (tables 2 and 5). The second incisor begins to resorb only a little later, and this seems to be due to the proximity of the large first permanent incisor. Resorption of the third incisor and canine teeth (like the first incisor) is coincident with the appearance of their permanent successor tooth germs (tables 2, 3, and 5).

Exfoliation.—Loss of the deciduous tooth takes place only slightly before the permanent successor emerges into the oral cavity (fig. 14 and table 5). Usually, three quarters or more of the root must be resorbed before exfoliation can take place (fig. 13).

PERMANENT INCISOR AND CANINE TEETH

Initiation.—The exact age for the beginning of tooth bud formation cannot be determined from radiographs, as the density of the surrounding bone masks the earliest tissue proliferations. However, the first radiolucency indicating the tooth follicle has been shown histologically to represent a tooth germ already well advanced toward the bell stage of tooth development, with matrix deposition ready to begin (fig. 9). Additional histologic analysis will be necessary to determine the chronology of this phase of development.

Crown Formation.—Enamel and dentin formation begin with the deposition of layer upon layer of enamel and dentin matrix by the ameloblasts and odontoblasts. After the matrix is deposited, calcification takes place; there is a lag between matrix deposition and its calcification in the enamel. Therefore, the chronology of enamel development as derived from radiographs will be slightly later than when it is derived from histologic sections.

The three permanent incisor and canine teeth begin to form at 6, 12, 20, and 27 months, respectively (table 3). The crowns of the first incisor, second incisor, and canine teeth are completed six months later, while the third incisor forms more rapidly, being completed only four months later (fig. 7).

Rate of Permanent Crown Formation.—• The crown of the first incisor, second incisor, and canine teeth require about six months to form, while the third incisor

Legend for Figures 8-12 (Plate 2) on Opposite Page

Fig. 8—Radiograph of the distal extremity of a dried mandible at birth. All crowns of the deciduous teeth are complete and one half or more of their roots are formed. Each appears at different levels of eruption. The midline separation is an artefact. (All the radiographs in this series are actual size).

Fig. 9—Radiograph of teeth of a 6-month-old female Holstein-Friesian. The deciduous incisors are completely formed. The tooth germs of the first permanent incisors are apparent as circumscribed radiolucent areas at the apices of the first deciduous incisors (A). The mental foramen lies below the developing tooth germ and appears as a smaller more sharply defined radiolucent area (B).

Fig. 10—Radiograph of teeth of a 10-month-old Holstein-Friesian heifer. Two thirds of the crown of the first permanent incisor is formed. The arrow indicates the crest of the alveolar process.

Fig. 11—Radiograph of teeth of a 12-month-old Hereford female. The crown of the first permanent incisor is almost completed and the crypt of the second incisor is visible just below the apex of the second deciduous incisor (B). Resorption of first deciduous incisor indicated by (A).

Fig. 12A and 12B—'Radiographs of a preserved specimen from an 18-month-old cross-bred Holstein-Friesian; (A) labiolingual view, (B) lateral view of one half of the jaw showing the alignment of the first permanent incisor crown at right angles to the other teeth and the lingual position of the second incisor. The arrows indicate areas of advanced resorption on the lingual surface of the first deciduous incisor.

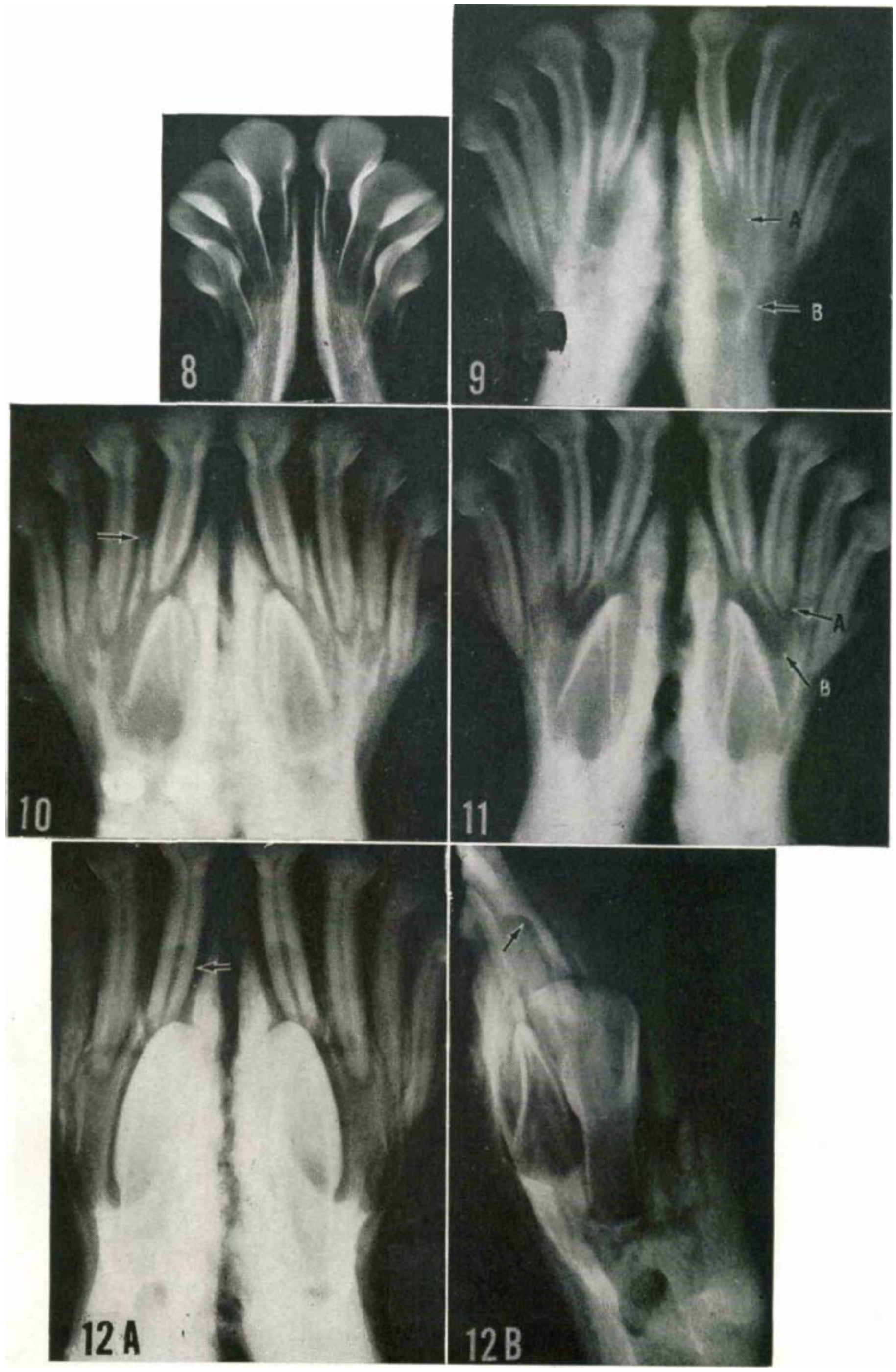

8
9
A
B
10
11
A
B
12 A
12 B

TABLE 5 — Composite Chronology of Development of Mandibular Teeth* (Anterior)

	Deciduous				Permanent			
	First incisor	Second incisor	Third incisor	Canine tooth	First incisor	Second incisor	third incisor	Canine tooth
Birth	3/4 erupted — root 2/3 formed	2/3 erupted — root 2/3 formed	1/2 erupted — root 1/2 to 2/3 formed	1/4 erupted — root1/2 formed	Absent	Absent	Absent	Absent
1/2-1 yr	Root formation	Root formation	Root formation	Root formation	Crown formation			
1-1 1/2 yr.	Root resorption advanced				Crown formation completed	Crown formation begins		
1 1/2-2 yr.	Exfoliated		Root resorption begins		Intra-osseous eruption begins	Crown formation completed	Crown formation	
2-2 1/2 yr.		Root resorption advanced		Root resorption begins	Emergence into oral cavity — root formation completed	Intra-osseous eruption begins	Crown formation completed	Crown formation begins
2 1/2-3yr.		Exfoliated	Root resorption advanced			Emergence into oral cavity	Intra-osseous eruption begins	Crown formation completed
3-3 1/2yr.			Exfoliated	Root resorption advanced		Root formation completed	Emergenc e into oral cavity	Intra-osseous eruption completed

31/2-4yr.			Exfoliated			Root formation completed	Emergence into oral cavity
4-4 1/2yr.							Root formation completed

TABLE 5—(Continued) Composite Chronology of Development of Mandibular Teeth*
(Posterior)

	Deciduous premolars			Permanent premolars			Permanent molars		
	First premolar	Second premolar	Third preraolar	First premolar	Second premolar	Third premolar	First molar	Second molar	Third molar
Birth		All roots complete 1-2 mo. later					1/3 of crown formed — completed at 2-3 mo.	Crown formation begins at 1 mo.	
1/2-l yrs.					Crown formation begins	Crown formation begins	Emergence into oral cavity	Crown formation completed	Crown formation begins
1- 1 1/2 yrs.				formation begins	Crown formation completed		Root formation completed	Emergence into oral cavity	
1 1/2-2yrs.		Root resorption present different degrees		Crown to formation completed		Crown formation completed			Crown formation completed
2– 2 1/2yrs.		Exfoliated		....	Emergence into oral cavity			Root formation completed	Emergence into oral cavity
2 1/2 - 3 yrs.				Emergence into oral cavity		Emergence into oral cavity			
3-3 1/2 yrs.			....	Root formation completed	Root formation completed	Root formation completed			Root formation completed

* Based on analysis of intra-oral radiographs of 8S9 living cattle selected for optimal nutritional status and accurate birth dates.

crown is completed in four months. The crown of the third incisor is smaller than the first and second incisor (fig. 3) and observation has shown that the canine tooth often appears larger and slightly different than the other three. This may be correlated with the fact that the fourth anterior tooth is in reality a canine tooth and only in the Oligocene era has come to have its present incisor-like form and position.[8]

The initiation of the first incisor crown formation lies within a narrow range of time (table 3). The second and third incisors have a larger range, while the permanent canine teeth may start development anywhere between 25 and 33 months.

The range of ages over which the crown of the first three incisors are completed are quite similar but the range is doubled for the canine teeth.

Intra-Osseous Eruption.—When a third or more of the permanent incisor roots are formed, migration within the mandibular bone begins. It commences for the first permanent incisor at 18 months and for the second incisor, third incisor, and canine teeth at 25, 30, and 38 months, respectively (table 3).

Emergence into the Oral Cavity.—Emergence into the oral cavity occurs when approximately four fifths of the root has been formed (fig. 7). This usually takes place approximately four to five months after intra-osseous eruption began.

Rate of Eruption.—Eruption commences when a third or more of the root is formed and it takes from four to five and one half months for each of the teeth to emerge into the oral cavity. However, eruption does not end with the appearance of the incisor into the oral cavity nor when it strikes the upper gum pad. Eruption still proceeds, but very slowly, to compensate for crown •wear.

Table 3 indicates a greater range in the time and rate of eruption for the third incisor and canine teeth than for the first and second incisors.

It will be apparent from the foregoing description of these processes, that there is a tendency for an increasing range in the ages at which they occur—from the first incisor to the canine in tooth sequences, and from the beginning of crown formation to the completion of root formation in time sequence.

Root Formation.—Root formation begins when the crown is completely formed. It is not completed until the tooth has been in active function within the oral cavity for approximately five months for the first and second incisors and nine months for the third incisors and canine teeth (table 3).

Rate of Root Formation.—The root takes from 15.7 to 19.5 months to form (table 3) in contrast to the six years required for human tooth root formation.[9] The range is larger for the second and third incisor

Legends for Figures 13-18 (Plate 3) on Opposite Page

Fig. 13—Radiograph of teeth of a 20-month-old Holstein-Friesian, the arrow indicates area showing the first evidence of calcification for the third incisor behind the crown of the second incisor. Root formation has begun for the second incisor. The first permanent incisor has started to rotate and erupt and resorption of the root of the first deciduous incisor is well advanced.

Fig. 14—Radiograph of teeth of a 23-month-old Holstein-Friesian heifer. The first incisor on the left is about to erupt into the oral cavity. Its rotation is nearly completed. The deciduous first incisors are ready to exfoliate.

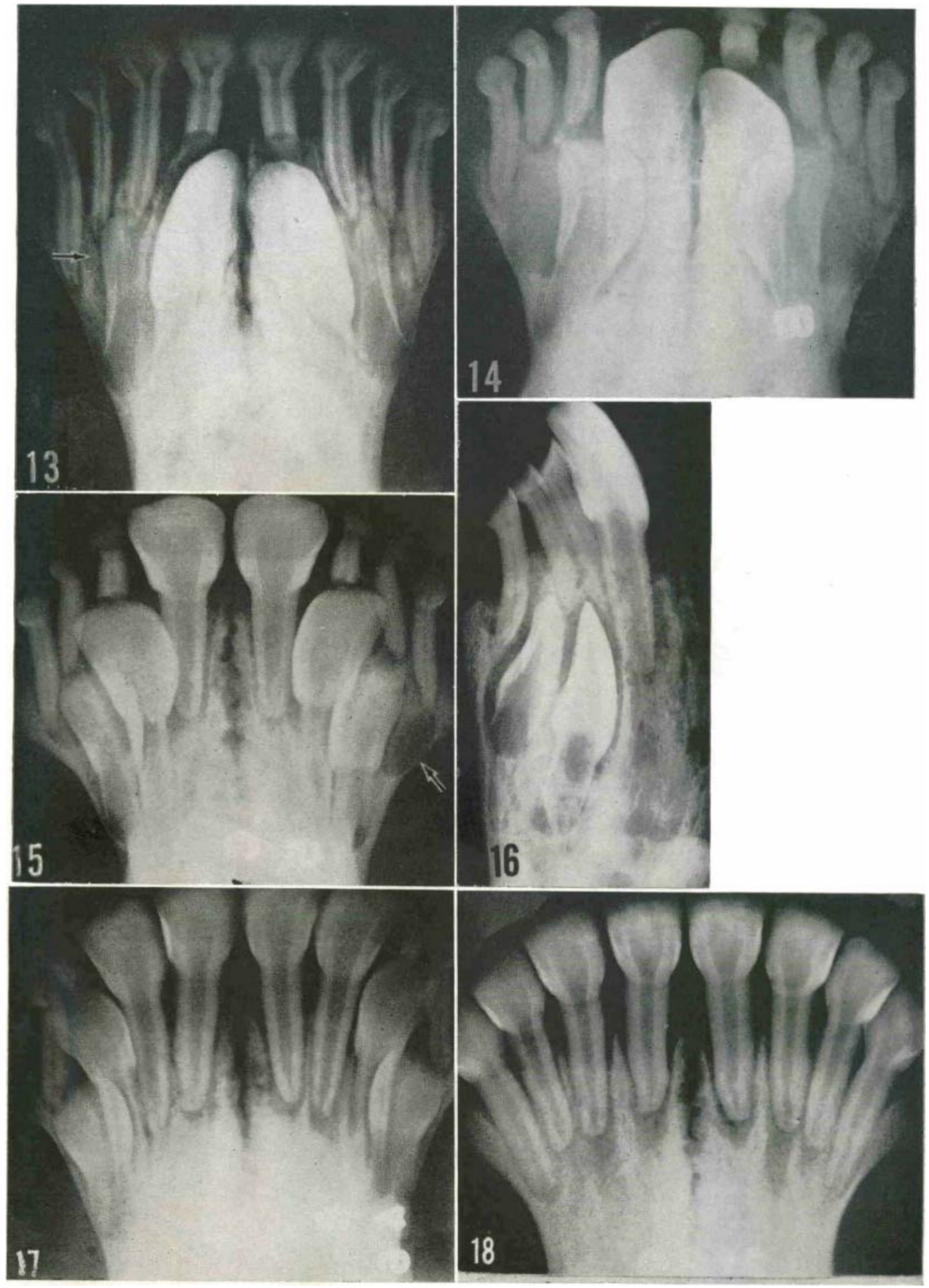
Fig. 15—Radiograph of teeth of a 27-month-old Holstein-Friesian heifer. Arrow indicates area showing beginning calcification of the canine tooth lingual to the crown of the third incisor. The crown of the third incisor is completed and its root has started to develop. The first incisor has erupted into the oral cavity.

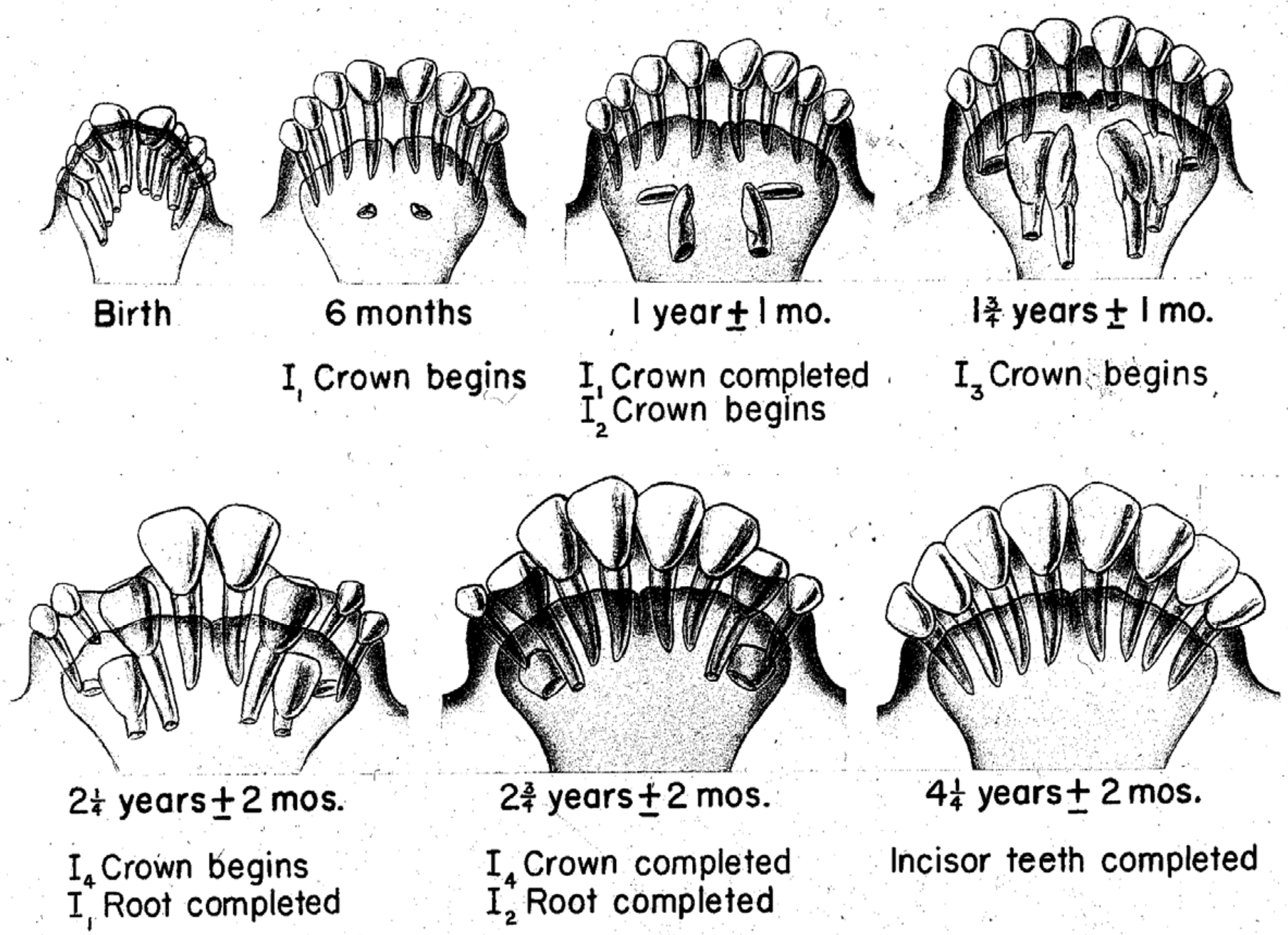
Fig. 16—Radiograph through one half of a mandible from an animal slightly younger than the one shown in figure 15. Notice the spatial arrangement of the three developing permanent

Fig. 17—Radiograph of teeth of a 3-year-old Holstein-Friesian cow. The third permanent incisor is about to emerge into the oral cavity as soon as the deciduous tooth is exfoliated. The root of the first and second permanent incisors are completed.

Fig. 18—Radiograph of teeth of a 4%-year-oId Holstein-Friesian cow. The permanent dentition is complete

is complete.




Birth
6 months
I_1 Crown begins
1 year ± 1 mo.
I_1 Crown completed
I_2 Crown begins
1¾ years ± 1 mo.
I_3 Crown begins
2¼ years ± 2 mos.
I_4 Crown begins
I_1 Root completed
2¾ years ± 2 mos.
I_4 Crown completed
I_2 Root completed
4¼ years ± 2 mos.
Incisor teeth completed

than it is for the first. There was inadequate data to show the frequency and distribution for the canine tooth, the estimate for completion at 52 ± 2 months being made from 28 animals ranging from 4 to 5 years of age.

Stages in Incisor and Canine Tooth Development

BIRTH

When the calf is born, nearly all the deciduous teeth have erupted, to different degrees (table 5 and fig. 8). The first incisor is usually fully erupted but the canine teeth may still be unerupted. Radiographs show that one half or more of the roots are formed and the pulp canals are still wide (fig. 8), but they show no signs of the permanent successors.

The jaws at birth are not large enough to accommodate the deciduous teeth, so the crowns and the roots are rotated and overlap each other (fig. 8). As the jaws enlarge, this crowding is relieved (fig. 10).

Six MONTHS

This age is characterized by the appearance of the tooth germ of the first permanent incisor in the radiograph (fig. 9). The earliest evidence of permanent incisor tooth development is the appearance of a circumscribed radiolucent area at the level of the first deciduous incisor. The radiographs do not show the calcified enamel at this stage, as calcification is of insufficient density to be contrasted with the investing bone. Below the permanent incisor follicle is another, but smaller, circular radiolucent area. This is the foramen for the mental nerve.

In the meantime, the roots of the deciduous incisor have been completed and a marked decrease in pulpal width is also apparent. The deciduous tooth roots begin to be resorbed with the appearance of the first permanent tooth follicle. Resorption starts in the apical region and, from there, spreads in an orderly manner up the length of the root until the tooth is exfoliated. Resorption is recognized on a radiograph by small areas of varying radiolucency in the dentin.

Periodo ntium.—The nature of the attachment of the tooth to the jaw is now apparent in the radiograph (fig. 9). A quarter or more of the root of the developing deciduous tooth has erupted beyond the crest of the alveolar process. The part of the root lying within bone is attached to the latter by the periodontal membrane, distinguished in the radiograph as a dark radiolucent band around the tooth root.

TEN MONTHS

This age is characterized radiographically by two thirds of the crown of the permanent first incisor being completed (fig. 10). The crown lies at right angles to the plane of ultimate alignment in the mouth as shown at 18 months (fig. 12A and 12B).

The Deciduous Incisors.—The radiograph shows a progressive reduction of crown size due to attrition and a narrowing of the pulp due to secondary dentin formation (fig. 10). Half of the incisor root now lies above the alveolar crest due to continued eruption of these teeth. As previously stated, this area of the root is supported by thick bundles of collagenous fibers which are covered by the attached gingivae. There is no evidence, clinically, of gingival recession. The periodontal membrane lies between the cementum covering the root and the alveolar bone which lines the tooth socket. This membrane (or ligament as it is sometimes called) is quite wide especially around the first and second deciduous incisors.

TWELVE MONTHS

Calcification of the permanent second incisor crown begins at 1 year, at the same time that the crown of the first incisor is completed.

The Deciduous Teeth.—Areas of resorption are well defined on the root of the first deciduous incisor (fig. 11). Early signs of resorption can also be seen on the root of the second incisor. Resorption of the second deciduous incisor begins sometime before the appearance of the follicle for the second permanent incisor due to impingement of the crown of the first permanent incisor upon the roots of the second, as well as the first, deciduous incisor. As seen in figure 4, the partly formed third permanent incisor lies behind the crown of the second permanent incisor.

-

TABLE 6—Composite Chronology of Mandibular Tooth Development

Teeth	Crown format-ion begins	Age of eruption	Sequence of development
DECIDUOUS			
1st jncisor	in utero*	0- 7 days	1
2nd incisor	in utero	0-14 days	2
3rd incisor	in utero	0-21 days	3
Canine tooth	in utero	14-42 days	4
1st premolar	in utero	0-14 days	3
2nd premolar	in utero	0-10 days	2
3rd premolar	in utero	0-10 days	1
PERMANENT			
1st incisor	6 mo.	23 ± 1 mo.	3
2nd incisor	12 ±. 1 mo.	30 ± 1 mo.	ii
3rd incisor	20 ±1 mo.	36 ± 2 mo.	8
Canine tooth	27.5 ± 2 mo.	42 ±2 mo.	9
1st premolar	13 mo.**	24-30 mo.t	1
2nd premolar	10 mo.	18-30 mo.	•I
3rd premolar	11 mo.	30-36 mo.	5
1st molar	in utero	5- 6 mo.	1
2nd molar	1 mo.	12-18 mo.	•1
3rd molar	10 mo.	24-30 mo.	4

* not available
** Standard deviation not determined.
*** Premolar and molar eruption age after Sisson,

The Permanent Incisor Teeth.—Development of the first permanent incisor proceeds rapidly. The crown is completely formed in six months.

The tooth germ of the second permanent incisor begins to deposit enamel and dentin within the dental follicle. This tooth lies lingual to the first incisor tooth crown, and is located at the apex of the second deciduous incisor (fig. 11).

TWENTY MONTHS

At 20 months, the third incisor begins to calcify and the second incisor is completed.

The Deciduous Incisor Teeth.—Besorption of the root of the first deciduous incisor is well advanced at 20 months due to the continued intraosseous movements of the first permanent incisor (tables 2, 3, and 5).

Boot resorption may be visualized as a biphasic process: (1) resorptiou at the apex of the root in response to the proximity of a developing tooth germ and (2) advanced semicircular resorption in response to the permanent successor's eruptive movements. In the latter phase of resorption, osteoclasts ascend along the lingual and mesial surfaces of the root on a broad semicircular front. This is better understood by comparing the two radiographs taken at right angles to each other as shown in figures 12A and 12B.

The labial surface of the root is the last to become resorbed. Sometimes it does not become resorbed at all and causes a lingual deflection of the erupting permanent incisor.

The Permanent Incisor Teeth.—By the 20th month, half of the root of the first incisor is completed (fig. 13). It has already begun its intraosseous eruption. Apparently eruption begins when approximately one third to one half of the root is completed.

The crown of the second incisor is completed and its root is just beginning to form. The outline of the follicle for the third incisor appears behind this crown near the root apex of the third deciduous incisor. This represents a stage two or three months in advance of the dissected specimen shown in figure 4. Three months later, at the age of 23 months, the right incisor is slightly in advance of the left (fig. 14). A slight difference in eruption is often observed between the two teeth of the pair. Also, the right permanent first incisor has rotated a quarter turn during its migration.

TWENTY-SEVEN MONTHS

This age is characterized by the beginning of calcification of the canine tooth.

TABLE 7—of Tooth Eruption in Cattle

.	Deciduous dentition		5mos.	6mos.	6mos.	6mos.	6mos.	6mos.
			M_1	M_2	I_1	I_2	I_3	C
	i_1 i_2 i_3 p_3 p_2 p_1	c				P_2 M_3	P_3 P_1	
Age	0-1/2 mo.	½-1 mo.	6 mos.	12 mos.	25 ≠ 1 mos.	30≠ 1 mos.	35≠2 mos.	42≠2 mos.
Crown Formation Begins	*in utero*		*in utero*	1 mo.	6 mos.	10 mos. 12 mos. 10 mos.	11 mos. 21 mos. 13 mos.	27 mos.

The crown of the third incisor was completed at 24 months. Meanwhile, the first incisor has erupted and, clinically, the mixed incisor dentition period has begun (fig. 2).

The. Deciduous Incisor and Canine Teeth —The pulp canals of these deciduous teeth are practically obliterated and only portions of the crowns remain (fig. 15). The roots often are apparently extruded above the level of the gum margin and worn quite a bit by the abrasive action of grass and other feed being pulled between the teeth (fig. 2).

The first deciduous incisor was exfoliated when the first permanent incisor erupted
three months previously. The root of the second deciduous incisor is almost entirely resorbed and the tooth is very mobile.

Resorption of the apices of the third incisor and canine teeth is well advanced and a small amount of bone supports these deciduous teeth (fig. 15).

The Permanent Incisor and Canine Teeth.
—The first incisor took its place within the oral cavity at 2 years of age when four fifths of the root was formed.   Now, the root is complete.

Three quarters of the root length of the second incisor is completed and intra-osseous eruption is well advanced. In three

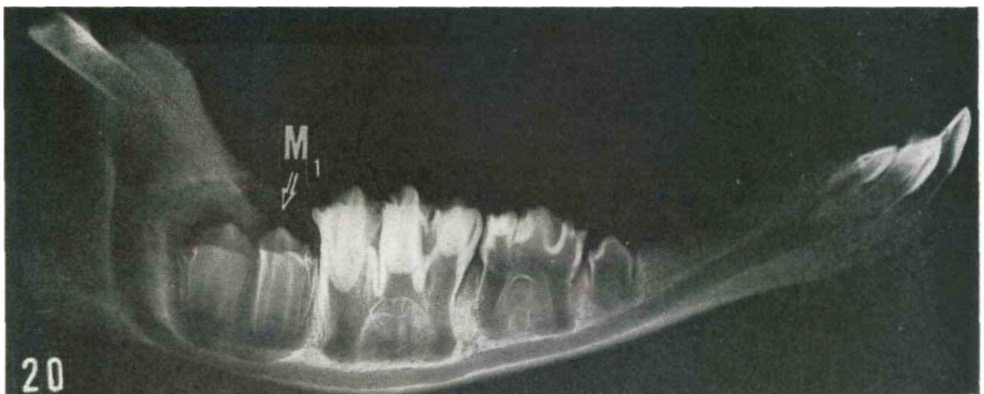


Fig. 20—Radiograph of a mandible of calf at birth showing relation of the deciduous incisors and premolars. The first deciduous incisor and third deciduous premolar are the first to emerge followed by the second incisor and the second premolar, then the first deciduous premolar and third deciduous incisor. The canine tooth is last to erupt. The developing crown of the first permanent molar (Mi) and the mandibular canal are visible.

Fig. 21—Radiograph of a 2-month-old bull's mandible. The three deciduous premolars are fully formed and are in functional occlusion. The crown of the first permanent molar is complete with a quarter of the root formed. The outline of the second molar follicle is seen with a third of its crown formed. The lamina dura shows around the roots of these teeth as compared with its absence around the anterior teeth.

months, the tooth, will emerge into the oral cavity.

One third of the root of the third incisor has formed, but there is as yet no evidence that the tooth has commenced to erupt. Its incisal edge still lies below the apex of its permanent successor.

The tooth follicles of the canine teeth are apparent in the radiograph, indicating the beginning of crown formation. In some cases, calcification at the incisor edge can just be detected (fig. 15).

A radiograph at a slightly earlier age through a half section of a mandible (fig. 16) demonstrates the spatial arrangement of the permanent anterior teeth and shows how they each lie one behind t'u other within the limited space of lie bony mandible.

The Arch Form.—From the earliest stages of development, with the eruption of the deciduous anterior teeth into the oral cavity, there has been a gradual enlargement of the mandibular complex which supports these teeth. In the beginning, the teeth were tightly packed together, but during the next two years, they have erupted farther into the oral cavity and spread out to form a smooth arch. Now, at 27 months, the crowns have become separated, partly from the wearing away of their broader incisal tips, but also because the eruptive movements are on a gentle curve carrying the teeth away from the midline.

This is part of the widening process of the mandible which allows for the development of the permanent teeth and, when they erupt, assures them adequate space to function.

THREE YEARS

The eruption of the third permanent incisor and exfoliation of its deciduous predecessors occurs at 3 years of age. Only a small part of the deciduous roots of the canine teeth are supported by bone (fig. 17).

The Permanent Incisor and Canine Teeth.—The first and second incisors have their roots completed. The third incisors are also erupted with four fifths of their roots formed. The canine tooth is not yet erupted but one third (or slightly more) of its root length is completed and it will shortly begin to move toward the oral cavity (fig. 17).

The Periodontium.—Until this stage is reached, it is not possible to see the periodontal membrane clearly, because of the overlapping teeth. The cervical third of the root of the first and second incisors are above the alveolar crest. The apical two thirds of the roots are embedded in bone. The roots are secured to the bone by collagenous fibers which form the periodontal membrane. This is seen radiographically as a narrow radiolucent band running between the root and the investing bone. It appears to be especially wide at the apex of the tooth (fig. 17). This probably represents an area of grouped collagen fibers which contributes to the cushioning of the tooth as it strikes against the upper gum pad.

FOUR AND A QUARTER YEARS

All the permanent incisor and canine teeth and their roots are completely formed (fig. 18).

TABLE 8—Chronology of Tooth Development in Different Breeds of Dairy and Beef Cattle

		A. Comparison of beginning crown formation				B. Comparison of completion of crown formation			
Breeds	No. animals	First incisor (months)	Second incisor (months)	Third incisor (months)	Canine tooth (months)	First incisor (months)	Second incisor (months)	Third incisor (months)	Canine tooth (months)
Dairy and beef	869	6.0	12.2 ± 1	20.0 ±1	27.5 ±2. 5	12.3 ± 1	18.6 ±1	24.0 ± 1	33.2 ±2
Dairy	495	6.0	12. 7 ±1	19.4 ± 1	27.3 ±2	12.0 ± 1	18.0 ±1	24.0 ± 1	33.4 ±2
Holstein-Friesian	365		11.8	19.5	26.5	11.6	17.4	24.0	33.0
Guernsey	76		14.0	19.0	27.6	13.0	18.0	24.7	33.0
Jersey*	33	6.0		19.0				24.0	84.0
Brown Swiss*	14		12.0	19.0	27.6		17.0		33.0
Ayrshire	7	6.0	13.0	21.0			19.0		
Beef	374	6.0	11.6 ±1	20.5 ±1	27.8 ±2	12.5 ±1	19.2 ±1	24.0 ± 1	33.0 ±2
Hereford	258	6.0	11.4	20.5	28.8	13.0	20.0	24.5	32.5
Aberdeen Angus	100	6.0	11.7	19.5	26.8	11.5	17.0	23.0	31.0
Shorthorn*	16	6.0				13.0			
Bulls (all breeds)	105	6.0	12.0 ±1		27.4 ±2	12.6 ±1	18.0 ±1	26.0 ±1	

A complete summary of these stages of incisor and canine tooth development is illustrated by composite drawing (fig. 19).

Comparison of Tooth Development in Different Breeds

There are marked physical, physiological, and developmental differences between the dairy and beef breeds. They attain body maturity at different ages and reach mature weights and heights at different ages. In addition, the body economy of each is geared toward different objectives—the dairy animals to produce milk and the beef animals to acquire flesh. Because of the different economies, farm management is based on different principles.

Furthermore, the breeds are individual types with different characteristics. It was, therefore, thought necessary to test whether the chronology of tooth development differed among the different breeds and sexes.

METHOD OF ANALYSIS

The .radiographs for all the dairy cattle were first arranged in sequence according to age, disregarding the different types or breeds of animals within this group. The same was then done for all the beef animals. Prom these radiographs, the mean and 1.5 standard deviations were then calculated for the following stages in the development of each of the incisors and the canine teeth:

1) Beginning and completion of crown formation
2) Eruption into oral cavity
3) Completion of root formation

The chronology of tooth development was then compared for all dairy and for all beef cattle (fig. 25).

When this was completed, the same data were computed and compared for the Holstein-Friesian, Guernsey, Hereford, and Aberdeen Angus breeds separately. There were inadequate data to compare on an equivalent basis the Jersey, Brown Swiss, and Shorthorn breeds, but by extrapolation it was possible to obtain some indication as to whether the chronology of their tooth development was similar or differed widely from the other breeds. The similarity of the chronology of tooth development among all the breeds studied, individually or collectively, is shown (table 8).

Finally, the chronology of tooth development was computed for all the bulls and compared with chronology of tooth development for the combined beef and dairy herds.

The findings in detail were as follows:

Beginning of Crown Formation.—The first incisor started to form for all the breeds within a remarkably limited range of age, and no significant difference was discernible for any of the breeds examined (fig. 25 and table 8). The same was true for the second and third incisors. Only the canine tooth differed slightly in that it tended to develop a little earlier in the beef breeds (fig. 25 and table 8).

Eruption into the Oral Cavity.—For the first three pairs of incisors, there was little distinction among the different breeds. Graph 2 and table 6 indicate that eruption of the first incisor in the Holstein-Friesian group was slightly in advance of the other

TABLE 8—(Continued)

		C. Comparison of eruption into oral cavity				D. Comparison of root completion			
Breeds	Number animals	First incisor (months)	Second incisor (months)	Third incisor (months)	Canine tooth (months)	First incisor (months)	Second incisor (months)	Third incisor (months)	Canine tooth (months)
Dairy and beef	869	23.0 ± 1	30.0 ± 1	35.7 ±2	42.0 ± 2	28.0 ±1	35.0 ±2	43.5 ±2	52.0
Dairy	495	23.0 ± 1	29.8 ±1	36.0 ±2	42.7 ± 2	28.2 ± 1	35.5 ±2	42.6 ±2	52.0
Holstein-Friesian	365	21.5	30.2	35.7	43.5	29.0		42.5	51.6
Guernsey	76	23.6	30.0	35.4	42.0	28.2	35.5	42.0	
Jersey*	33			37.0		27.0		42.0	
Brown Swiss*	14					28.0	35.6		
Ayrshire	7								
Beef	374	23.0	30.6	35.3 ±2	41.0 ±2	28.0 ± 1	34.7 ±2	44.4 ± 2	52.0
Hereford	258	23.1	31.0	34.8	41.0	28.5	34.3	45.5	52.6
Aberdeen Angus	100	24.0	30.0	36.0		28.0	35.0	44.0	
Shorthorn*	16					28.0			
Bulls (all breeds)	105		29.0 ±1	35.5 ±2	40.0 ±2	28.4 ±1	35.6 ±	42.0 ± 2	

* Extrapolated. Omitted figures inadequate material .

breeds. In general, the canine teeth appeared to develop and to erupt a little earlier in the beef than in the dairy breeds (fig. 25 and table 8).

Completion of root formation.—Little difference was discernible for the first and second incisors and the canine teeth, but the third incisor appeared to complete its root formation a little earlier in the dairy animals (fig. 25 and table 8).

The bulls showed no consistent differences from the cows (table 8).

Conclusions.—The chronology of tooth development was found to be remarkably similar in all breeds of beef and dairy animals in spite of striking differences in other developmental processes and in genetic makeup. The chronology of tooth development in cattle appears, at first sight, to be a basic factor common to all breeds and does not appear to be linked to changing genetic factors or other developmental characteristics. However extensive experimentation would be necessary to prove this point.

Chronology of Premolar and Molar Development

It was thought that the chronology of tooth development would be incomplete without reference to the premolars and molars. Huidekoper[5] writing in 1891, tabulated the ages for the eruption of the anterior teeth, premolars and molars which had been worked out by different authors during the nineteenth century. Sisson, in 1953,[11] published a similar table of tooth eruption in cattle. None of these studies indicated the chronology of other phases of tooth development to cattle.

Methods.—Unfortunately, no simple technique was available for obtaining radiographs of the premolar and molar region in living animals. To overcome this lack, mandibles from animals of known ages were obtained from slaughterhouses. The mandibles were dissected free of other tissues and radiographs were obtained of the incisor and molar areas using our ordinary radiographic technique.

Because of the comparatively small number of specimens, it was necessary to extrapolate for the different stages of tooth development. The figures given (table 4) are therefore approximations.

Since many of the ages of the specimens were approximations, the physiologic age was determined by comparison with the stage of incisor development in the same jaw. This method of cross-dating proved satisfactory in that the stage of premolar and molar development was related to the stage of incisor development; and so permitted the determination of the sequence of tooth development (table 6).

Materials.—The dental material came from a slaughterhouse so the data was limited to 75 animals of indeterminable breeds and nutritional background, but of known ages which were equally distributed from birth to slightly more than two" years.

Stages of Development

BIRTH

When the calf is born, the third deciduous premolar is usually erupted. It is followed soon by the second and first premolar so that by the second week, the deciduous dentition is complete except for the slow developing canine teeth. Interestingly, the order of development in the deciduous premolars (3rd, 2nd, 1st) is the reverse in the deciduous incisors (table 6).

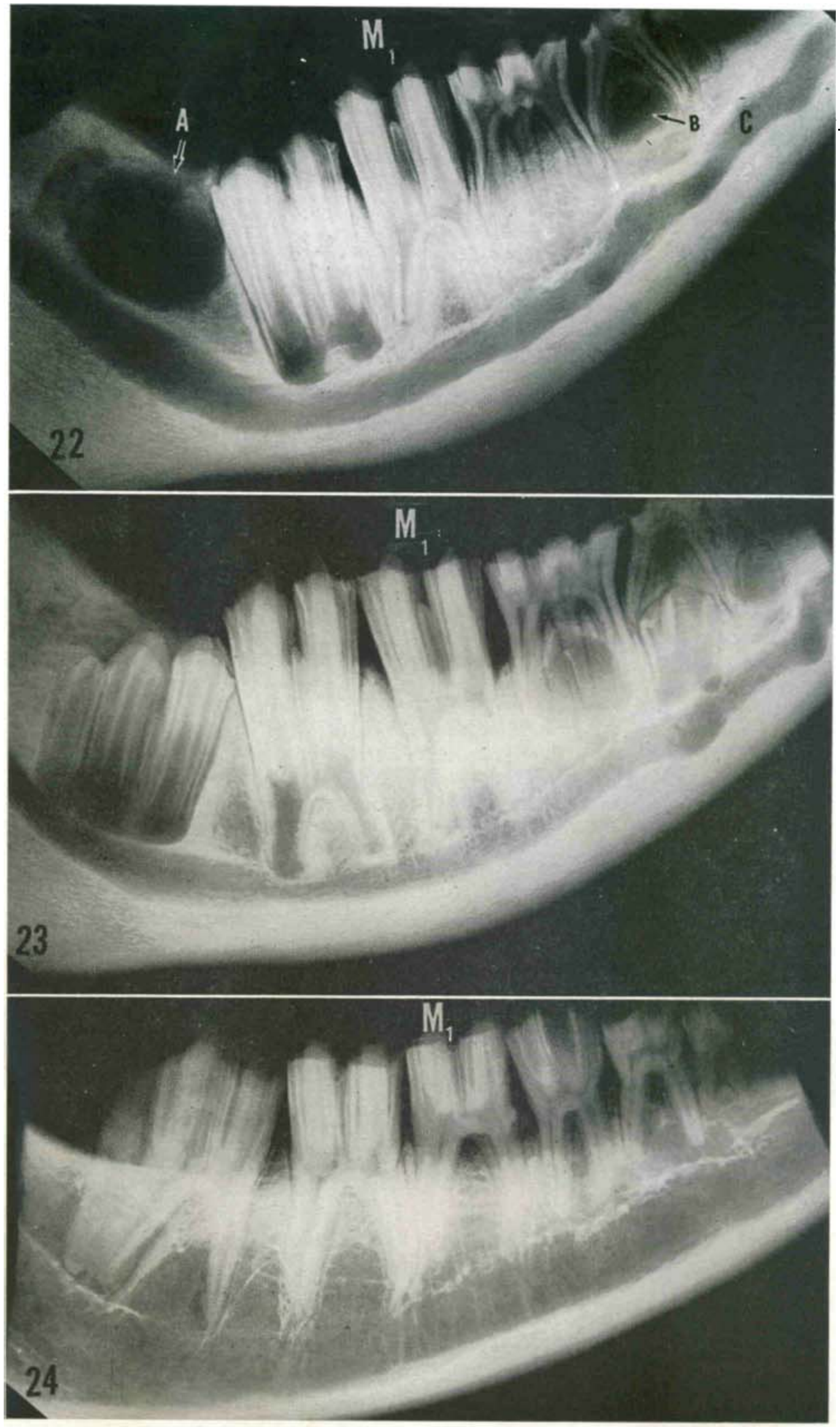
At birth, the crowns of all the deciduous premolars (like the deciduous anterior teeth) are completely formed, while the roots are at different levels of development

Legends for Figures 22-24 (Plate 4) on Opposite Page

Fig. 22—Radiograph of mandible of a 12-month-old Hereford steer. The first permanent molar is erupted and the second permanent molar has started to erupt, while the calcification of the third molar crown has just begun (A). The follicle of the second permanent premolar (B) is seen between the roots of its deciduous predecessor. Notice the large mandibular nerve canal (C).

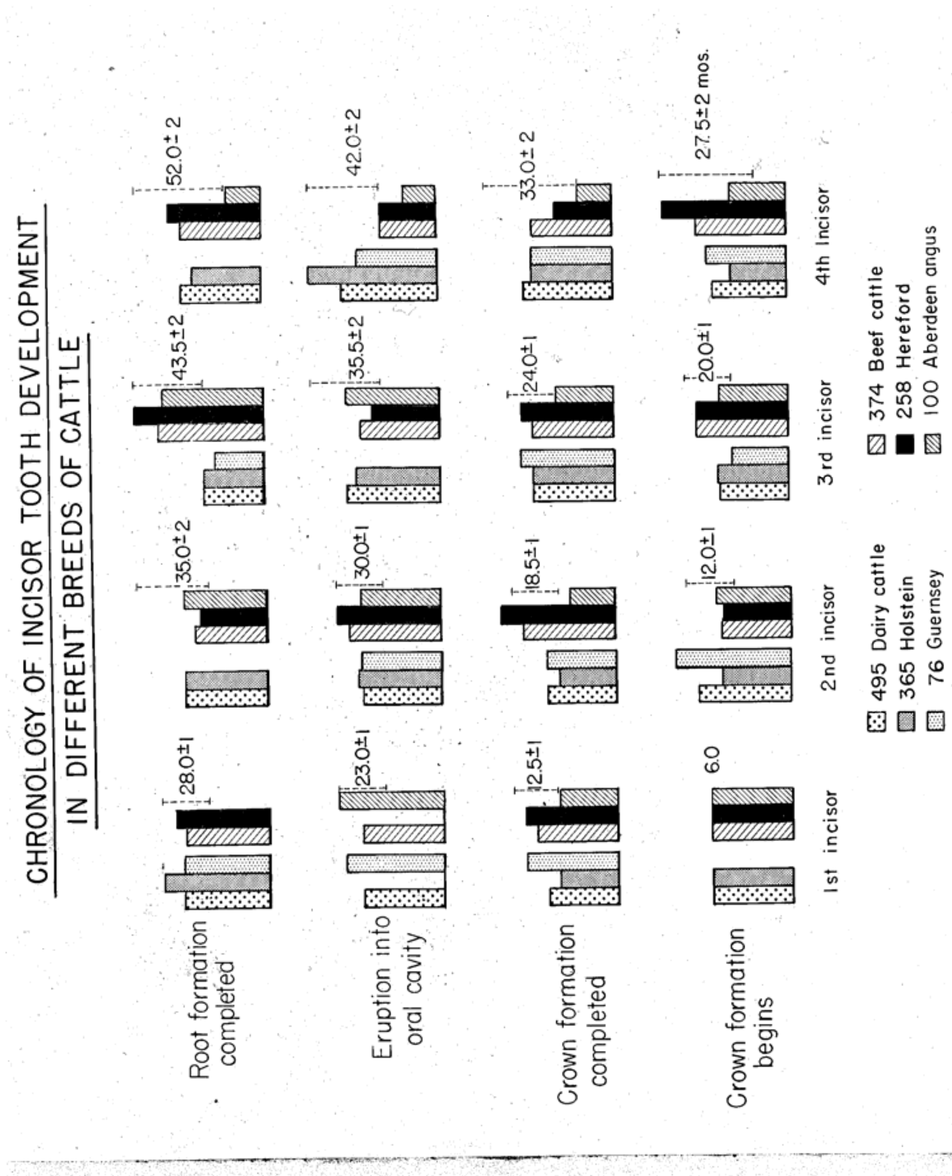
Fig. 23—Radiograph of mandible of a 16-month-old Hereford cross-bred steer. The tooth germs of the three permanent premolar crowns can be seen lying between the roots of their predecessors. The second permanent molar crown is nearly completed.

Fig. 24—Radiograph of an adult Holstein-Friesian cow's mandible. The permanent dentition is complete.



-34

Plate 4


CHRONOLOGY OF INCISOR TOOTH DEVELOPMENT
IN DIFFERENT BREEDS OF CATTLE
Root formation completed
Eruption into oral cavity
Crown formation completed
Crown formation begins
1st incisor
2nd incisor
3rd incisor
4th incisor
28.0±1
23.0±1
12.5±1
6.0
35.0±2
30.0±1
18.5±1
12.0±1
43.5±2
35.5±2
24.0±1
20.0±1
52.0±2
42.0±2
33.0±2
27.5±2 mos.
495 Dairy cattle
365 Holstein
76 Guernsey
374 Beef cattle
258 Hereford
100 Aberdeen angus

(fig. 20). Root formation is completed approximately two months later (fig. 21).

Development of the first permanent molar teeth begins *in utero.* At birth, one third of the crown is calcified, and may be seen lying in its follicle posterior to the last deciduous premolar (fig. 20). Also visible is the mandibular canal which carries the nerve and blood vessels for the teeth and surrounding tissues. It runs from the middle of the ascending ramus, between the developing teeth and the lower mandibular border to the incisor region. It increases markedly in width with age (fig. 20 to 24).

Six MONTHS

From birth until 6 months is the period of the deciduous dentition. With the eruption of the first permanent molar at 5 to 6 months of age, the mixed dentition period begins. This lasts until the deciduous canine teeth are exfoliated in the fourth year. The eruption of the first permanent molar into the oral cavity is coincident with the beginning of crown formation for the first permanent incisor (fig. 9).

The first permanent molar is the smallest of the permanent molar series, while the second and third are the larger.

Since the first permanent molar begins to calcify before the animal is born and does not complete its crown until the third mouth of life, the neonatal line marking the trauma of birth should be found within the enamel and dentin which was forming and calcifying at the time of birth.

TWELVE MONTHS

The second permanent molar may be partly erupted at 12 months of age (fig. 22). This molar begins to calcify soon after birth (fig. 21) and it takes approximately a year for the crown to form (table 4). This is twice as long as required for the formation of a permanent incisor crown.

Intra-osseous eruption of the molars begins soon after the crown is completed. This is much earlier than was observed in the incisors, which do not begin to erupt until their roots are one third completed. Formation and calcification of the third molar, and the three premolars begin at approximately the same time, between 9 to 13 months of age (fig. 23). The crowns are completed approximately one year later (table 4). Emergence into the oral cavity follows soon after the crowns are completed, between the second and third year of life, the order being second premolar, third molar, first premolar, and third premolar. The molars erupt into the oral cavity soon after intra-osseous movement begins because, unlike the anterior teeth, the crowns of these teeth develop close to the surface of the jaws. Intra-osseous eruption begins early (when the crown is completed) and terminates quickly because little movement is necessary to bring these teeth into function. The incisors and canine teeth, when they have erupted, lie high above the basal bone, almost entirely within the alveolar process, while the molars, when they first erupt, are largely within the basal bone and have only a small alveolar process. However, as the molars continue to erupt slowly during function, they migrate away from the lower border of the mandible and the basal bone. At the same time, bone forms at the alveolar crest to give additional support to the erupting tooth, and thus the height of the alveolar process increases throughout life (fig. 20 and 24).

Two YEARS

The second and first premolar teeth erupt into the oral cavity at 24 to 30 months, between the appearance of the first and second permanent incisors followed soon after by the third and. first premolars (table 5). The second year is, therefore, characterized by a rapid displacement of many of the deciduous incisors and premolars by their permanent successors.

THREE YEARS

By the third year of life, all the premolars and molars are erupted and three of

Legend for Figure 25 on Opposite Page

Fig. 25—Composite graphs comparing the chronology of tooth development in different breeds of dairy and beef cattle (± indicates 1.5 standard deviations around the mean and is indicated by the vertical dotted line).

the four permanent anterior teeth are also erupted (fig. 24). The permanent dentition is almost complete, except for the canine teeth. The last tooth emerges after an interval of approximately six months (81/2 years) to complete the permanent dentition. This delay supports the thesis that the fourth anterior tooth is related to the late developing canine tooth of other species.

Discussion

GENETIC DIFFERENCES

Little difference was observed in the chronology of any phase of tooth development, including eruption, between the various breeds (fig. 25). When a marked difference did occur, it was usually associated with a shortage of data. This suggests that the chronology of tooth development may not be related nor influenced by genetics in the same way that tooth or jaw morphology are. It suggests that the differences in eruption age observed in man may be better related to environment factors such as diet, occlusion, size of jaws, etc., rather than to genetic differences. However, these considerations can only be confirmed by planned experimentation.

SEX DIFFERENCES

The bulls were not consistently more precocious nor more retarded in any one of the tooth developmental processes considered.

The fact that all the animals were on optimal levels of nutrition may well be a contributing factor to the small difference of tooth chronology found.

Perhaps the chronological pattern may be a guide to nutritional status. The analysis of chronology of tooth development of a sample of continuously undernourished animals would be a worth while study.

ORDER OF ERUPTION

The six-month (first permanent) molar is the bovine equivalent of the human 6-year-old molar, while the 12-month second permanent molar is equivalent to the human 12 year (second permanent) molar.

The third permanent molar and the three premolars erupt as a group, just as the premolars and second molars do in man.

A fixed and definite order in the eruption of this premolar and molar group (P2-M3-P1-P3) is implied (table?). However, this order may well be changed in a larger or wider sample under different local conditions, diet and occlusion, as it does in man.

THE "AGING" OF ANIMALS

From time immemorial, the age of many species of domestic animals has been assessed by the state of eruption and wear of their teeth. This study suggests the possibility of using intra-oral radiographs for assessing the age of animals more accurately during the first four years of their life. The accuracy of this method is indicated by the narrow range in which the developmental process takes place.

A controlled, double-blind study comparing estimations of age from clinical observations of teeth with estimations made from radiographs in a group of animals with accurate birth records would be most revealing.

TOOTH RING ANALYSIS

As indicated before, the enamel- and dentin-forming cells are extremely sensitive to systemic changes in their environment while they are actively engaged in the deposition and calcification of the enamel and dentin matrix. Any metabolic change in the organism affects the quality and sometimes the quantity of matrix deposited by these cells. These are seen as accentuated incremental lines in the enamel and dentin and, if the disturbance is severe enough, hypoplastic defects result.[12]

In human teeth, examination of the rings or layers of enamel and dentin formed during different periods of development show that the prenatal enamel is much better and homogeneously calcified than the postnatal enamel, the two portions being separated by a prominent incremental line or ring at the exact level of enamel and dentin forming at birth. This neonatal ring is a valuable landmark which aids in the assessment of prenatal as well as postnatal injuries or defects in development. Massler, Schour, and Poncher[12] also describe differences in the degree of calcification of enamel formed during infancy, early childhood and later childhood. They found accentuated lines occurring constantly at the level formed at 10 months of age (infancy ring), $2y_2$ years (early childhood ring), and at $4^/{}_2$ years (later childhood ring). They suggest that such metabolic changes as weaning and puberty should leave permanent records in the structure of the enamel and dentin.

The teeth of cattle offer a valuable opportunity to study the effects of other metabolic episodes on the form and calcification of enamel and dentin. It is certain that there is a neonatal line in the first permanent molar and, since cattle are bred while enamel and dentin are still forming, the effects of pregnancy should, therefore, be registered in the enamel and dentin forming at 18 to 24 months (cervical area of 1_2 and 1_3). Clearly this hypothesis may be tested by comparison of the teeth of cows with the teeth of bulls or steers.

Preliminary observations in a number of ground sections of teeth indicate that the enamel and dentin of the incisors contain a relatively large number of prominent incremental lines; also, that this rapidly growing structure is extremely sensitive and surely records equivalent metabolic periods observed in the slower growing human enamel. Furthermore this enamel may register the effects of nutritional variations (summer and winter feed) in its enamel as well as minor infections and systemic ailments.

With the chronology of tooth development in cattle better established, it will be possible to make a detailed analysis of the different incremental lines that have been noticed. By examining the teeth of animals with precisely recorded developmental and nutritional histories, these incremental lines may be correlated to different physiological stresses as weaning, pregnancy, and lactation or different nutritional experience. Furthermore, the severity of mottling as caused by ingestion of excessive amounts of fluorides can be related to the animal's physiologic development.

Summary and Conclusions

This study was designed to establish the chronology of enamel and dentin formation in cattle as accurately as possible in order to lay a firm foundation for future studies in tooth ring analysis, *i.e.,* the effects of specific physiologic and pathologic stresses on enamel and dentin formation.

The chronology of development of the permanent incisor and canine teeth was established from analysis of radiographs obtained *in vivo* from 869 purebred cattle living under optimal nutritional conditions. It was found that development of the incisor and canine (anterior) teeth followed an orderly sequence. The first incisor began to develop enamel and dentin when the calf was 6 months of age; the second incisor at 12 months, when the crown of the first incisor was completed; and the third incisor at 20 months, soon after the crown of the second incisor was completed at 18 months. The canine tooth began its enamel and dentin formation at 27 months, three months after the third incisor crown was completed.

Eruption and root formation followed a similar orderly sequence from the first incisor to the canine tooth. The first incisor emerged into the oral cavity at 23 months, the second incisor at 30 months, the third incisor at 36 months and the canine teeth at 42 months. Root formation was four fifths completed at the time of emergence.

No significant differences in the chronology of tooth development in the different breeds or sexes was found in spite of rela-
ferences between dairy and beef cattle, tively
large developmental and genetic dif-

It is hoped that this study will provide a satisfactory baseline for future studies which relate the effects of physiologic stress such *as* birth, weaning, pregnancy, and lactation as well as pathologic factors as nutritional deficiencies, fluorosis intoxication, and infectious diseases upon the enamel and dentin (tooth ring analysis).

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