DENTITION OF THE NORTHERN FUR SEAL

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ABSTRACT

Gross morphology and development of deciduous and permanent teeth of *Callorhinus ursinus* are described. The deciduous teeth are essentially nonfunctional; two-thirds of them are usually shed in fetal life. The permanent teeth begin to calcify very early; all have erupted from the jaw, though not all from the gum, at birth. Root growth continues through life, especially in teeth which retain an open pulp canal for 20 years. The 1st premolar and all molars in each quadrant are primary permanent teeth. A "lower 1st incisor" was presumably lost in the evolution of the seal. Cusplets and a double root on certain teeth suggest that modern teeth are derived from more complex ones. In 11 percent of specimens, supernumerary or prenatally absent teeth are recorded.

Purpose

Since 1867 the U.S. Government has managed the Alaska fur seal herd. The seals breed on the Pribilof Islands, and their population in midsummer is about 1,800,000. To improve the management of the herd, the Government obtains zoological information about the animals in its care. In 1949, in the course of exploratory research, Fish and Wildlife Service biologists found that fur seal teeth have layers which correspond in number to the age of the individual in years (Scheffer, 1950). This finding has proved to be useful, and biologists now engaged in applied research have identified the ages of more than 50,000 seals killed during the past decade.

The study of fur seal dentition has continued so that we could gain a better understanding of variation in the teeth and jaws with age and sex. One purpose of the present paper is to trace the origin, growth, and disappearance of the deciduous (milk) teeth which erupt from the bony alveolus in early fetal life. Another purpose is to trace the origin and growth of the permanent teeth which normally erupt from the bony alveolus in late fetal life.

Previous Research

While the dental formula for the fur seal *Callorhinus ursinus* has been known for nearly a century, the ontogeny of the dentition has not been well described. The young fur seal is extremely precocious, and its dentition is determined and developed in utero during winter and spring when the pregnant female is at sea. Because of prohibitions against killing seals at sea, biologists were unable, until 1950, to obtain fetuses. Between 1958 and 1962 they took annually for research purposes about 900 pregnant females along the oceanic migration routes.

Certain papers have contributed to our understanding of the teeth of *Callorhinus*. Allen and Bryant (1870) presented drawings of the skulls of young and adult *Callorhinus* and the first description of fur seal permanent dentition.

Allen (1880) stated that the teeth of *Callorhinus* are weaker than those of the southern fur seal *Arctocephalus*, the Steller sea lion *Eumetopias*, or the California sea lion *Zalophus*.

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Kükenthal (1894) reviewed the literature on deciduous teeth of seven phocids and one otariid (the southern fur seal). In all he reported three deciduous premolars antecedent to the 2d, 3d, and 4th permanent premolars in each quadrant.

Lucas (1899) gave the deciduous and permanent dental formulas of *Callorhinus* as known today. He examined only one fetus younger than full term and identified as premolars the first four postcanines in each quadrant, after observing that the three deciduous premolars are adjacent to the alveoli of the 2d, 3d, and 4th permanent premolars.

Osborn (1907, p. 143) believed that "the teeth of the . . . Pinnipedia are so much modified secondarily that until we trace their ancestral history we cannot feel any confidence in attempts either to homologize the cusps or to trace these teeth back to a tritubercular or triconodont stage."

Todd (1918, p. 175) stated that "it does not take very long, geologically speaking, for a tritubercular molar to retrogress into a simple conical tooth." His remarks on the California sea lion *Zalophus* apply also to *Callorhinus*: "The premolars and molar of the maxilla are secondarily simple teeth, each with a well-marked cingulum surrounding the base of the crown. Their single cusps probably represent the paracone. The mandibular cheek teeth are also simple but the basal cingulum rises into a small cusp in front and behind the apex [crown tip] of the tooth, which may be the homologue of the protoconid" (p. 186).

Kellogg (1922) concluded that the terrestrial ancestors of the Pinnipedia may have had six more teeth than has modern *Callorhinus*. They may have had, on each side, one more upper posterior molar, one more lower medial incisor, and one more lower posterior molar. "In studying the dentition of the Otariidae," wrote Kellogg (p. 64, 100), "the fact is gradually forced upon one that the earliest otarids slowly retrogressed from the complex, flesh-tearing dentition of the land carnivores and reverted back toward a simple, conical tooth most favorable for the capture of elusive prey. . . . The evidence shows that the reduction of the true molars was very rapid in the Otariidae, at least."

Howell (1929) gave a dental formula for otariids which included one, two, or three lower molars on each side. Reference to three lower molars is puzzling. While the Miocene pinniped *Allodesmus* had two lower molars, no modern pinniped normally has more than one on each side.

Simpson (1945, p. 233) stated that "probably the pinnipeds are an early offshoot of the little differentiated late Eocene and early Oligocene canoid ancestry, paralleled by the otters, which had the same ultimate origin and a similar adaptive trend, and in other features by the bears, also with the same remote origin." The oldest known pinniped remains are from Miocene beds, perhaps 35 million years old. The remains are fossil skulls and skeletons, and are obviously those of pinnipeds. Their progenitors are completely unknown (Scheffer, 1958).

Rand (1950) studied the dentitions of 42 pups of the southern fur seal *Arctocephalus*. The teeth are like those of *Callorhinus*, although deciduous canines may persist for 5 months and deciduous premolars for 4 months after birth.

Gregory (1951, p. 405) stated that the teeth of seals "are usually 'simple' pegs, with a basal cingulum, a small basal cusp and conical, slightly recurved crowns adapted for fish-catching. Very probably this is a retrogressive, secondarily simplified dentition." He stated that there are four premolars in each quadrant, and he supposed that all have deciduous predecessors.

In a random sample of 38 female fur seal skulls, Chiasson (1955) found 6 that lacked one or more upper teeth, usually including the posterior upper molar. He stated (p. 564) "due to the fact that fur seals may replace the 6th upper postcanine [m2], this deciduous tooth might, upon accidental extraction, be replaced by the permanent tooth."

In 1957 Chiasson presented a discussion of the dentition of the fur seal. He emphasized the "double-rooted tooth development" of the posterior postcanines, stating that it "appears in the alligator and perhaps in other reptiles but not, to my knowledge, in any other mammal." Chiasson implied that the fur seal can have only three premolars in each half of each jaw since it has only three deciduous postcanines. He surmised that pinnipeds could not have evolved from creodont (precarnivore) stock because the creodonts had complicated teeth and modern seals do not.

Sergeant (1959) and Laws (1962) discussed the rhythmic deposition of dentin and cementum on the teeth of seals and cetaceans. The result is often a series of annual growth layers or ridges, useful as indicators of age (see page 308).

An Interim Convention on Conservation of North Pacific Fur Seals was signed in 1957 by representatives of four nations. The Convention resulted in anatomical studies by biologists of Canada, Japan, and the United States. The studies have produced six recent reports on dentition, namely, theses by Bokstrom (1961), Takano (1961), and Lamb (1962), written with the guidance of Kraus; and three publications by Kubota, Komura, Nagasaki, Tsuboi, and Matsumoto (1961a, b) and Kubota, Nagasaki, Matsumoto, and Tsuboi (1961). We shall discuss these later.

In critically reviewing previous research, the following points are important: (1) The number of permanent premolars in each quadrant has been given, variously, as three and four; four is correct. (2) In the southern fur seal, the deciduous canines may persist for 5 months, as against 3 months in the northern genus (p. 300). (3) While fossil evidence is lacking, the teeth of pre-Miocene seals were presumably more numerous and were more elaborately cusped than those of Recent seals. (4) One author has emphasized the evolutionary importance of the simple crown of all postcanines, and the double root of certain postcanines. In our opinion, there has been ample time—at least 35 million years—for the development of both features. (5) From six recent reports issued in 1961 and 1962, pertinent data have been extracted and will be used in the present paper as supplementary and comparative material, with appropriate citations.

MATERIALS AND METHODS

Numbers of Specimens

The specimens of the present study were collected on the Pribilof Islands, or at sea along the northwest coast of North America. They include material in formalin, dry skulls, dental arches only, isolated teeth, and photographs only, as follows:

	Number
Fetal and prematurely born (aborted)	20
Newborn and full-term fetal	18
Pups older than newborn	34
Yearling, pelagic	5
Yearling, autumn (on land)	4
Ages 2 to 10 years	62
Over 10 years	24
Total	167

Of these, about half are represented by skulls in the permanent collection of the National Museum or in the Bureau of Commercial Fisheries Marine Mammal Biological Laboratory. The others are represented by specimens which have been dissected, photographed in the field, or otherwise treated as temporary study materials.

We have also examined, in order to estimate the incidence of anomalous teeth, the skulls of 42 seals taken pelagically in 1952, and several hundred isolated teeth (right upper canines) taken in the course of fur seal population studies.

Dr. Tadahiro Ohe (Tokyo Medical and Dental University), while studying at the University of Washington School of Dentistry in 1962, made special preparations of several early fetuses and has generously allowed us to use certain of his unpublished findings. These are noted at appropriate places.

With minor exceptions, the specimens represent seals killed at random from a normal population. They do not represent a pathological group or a group of individuals found dead and salvaged for scientific use. The demonstrated variability in dentition is believed to be typical of the population at large.

Ages of Specimens

The exact ages of the fetal specimens are not known. From embryological evidence, however, it is possible to estimate for a fetus of given weight, its implanted age and its progress toward full-term size. The evidence is sketched below.

Date of implantation.—Pearson and Enders (1951) examined the genital tracts of 99 adult female seals killed on a Pribilof breeding ground on October 27, 1949. The seals were 4 years old or older. In each of 10 tracts the investigators found a single blastocyst, and they noted that around 6 of the blastocysts an implantation pocket was beginning to form. The general conclusion may be drawn that, by late October at least, no embryo of macroscopic size is present.

Scheffer (1960) examined another collection of adult female tracts obtained on the same breeding ground, though later in the year, as follows: four tracts on November 18, 1958, three tracts on 28 November 1951, and five tracts on December 3, 1958. Only in the December sample did he find embryos of macroscopic size: three embryos 10, 10, and 20 mm. in crown-rump length.

Douglas G. Chapman (in letter of October 15, 1957) analyzed the weights of 398 fetuses collected between mid-January and the end of June. The weights "were plotted on arithmetical probability paper (time versus percent of final value). This is essentially equivalent to assuming that the growth curve follows the logistic form." Extrapolation suggested a fetal weight of 10 g. for both male and female on November 21. Considering all the evidence available, we tentatively conclude that the mean date of implantation is in mid-November.

Fetal growth rate.—The weights of the 398 fetuses have been published (Scheffer, 1962). A chart of the weights up to the 10-day period centering on June 28 is shown in figure 1. During this last period, the mean weight of four males was 5.6 kg., and of seven females was 5.5 kg.

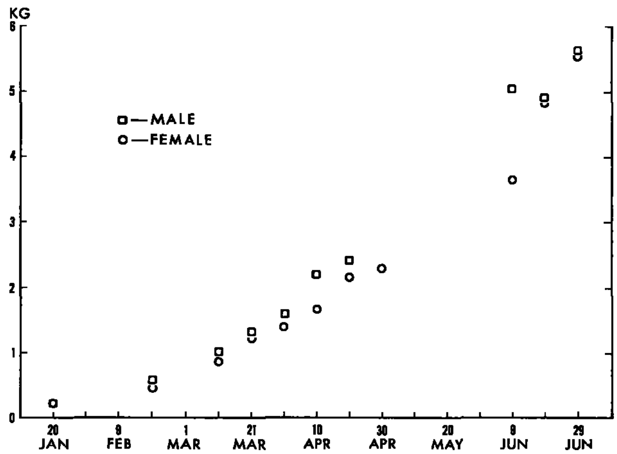

FIGURE 1.—Body weight of the fetal male and female, January to June. (Based on the weights of 209 males and 189 females (Scheffer, 1962, tables 1 and 2).)

Date of birth and weight of the newborn pup.—On a breeding ground where at least 782 pups were born in the summer of 1951, Bartholomew recorded the number born per day (Bartholomew and Hoel, 1953). The mean birth date was July 13.

At various times in summer on the breeding grounds, a total of 39 newborn and full-term fetal pups have been weighed (Scheffer and Wilke, 1953). The mean weight of 23 males was 5.4 kg., and of 16 females, 4.8 kg. These values are slightly less (7 percent) than those obtained for 11 fetal seals collected at sea in late June (see above). The discrepancy is probably a small-sample effect, though perhaps it may also be due to natural variation, from one year to the next, in newborn size. For purposes of the present paper, mean newborn weight (MNW) is 5.4 kg. for males and 4.8 kg. for females.

Ages of postnatal specimens.—From the time it is born in midsummer to the time it departs from land in late autumn, a pup, or individual in the calendar year of its birth, is identifiable as such. At birth it wears a distinctive black pelage. By age 3 months, the black coat has been replaced by a silvery, adult-type pelage. At this stage the pup can be distinguished in the field from a yearling by its smaller size and less prominent canine teeth. We will show (table 15) that the length of the upper canine root is only 3 mm. in the late autumn pup as against 9 mm. in the yearling. Between the pup and the yearling there may be some overlap in body weight and length, but apparently none in erupted length of the canines.

The ages of many specimens older than pups have been estimated quite closely from counts of annuli on the roots (Scheffer, 1950). The exact ages are known for other specimens which had been captured, marked, and released during their first summer and recaptured in later years. Through 1962, about 527,000 pups had been marked on the Pribilof Islands by a permanent metal tag clamped to a flipper.

Dental Terminology

Dental terminology for the fur seal and, indeed, for many mammals including man, is still controversial. The terminology used in the present paper is described below.

Primary tooth (indicated by small letter).—A tooth without a fetal antecedent.

Secondary tooth (indicated by large letter).—A tooth which develops near the locus of, and eventually replaces, a primary tooth.

Deciduous tooth.—A tooth which is exfoliated *in utero* or before age 14 weeks. All deciduous teeth are primary.

Permanent tooth.—A tooth which is normally retained through life. Most permanent teeth are secondary; certain ones are primary. During perinatal life while certain teeth of both deciduous and permanent series are present in the oral cavity the dentition is referred to as mixed.

Classified on the basis of their position in the dental arch, the permanent teeth are of four types.

Starting with the midline, the following teeth are present in each quadrant:

Incisors (I).—The most anterior teeth; rooted in the premaxillary bone (=intermaxillary bone=incisive bone) or mandibular bone; aligned approximately in a right-and-left (transverse) direction.

Canine (C).—The large tooth at the anterolateral corner of the jaw; rooted in the maxillary or mandibular bone.

Premolars (p and P).—The first four postcanines; rooted in the maxillary or mandibular bone.

Molars (m).—The most posterior teeth, being the 5th and 6th upper postcanines and the 5th lower postcanine; rooted in the maxillary or mandibular bone.

The deciduous teeth bear the names of the teeth which replace them.

The surfaces of the teeth are designated as:

Lingual.—That surface which is in contact with the tongue.

Labial.—That surface of the incisors which is in contact with the lips.

Buccal.—That surface of the canines and postcanines which is in contact with the cheek.

Occlusal.—That surface which comes into contact with the opposing teeth.

Mesial.—That surface which contacts (or nearly contacts) the tooth anterior to it in the dental arch.

Distal.—That surface which contacts (or nearly contacts) the tooth posterior to it in the dental arch.

The crown is the exposed, enamel-covered portion of the tooth. Near the gingival line, the enamel may form a shelf-like ridge or cingulum around the base of the crown. The neck is the region of the cementoenamel junction. The root is normally the hidden, cementum-covered portion of the tooth. The basal or apical end of the tooth is the attached end; the opposite end is usually referred to as the tip of the crown. The tooth is rooted in a socket, the bony alveolus.

Height of tooth is measured from the tip of the crown to the midpoint of the buccal or labial rim of the bony alveolus (=alveolar height=morphological height) or to the rim of the gingiva (=gingival height), along the outer surface of the tooth. Special cases are: (1) on upper incisors I1 and I2, the tip of the crown is considered to be the more anterior of the two cusps; (2) for each canine, the measurement line is along the anterolateral "prow"; (3) where the root of the molar is longitudinally furrowed, a small peak of bone may extend into the furrow, toward the crown, from the bony alveolar rim, particularly on old seals; this peak is ignored in measuring alveolar height. A value given for "height" is the mean height of right and left teeth of a pair.

Length of root is measured on the extracted tooth, on the lingual surface from the cementoenamel junction to the base (apex). If the tooth is double-rooted, the mean length of the two roots is given. On canines, especially, the lingual surface is identified by a distinct "keel" that runs the length of the crown.

Condylobasal length (CBL) is measured from a transverse line touching the most posterior points on the occipital condyles to a transverse line touching the most anterior points on the premaxillary bones. In other words, it is a midline measurement between a tangent to the most posterior points of the condyles to the most anterior points of the midsagittal plane of the premaxilla. On fetal skulls having a CBL of less than 75–80 mm., the condyles slope into the parietal region and the "most posterior points" are difficult to identify.

Cranial width (CW) is calvarial width, or the greatest transverse width of the brain case posterior to the zygomatic arches. In males, it exceeds mastoid width until ages 4 to 6 years, when mastoid width overtakes it. Thus, in fully adult males, cranial width equals mastoid width. In females, cranial width is always greater than mastoid width. Scheffer and Wilke (1953) defined and illustrated mastoid width as the greatest width of the skull across, "or near," the mastoid processes. Modern opinion is that the term mastoid width should be restricted to the width across the processes.

Length of postcanine series is measured on a straight line along the axis of the tooth row from the distal (posterior) margin of the bony alveolus of the posterior molar to the mesial (anterior) margin of the bony alveolus of the anterior premolar.

The principal events that we shall be concerned with in the development of the dentition are as follows: Crown calcification, or formation of enamel and dentin, begins in deciduous and permanent teeth in early fetal life. Root formation begins in each tooth before crown calcification has ceased. Growth of the root is accompanied by alveolar eruption, when the tip of the crown rises above the bony alveolar rim, and later by gingival eruption (=clinical eruption) when the tip cuts the gum and enters the oral cavity. Root closure, or closure of the apical foramen, is followed by exfoliation (=shedding) in the deciduous teeth. Root closure in the permanent teeth is apparently followed by slow deposition of cementum; the teeth remain in place. (In the development of the deciduous dentition of the fur seal a curious and unexplained sequence is observed. In all teeth except the canines, root closure takes place a week or more in advance of gingival eruption.)

DECIDUOUS TEETH

Morphology of Deciduous Teeth

The deciduous formula (plates 1 and 2) is:

$$\frac{\text{i1—i2—i3 c p2—p3—p4}}{\text{i2—i3 c p2—p3—p4}}$$

The deciduous teeth are small and, excepting the canines, are nonfunctional. They are haplodont (with simple crown), though the premolars have small anterior and posterior bulges suggesting cusps. All are weakly rooted; some occasionally do not erupt from the gum; none remains after the first 13 weeks of the 3- to 4-month suckling period. Excepting those of the canines, the roots attain full size in utero. In the dentitions of two fetal males and two fetal females, ranging in body weight from 1.36 to 2.27 kg. (25 to 42 percent MNW), the following teeth are found to be double-rooted; upper p2, upper p4, and lower p4. The others are single-rooted. Kubota et al. (1961b) reported a similar finding.

Calcification, Alveolar Eruption, and Root Closure of Deciduous Teeth

Calcification.—Takano (1961), who studied stained sections and radiographs, found that the lower deciduous teeth "begin calcifying after 1 percent MNW (mean newborn weight). All of the [lower] deciduous teeth showed calcification before 2.1 percent MNW in the female and 2.4 percent MNW in the male" (p. 25).

Lamb (1962) determined the time of appearance of both dentin and enamel in the deciduous teeth of the lower jaw (table 1). His findings agree with Takano's, that calcification of all lower deciduous teeth is initiated before or soon after the fetus has attained 2 percent MNW.

As for the upper deciduous teeth, the radiographs of Kubota et al. (1961b) show that the teeth calcify at about the same time as the lower ones. Those authors, however, did not give the

TABLE 1.—*Presence of dentin and enamel in the mandibular dentition of the fetus* [1]

[For dental terminology used in this and subsequent tables, see pages 296 to 298]

Teeth	Weight of fetus, as percentage of mean newborn weight				
	1 percent	2 percent	3 percent	4 percent	5 percent
	Presence of dentin and enamel [2]				
Deciduous:					
i2	—	DE	DE	DE	DE
i3	—	D	DE	DE	DE
c	—	D	DE	DE	DE
p2	D	DE	DE	DE	DE
p3	D	DE	DE	DE	DE
p4	D	DE	DE	DE	DE
Permanent:					
I2	—	—	—	—	—
I3	—	—	—	—	—
C	—	—	D	—	D
p1	—	—	—	D	D
P2	—	—	—	—	—
P3	—	—	—	—	—
P4	—	—	—	—	—
m1	—	—	—	—	—

[1] After Lamb (1962, p. 35) based on five male fetuses.
[2] D=dentin, E=enamel, identified by radiography and examination of stained frontal sections.

weights of the fetuses nor did they indicate the sequence of calcification of the upper deciduous teeth, beyond stating that calcification starts in the incisors.

Takano (1961, p. 25) stated that "the deciduous . . . teeth do not form completely enclosed within bone" but, rather, "crown formation takes place within a soft tissue mass which is directly connected to the gingival tissue." In other words, all deciduous teeth except the canines develop in shallow depressions rather than in true bony alveoli. Lamb (1962) concluded that histodifferentiation during tooth formation in the seal is essentially the same as in man.

In summary, we conclude that crown calcification of the deciduous teeth is progressing while the fetus is increasing in weight from about 100 g. (2 percent MNW, implanted age about 7–8 weeks) to 150 g. (3 percent MNW, implanted age about 8–9 weeks), in January.

Alveolar eruption.—Alveolar eruption of the deciduous teeth has no distinct beginning, for the smallest teeth, the medial incisors, begin to calcify at the level of the bony alveolar rim. In our smallest specimen preserved as a cleaned skull, all deciduous teeth have erupted beyond the bony alveolar rim. This is a female of 438 g. (9.1 percent MNW). Here the tooth with least alveolar height (0.5 mm.) is the upper 4th premolar, and with the greatest alveolar height (2.2 mm.) is the upper 3d incisor.

TABLE 2.—*Alveolar height of deciduous teeth*

Teeth	Specimen catalog number [1]						
	39	40	34	41	36	37	29
	Alveolar height (mm.)						
Upper:							
i1	1.0	1.0	1.0	0.5	lost	1.3	1.0
i2	1.0	1.2	1.0	1.0	1.6	1.3	1.0
i3	2.6	1.6	2.6	2.0	1.9	2.2	2.7
c [2]	4.2	4.3	4.3	5.0	4.8	4.6	4.6
p2	2.0	2.1	2.3	3.1	2.6	2.6	2.9
p3	1.7	1.3	2.5	2.2	2.2	2.0	2.2
p4	1.8	2.2	2.6	2.5	2.1	2.2	2.5
Lower:							
i2	1.0	1.9	0.8	1.0	2.0	1.5	lost
i3	1.0	2.2	1.0	2.0	2.7	1.5	3.0
c [2]	3.3	3.2	3.0	3.5	3.4	3.1	4.1
p2	2.7	2.1	2.6	2.9	2.6	3.0	3.1
p3	2.0	2.2	2.5	1.9	2.0	2.8	2.5
p4	2.3	2.2	2.3	2.3	2.3	2.4	2.5
Total tooth heights	26.6	27.5	28.5	29.9	30.2	30.5	32.1
	Specimen data						
Sex	Male	Female	Male	Male	Male	Female	Female.
Date	Mar. 30	Apr. 1	Mar. 28	Apr. 1	Mar. 30	Mar. 30	Mar. 28.
Condylobasal length, mm	72	79	85	90	81	84	85.
Body length, cm	40	41	42	47	42	42	43.
Body weight, kg	1.4	1.4	1.8	2.3	1.8	1.6	1.8.
Percent MNW	25	28	33	42	33	33	38.

[1] All specimens are in the "Sitka 50" series; all are fetal and are listed according to increasing total tooth height.
[2] The canines continue to grow in perinatal life. Maximum recorded heights are: upper, 8.2 mm; lower, 5.5 mm.

In a slightly larger fetus (female, 660 g., 13.7 percent MNW) alveolar eruption of the deciduous teeth is also complete. For seven still larger specimens, the alveolar height of each tooth is shown in table 2.

We conclude that alveolar eruption begins shortly after crown calcification in the fetus of 200 g. (4 percent MNW, implanted age about 10 weeks), and has begun in all teeth in the fetus of 400 g. (8 percent MNW, implanted age 12–13 weeks), in January and February.

Root closure.—In a fetal male of 1.36 kg. (25 percent MNW) the root of upper c is open; the roots of upper i1, i2, and p4 are nearly closed; the roots of upper i3, p2, and p3 are closed; the roots of lower c and p4 are open; the roots of lower i2, i3, p2, and p3 are closed. In two fetal females of 1.36 and 1.59 kg. (28 and 33 percent MNW) all roots are closed except those of upper and lower c (plate 2).

We conclude that, in certain deciduous incisors and premolars, the roots close when the fetus has attained a weight of about 1.0 kg. (20 percent MNW). In the remaining incisors and premolars, the roots close when the fetus has attained a weight of about 1.50 kg. (30 percent MNW), when the first teeth are about to erupt from the gum. In the canines, the roots close near time of birth, earlier in the lower pair than in the upper.

Gingival Eruption of Deciduous Teeth

In two fetuses similar in appearance, both 1.35 kg. (27 percent MNW), no teeth have erupted from the gum, though the site of each tooth is evident as a mound. Two larger fetuses present a similar picture, with teeth unerupted, though by now the upper medial incisors (i1) show through the gingival tissue as slender dark lines, and in a 1.70 kg. specimen (34 percent MNW) lower i2 is about to erupt (plate 3).

The next fetus in size (2.3 kg., 45 percent MNW) is the first-listed of table 3. Here 9 teeth out of 26 have erupted. The specimens of table 3, collected between April 21 and July 5, suggest, but do not show clearly, the sequence of eruption. We have, therefore, rearranged the data of Kubota et al. (1961a, p. 330–333), based on 25 fetal specimens, mainly collected in April when eruption is most active. The sequence of eruption is as follows:

Upper:	i1	i2	i3	c	—	p2	p3	p4
Sequence:	7	11	3	1		2	6	8
		4	13	5		10	12	9
Lower:	—	i2	i3	c	—	p2	p3	p4

TABLE 3.—*Gingival eruption of deciduous teeth*

Teeth	NWC 53 3119	NWC 52 3122	NWC 52 3121	US 58 790 R
	Specimen catalog number [1]			
	Stage of eruption [2]			
Upper:				
i1	(x)	(x)	(x)	(x)
i2	/	(x)	(x)	(x)
i3	x	o	x	(x)
c	/	x	x	x
p2	/	x	x	x
p3	—	—	x	x
p4	—	—	o	x
Lower:				
i2	o	(x)	(x)	(x)
i3	(x)	(x)	(x)	(x)
c	—	o	x	x
p2	—	—	x	x
p3	—	—	—	x
p4	—	—	x	x
	Specimen data			
Age	Fetal	Fetal	Fetal	Fetal.
Sex	Female	Female	Male	Female.
Date	April 21	April 21	April 21	May 9.
Condylobasal length, mm.	97	96	105	108.
Body length, cm	46	50	51	54.
Body weight, kg	2.3	2.4	2.7	3.4.
Percent MNW	45	50	50	71.

TABLE 3.—*Gingival eruption of deciduous teeth*—Con.

Teeth	26-6-60 A	5-7-60 A	BDM 549	NWC 52 3214	29-6-60 A
	Specimen catalog number [1]				
	Stage of eruption [2]				
Upper:					
i1	(x)	(x)	(x)	(x)	(x)
i2	(x)	(x)	(x)	(x)	(x)
i3	(x)	(x)	(x)	x	(x)
c	x	x	x	x	x
p2	(x)	(x)	(x)	x	(x)
p3	(x)	(x)	(x)	x	(x)
p4	/	x	x	x	x
Lower:					
i2	(x)	(x)	(x)	(x)	(x)
i3	(x)	(x)	(x)	(x)	(x)
c	x	/	x	x	(x)
p2	(x)	(x)	(x)	x	(x)
p3	(x)	(x)	(x)	x	(x)
p4	(x)	/	x	x	x
	Specimen data				
Age	Newborn	Newborn	Days?	Fetal	Fetal.
Sex	Female	Male	Male	Male	Female.
Date	June 26	July 5	July	June 20	June 29.
Condylobasal length, mm	122	124	135	132	133.
Body length, cm	65			66	69.
Body weight, kg	4.4		6.5	6.8	7.1.
Percent MNW	92		120	126	147.

[1] Specimens are listed in order of increasing weight or condylobasal length.
[2] Symbols: Dash (—)=tooth not erupted; o=tooth about to erupt; /=one tooth of a pair erupted; x=both teeth of a pair erupted; (x)=erupted but exfoliated.

We conclude that gingival eruption of the deciduous teeth is progressing while the fetus is increasing in weight from 1.65 kg. (33 percent MNW, implanted age about 20 weeks) to 3.0 kg. (60 percent MNW, implanted age about 25 weeks), in April and May. Eruption does not proceed in an anterior to posterior direction, as in the permanent teeth. The upper deciduous teeth tend to erupt slightly in advance of the lower ones. For reasons undetermined, all of the teeth except the canines erupt after root closure has taken place.

Exfoliation of Deciduous Teeth

Table 3, which shows gingival eruption, also indicates when certain teeth exfoliate.

The incisors, first to exfoliate, are usually shed before birth, perhaps as a result of "mouthing" movements of the fetus. They begin to exfoliate soon after the onset of gingival eruption. However, in the jaws of a fetal individual of 3.4 kg. (71 percent MNW) one incisor (left upper i2) is still attached to the gum. In the jaws of a newborn male, one lower i3 is persistent. In the jaws of a male a few days old, upper i1 can be seen as a white speck on the surface of the gum, most of its length buried.

The premolars (p2, p3, and p4) disappear just before or soon after the pup starts to nuzzle and suck. In six specimens including late-term fetuses and newborn young, only one, a large full-term fetus, has retained all of its deciduous premolars. A male several days old has retained only the posterior pair (p4) in upper and lower jaws.

The canines are far more deeply rooted than are other deciduous teeth and are functional after birth, the upper ones for a longer period than the lower ones. In our sample, the maximum alveolar height of upper c is 8.2 mm. in a male about 2 weeks old. Maximum height of lower c is 5.5 mm. in a full-term fetal male. One or more deciduous canines are present in 5 out of 14 skulls of known-age pups ranging in age from 23 to 103 days, as follows:

Age in days	Upper right	Upper left	Lower right	Lower left
	Deciduous canines present (X)			
23	X	X	X	X
23	X	X	X	X
25	—	—	—	—
32	—	—	—	—
39	—	—	—	—
50	—	—	—	—
63	—	—	—	—
66	—	—	—	—
66	—	—	—	—
73	X	X	—	—
73	—	—	—	—
83	—	—	—	—
92	X	—	—	—
103	—	—	—	—

The status of exfoliation near time of birth is shown in plate 4, and is indicated in table 3 by the data for the five last-listed individuals. These include two full-term fetuses, one pup on the day of its birth, and two pups a few days old. The deciduous teeth present or absent in each upper and lower quadrant are as follows:

Number of—	Upper (full complement 7 teeth)	Lower (full complement 6 teeth)
Teeth exfoliated	2–5.5 (mean 4.5)	2–5 (mean 4.2).
Teeth in situ	1.5–5 (mean 2.5)	1–4 (mean 1.8).

We conclude that exfoliation may begin in the fetus of 2.0 to 2.5 kg. (40 to 50 percent MNW, implanted age 22 to 24 weeks), in April and May. By time of birth, about 18 of the 26 teeth have exfoliated. The four posterior premolars (p4 in each quadrant) usually persist for a few days after birth. The four deeply rooted canines begin to exfoliate within a week or two after birth; all have been shed by age 14 weeks.

Evolutionary Implications

From modern embryological evidence the evolution of the deciduous dentition in *Callorhinus* may hypothetically be reconstructed, as follows: The protopinniped lived in a den near the sea or a brackish lagoon. The food of the growing individual was at first milk, then milk-plus-flesh, and finally flesh alone. As members of the evolutionary line began increasingly to exploit the advantages of a marine environment, the den life of the individual became shorter. Concurrently, a long gestation period began to gain survival value, since mutations in the direction of greater precocity at birth resulted in a pup which was sooner able to leave the den and join its mother in the food-rich waters. Today, the deciduous or "den" teeth, essentially nonfunctional, persist in the ontogenetic sequence, while gestation is now so extended that the permanent teeth have time to develop in utero and be ready to meet a sudden demand at prenatal age of 3 or 4 months. At this stage, around the first of November, the mother seal leaves the nursing ground for the open sea. The pup is forced to convert abruptly from a diet of milk to one of fish and squid. (Or so we believe. Certainly the pup receives no milk after its mother fails to return periodically to the beach. No stomachs of pups taken at sea before January have yet been examined. We can only assume that the diet of the pelagic young seal in November and December is similar to that observed for seals in January and later.)

We do not wish to leave the impression that the deciduous teeth of the protopinniped have remained essentially unchanged in form, size, and number. On the contrary, evidence suggests that the teeth have become smaller, simpler in form, and more weakly rooted. Certain incisors have almost disappeared; presumptive lower "i1" has disappeared without trace. Nor do we wish to leave the impression that the fetal time gap between development of the deciduous and permanent teeth has remained unchanged. As we will point out in the next section, there has apparently been a fetal telescoping with the result that calcification of permanent teeth now begins when the fetus has attained only 3 percent of its ultimate newborn weight, and while calcification of certain deciduous teeth is still being initiated.

PERMANENT TEETH

Morphology of Permanent Teeth

The permanent formula (plates 5 to 7) is:

$$\frac{\text{I1—I2—I3 \quad C \quad p1—P2—P3—P4 \quad m1—m2}}{\text{I2—I3 \quad C \quad p1—P2—P3—P4 \quad m1}}$$

The incisors.—Pinnipeds (Order Pinnipedia) have fewer permanent incisors than do carnivores (Order Carnivora). The incisor formulas for members of the Pinnipedia are as follows:

Family Otariidae (on each side)		3/2
Family Odobenidae		3/2
Family Phocidae,	Subfamily Phocinae	3/2
	Subfamily Monachinae	2/2
	Subfamily Cystophorinae	2/1

By comparison, all members of the Order Carnivora except the sea otter (*Enhydra lutris*) have three incisors on each side (3/3). It is assumed that, where pinnipeds have lost certain upper or lower incisors, they have lost the more medially placed ones and have retained the outer, more laterally placed ones (see formula at head of section).

For example, "in walrus [*Odobenus*] the first incisor, upper and lower, is certainly the smallest and least often present in both the deciduous and permanent dentitions" (Francis H. Fay, in letter of November 29, 1961). In the skulls of nine

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walrus calves, Fay[1] noted the frequency of occurrence of permanent incisors:

Incisors	I1	I2	I3
	Percent	*Percent*	*Percent*
Upper	56	78	100
Lower		22	66

In the skulls of 24 adults, however, he found no upper I1 and no lower incisors. He concluded that upper I3, the caniniform, is the only incisor consistently present in the adult, and that, in the evolution of the walrus, there has been a tendency toward absence of the medial rather than the lateral incisors.

Evidence for evolutionary loss of the lower medial incisors in *Callorhinus* is weaker. Unlike the walrus, the fur seal retains all of its permanent incisors through life. In the fur seal, however, in both deciduous and permanent dentitions and in both upper and lower arches, there is a gradient of incisor size decreasing in the direction of the midline. We agree with Kubota et al. (1961b, p. 393) that "the lower tooth opposite to the most rudimentary upper central incisor . . . has been lost."

The first two upper incisors (I1 and I2) on each side are notched transversely to accept the crown tips of the two lower incisors, which are chisel-shaped (plate 7). To the best of our knowledge, no members of the Order Carnivora have notched incisors, whereas all members of the Family Otariidae of the Order Pinnipedia do. When the seal's mouth is closed, the incisors, as well as other teeth, interlock to form a tight-fitting trap from which small fish or squid would have difficulty in escaping. The lower medial incisors (I2) are essentially tricuspidate (plate 8, *A*). The cusps become worn within a few weeks after birth and are not conspicuous in the adult. The incisors are usually single-rooted. We have seen only one specimen in which upper I1 and I2 are double-rooted (plate 9, *A*).

The canines.—The canines are like those of the Carnivora, with simple pointed crown and single root. We will discuss later (p. 308) the protracted growth period of the canine roots.

[1] Investigations of the Pacific walrus. Terminal report, Project No. 26, Arctic Institute of North America, March 1960. 3+72 typewritten pages.

The postcanines.—The permanent molariform teeth, six postcanines in each upper quadrant and five in each lower, are superficially alike. We designate the most anterior four above and below as premolars, the rest as molars, for these reasons: (1) On histological evidence there is a discontinuity between the 4th and 5th postcanines, above and below, in the sense that the 4th is a secondary tooth while the 5th is a primary. (2) In eruptive sequence the upper first four (p1, P2, P3, and P4) fall in one group, the fifth (m1) in another. That is, in each upper quadrant the first four postcanines erupt from the gum in regular order, from anterior to posterior, but the 5th erupts out of turn, earlier than the 4th. (3) In the Superfamily Canoidea, nearest relatives of the Pinnipedia, the first four postcanines have long been regarded as premolars (Frechkop, 1955; Grassé, 1955; Gregory, 1951; Weber, 1928).

To elaborate on point 1 (above), the first upper and lower postcanine (p1), the 5th and 6th upper postcanines (m1 and m2), and the 5th lower postcanine (m1) are primary teeth. They have no surviving (functional) successors, though during fetal development each is paired for a short time on its lingual margin with the anlage of a secondary tooth (Tadahiro Ohe, in a letter of July 25, 1962).

Each postcanine may have a small anterior and a small posterior cusp or cusplet (plate 8, *B*). A carnassial (shearing) cusp is never found as on certain posterior teeth, usually the 5th upper and 4th lower postcanines, of Carnivora. A cingulum is conspicuous only on the postcanines of the seal, especially on the lingual side of the teeth.

The roots of the first three premolars (p1, P2, and P3), upper and lower, have a vertical groove which tends to be deeper in the posterior series of teeth. Upper m1 is nearly always double-rooted; lower m1, usually; upper m2 and upper and lower P4, occasionally (tables 4 and 5; plate 9, *B*). There is no apparent sex difference in shape of root of the postcanines. (Tables 4 and 5 are based on specimens 8 years old or younger. Above 6 to 8 years, unless the root is distinctly bifurcated, cementum deposition tends to obscure the original shape.)

The posterior upper tooth, m2, is consistently the smallest of the molariform teeth, and it has no antagonist. It may be absent without trace from adult skulls (p. 311). The root of m2 turns

TABLE 4.—*Shape of root in permanent posterior postcanines, male*

Catalogue No.	Age of specimen	Upper teeth			Lower teeth	
		P4	m1	m2	P4	m1
		Shape of root [1]				
BDM 417	9 months	D	C	D	D	D
BDM 476	14 months	D	A	A	D	C
BDM 290	14 months	C	A	C	C	C
BDM 552	2 years	D	A	A	C	A
27-7-60A	2 years	D	A	B	D	C
BDM 50	3 years	D	A	D	D	A
BDM 53	3 years	C	B	C	D	C
BDM 51	4 years	B	A	B	D	A
BDM 68	4 years	A	A	C	A	A
BDM 107	5 years	C	A	C	C	B
BDM 149	6 years	C	A	B	D	B
Mean score [2]		3.2	1.3	2.5	3.4	2.2

[1] Symbols: A=root double and distinctly bifurcated; B=root double but not distinctly bifurcated; C=root deeply furrowed but not double; D=root single, not furrowed.
[2] The tooth which is most consistently double-rooted has the lowest score, based on a system where A=1, B=2, C=3, and D=4.

TABLE 5.—*Shape of root in permanent posterior postcanines, female*

Catalogue No.	Age of specimen	Upper teeth			Lower teeth	
		P4	m1	m2	P4	m1
		Shape of root [1]				
BDM 545	7 months	D	A	B	D	C
BDM 16	15 months	C	A	B	D	B
BDM 407	2 years	C	A	D	D	A
NWC 52-3097	3 years	C	B	C	C	C
BDM 405	3 years	C	A	A	D	B
NWC 52-3632	5 years	B	A	B	C	A
BDM 460	5 years	C	A	B	B	B
NWC 52-3661	7 years	B	A	D	B	A
BDM 463	7 years	B	A	D	A	A
NWC 52-3272	8 years	B	A	D	B	C
Mean score [2]		2.7	1.1	2.8	2.9	1.9

[1] Symbols: A=root double and distinctly bifurcated; B=root double but not distinctly bifurcated; C=root deeply furrowed but not double; D=root single, not furrowed.
[2] The tooth which is most consistently double-rooted has the lowest score, based on a system where A=1, B=2, C=3, and D=4.

anteriorward, perhaps thereby securing a better hold in the thicker part of the maxillary bone.

Calcification and Alveolar Eruption of Permanent Teeth

Calcification.—Calcification of the permanent teeth starts in the lower canine at fetal weight of 150 g. (3 percent MNW, about 9 weeks implanted age), in January. This is remarkably early compared with man. Kraus (1959) found that the first human permanent tooth begins to calcify at about time of birth, or 40 weeks implanted age, much later than in the seal. The permanent 1st mandibular molar of the rhesus monkey begins to calcify after the first three-quarters of prenatal development (Swindler and Gavan, 1962). Possibly this indicates a trend toward delayed calcification of permanent teeth in human evolution.

Initial calcification in the permanent dentition overlaps that in the deciduous, though is much more prolonged. That is, initial calcification is occurring in deciduous teeth at fetal stages of 2 to 3 percent MNW, while it is occurring in permanent teeth at fetal stages of 3 to 70 percent MNW. Initial calcification is last to start in the posterior upper molar, m2, in the fetus of about 3.5 g. (70 percent MNW, implanted age about 27 weeks) (Bokstrom, 1961; Takano, 1961; Kubota et al., 1961b; Lamb, 1962).

The sequence of calcification as described by Bokstrom, Takano, and Lamb was given separately for upper and lower teeth. We are unable to coordinate the sequence for the dentition as a whole, except to state that the lower teeth tend to calcify before their upper counterparts. Thus calcification has started in all of the lower teeth by fetal weight 0.9 kg. (18 percent MNW) as compared with 3.5 kg. (70 percent MNW) for the uppers. The sequence is as follows:

	Maxillary	*Mandibular*
1.	C and p1	C and p1.
2.	I3 and m1	I2 and m1.
3.	I1 and I2	P3.
4.	P2, P3, and P4	I3 and P2.
5.	m2	P4.

Alveolar eruption.—The sequence of alveolar eruption of the permanent teeth is difficult to demonstrate in our specimens, which are skulls cleaned by beetle larvae. In many skulls which ought to show the sequence of eruption, beetles have eaten the periodontal membranes around the partly formed teeth, allowing the loose teeth to sink into the alveoli. In the skull of a fetus of 660 g. (13 percent MNW), however, the following permanent teeth can be seen: upper canines and first three postcanines (p1, P2, and P3), lower canines and all five postcanines (p1, P2, P3, P4, and m1). All upper and lower incisors are hidden beneath dried remains of the gingiva. The last three upper postcanines (P4, m1 and m2) cannot be seen.

In a sample of seven older skulls taken from fetuses ranging in size from 1.36 to 2.27 kg. (25 to 42 percent MNW) all of the permanent teeth, except the posterior upper molar m2, are visible within their alveoli. The tips of their crowns are white, hard, and well calcified. From the stage of advancement of the tips we conclude that the first teeth—the incisors—erupt from the jaw when the fetus has attained a weight of about 2.5 kg. (50 percent MNW, implanted age about 24 weeks), in early May.

The status of alveolar eruption near time of birth is shown in table 6 and plates 10 and 11. All of the permanent teeth have usually erupted in utero to the level of, or beyond, the bony alveolar rim.

Alveolar eruption evidently continues through life. Increase in alveolar height between ages 5 and 10-plus years is shown in table 7. Table 7 suggests that, in the female, most of the teeth grow less than 1 mm. in root length after age 5 years. Exceptions are the large caniniform incisor (upper I3) and the canines. Alveolar height of the permanent teeth in fully adult skulls of both sexes is shown in table 8 and figure 2. The causes of increase in alveolar height during adult life are not clear, though cementum deposition on the roots is quite certainly one of them. Resorption of the bony alveolar rim is perhaps another (plate 20, A).

TABLE 6.—*Alveolar height of permanent teeth in fetal and newborn pups*

Teeth	Specimen catalog number [1]			
	BDM 325	BDM 547	BDM 225	BDM 450
	Alveolar height (mm) [2]			
Upper:				
I1	2.0	5.8	5.1	5.3
I2	2.0	5.6	5.5	6.0
I3	1.2	8.0	8.2	8.4
C	2.0	4.0	6.8	7.8
p1	1.9	4.7	6.9	6.9
P2	—	3.9	6.1	4.7
P3	—	3.9	4.0	4.6
P4	—	.8	3.5	2.4
m1	.2	3.6	4.3	4.1
m2	—	.8	—	2.0
Lower:				
I2	3.9	6.3	5.9	6.2
I3	2.9	6.3	6.2	7.0
C	.1	.1	7.0	6.9
p1	3.3	6.7	6.3	7.0
P2	1.0	6.6	6.0	6.6
P3	.2	7.0	6.2	6.4
P4	—	1.0	3.5	3.5
m1	.5	2.0	2.0	4.1
Total tooth heights	21.2	77.1	93.5	99.9
Specimen data				
Age	Fetal	Fetal	Days?	Days?
Sex	Female	Male	Female	Female.
Date	July 18	July 31	July 23	August 11
Condylobasal length, mm	99	122	123	121.
Body length, cm	49		67	67.
Body weight, kg	2.8	6.0	4.8	5.2.
Percent MNW	56	111	99	109.

[1] Specimens are listed by increasing total tooth height.
[2] A dash indicates an unerupted tooth.

TABLE 7.—*Alveolar height of permanent teeth in the female at ages 5 and 10+ years*

Teeth	Six specimens age 5 years			Seven specimens age 10+ years [1]			Difference between means (increase)
	Alveolar height (mm)			Alveolar height (mm)			
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	
Upper:							
I1	6.3	7.7	6.95	7.0	8.6	7.85	0.90
I2	7.2	8.0	7.38	7.0	9.0	7.93	.55
I3	9.4	10.5	10.08	10.1	14.0	11.62	1.54
C	19.0	19.5	19.20	21.0	27.0	24.30	5.10
p1	7.8	9.8	8.78	8.7	10.9	9.47	.69
P2	7.3	9.0	8.33	8.3	9.7	8.94	.61
P3	6.7	8.5	7.77	7.4	9.2	8.21	.44
P4	6.3	8.0	7.48	7.2	8.6	8.09	.61
m1	6.1	8.0	7.03	6.2	9.0	7.81	.78
m2	6.3	7.0	6.73	5.5	9.0	7.27	.54
Lower:							
I2	6.4	7.3	6.95	6.5	7.9	7.18	.23
I3	6.9	8.2	7.25	7.0	9.0	7.63	.38
C	15.0	18.0	16.75	20.0	22.0	21.00	4.25
p1	7.0	8.8	7.77	7.6	9.8	8.56	.79
P2	6.2	8.8	7.90	7.6	9.1	8.40	.50
P3	7.1	9.1	8.57	8.2	10.0	9.34	.77
P4	7.1	9.1	8.25	7.8	9.3	8.67	.42
m1	6.3	8.1	7.42	7.7	9.6	8.63	.21

[1] For these old specimens, the height of the canine teeth has been "restored" by small amounts, averaging 1.1 mm. to eliminate the factor of crown-wear. The aim has been to show alveolar height as an indirect measure of root increase.

TABLE 8.—*Alveolar height of permanent teeth in the adult*

Teeth	Mean alveolar height of tooth (mm)	
	In seven males [1]	In seven females [2]
Upper:		
I1	9.9	8.5
I2	10.2	8.5
I3	15.1	12.2
C	36.0	24.5
p1	12.7	10.7
P2	11.6	9.4
P3	11.6	8.8
P4	10.4	8.6
m1	10.4	8.8
m2	9.9	8.3
Lower:		
I2	8.3	7.4
I3	8.3	7.5
C	32.2	20.7
p1	10.3	9.0
P2	9.7	8.9
P3	10.9	9.5
P4	10.7	9.0
m1	10.7	9.0

[1] The sample included one 9-year-old, three 10-year-olds, and three older than 10, though the value shown for each tooth is the mean of the highest three. By this expedient, an attempt is made to show the height of the fully grown, but yet unworn, tooth.
[2] The sample included three 9-year-olds, one 10-year-old, and three older than 10, though the value shown for each is the mean of the highest three.

Gingival Eruption of Permanent Teeth

We have measured the height of the teeth above the gum in the jaws of 9 male and 10 female pups ranging in age from full-term fetal to 103 days (tables 9 and 10). We have also measured gingival height in five fully adult males and five fully adult females (table 11). As a basis for estimating the sequence of gingival eruption (table 12), we have analyzed the data for the six youngest specimens listed in table 9.

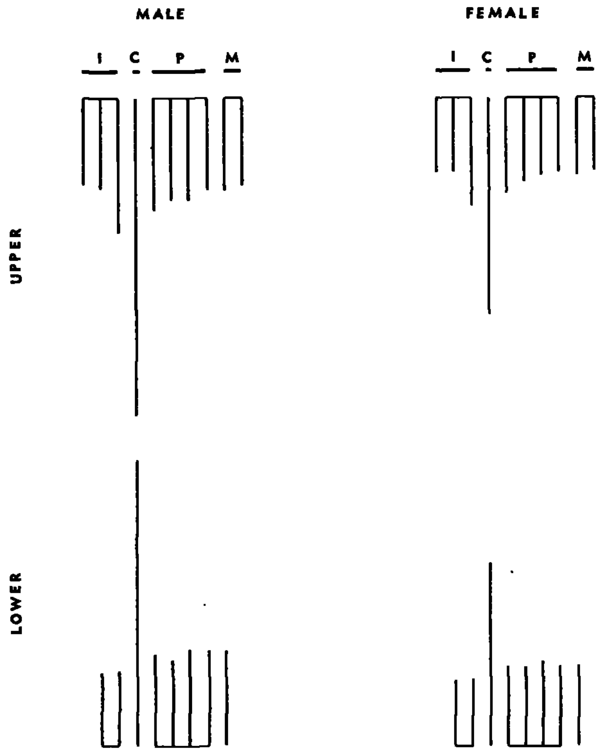

FIGURE 2.—Relative alveolar height of permanent teeth in the adult male and female. The length of each vertical bar represents the height of the tooth above the bony alveolar rim. The upper teeth are represented as pointing downward, the lower teeth as pointing upward. I=incisors, C=canines, P=premolars, M=molars. (Data from table 8.)

These represent an important perinatal period ending when the last tooth (upper m2) is about to erupt. One clue to the sequence is the number of specimens, in an age-graduated series, in which a particular tooth is present in the oral cavity. That is, a particular tooth present in six out of six specimens is assumed to have erupted earlier than another which is present in only four out of the same six specimens. A second clue is the eruptive maturation, or progress of a particular tooth toward its adult height. That is, a tooth which has already attained 80 or 90 percent of its estimated ultimate height is assumed to have erupted earlier that one in the same specimen which has attained only 60 percent of its estimated ultimate height. The estimated sequence of eruption is as follows:

Upper:	I1	I2	I3	C	p1	P2	P3	P4	m1	m2
Sequence:	2	4	7	16	6	9	12	13	14	18
		1	3	15	5	8	10	11	17	
Lower:		I2	I3	C	p1	P2	P3	P4	m1	

TABLE 9.—*Gingival height of permanent teeth in the pup, male*

Teeth	Specimen catalog number [1]				
	BDM 549	5-7-60 A	NWC 52 3214	24-7-60 A	23-8-60 A
	Gingival height (mm) [2]				
Upper:					
I1	2.8	2.7	3.5	3.5	4.3
I2	2.8	2.8	3.2	3.7	4.4
I3	—	3.8	3.3	4.7	7.1
C	—	—	—	—	.2
p1	—	2.4	2.9	3.4	4.7
P2	—	.2	.2	.2	4.1
P3	—	—	—	—	2.0
P4	—	—	—	—	1.5
m1	—	—	—	—	2.0
m2	—	—	—	—	—
Lower:					
I2	2.3	2.2	3.4	2.5	3.2
I3	3.5	2.7	4.3	4.0	4.3
C	—	1.5	—	—	—
p1	2.4	.4	2.6	2.6	4.1
P2	.6	—	1.0	.8	4.7
P3	.2	—	.1	.3	4.6
P4	—	—	—	.8	1.8
m1	—	—	—	—	—
Total tooth heights	14.6	18.7	24.5	26.5	53.0
Specimen data					
Age	Days?	Newborn	Fetal	Newborn	Days?
Date	July	July 5	June 20	July 24	August 23
Body length, cm			66		
Body weight, kg	6.5		6.8		
Percent MNW	120		126		

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Teeth	Specimen catalog number [1]			
	15-8-60 A	D 3 62	D 2 62	D 7 62
	Gingival height (mm) [2]			
Upper:				
I1	3.0	4.5	4.0	5.0
I2	3.7	4.7	4.5	5.5
I3	7.0	8.3	7.6	6.5
C	3.3	.3	4.0	7.2
p1	5.8	5.9	5.9	5.4
P2	3.3	5.0	5.8	6.9
P3	2.7	5.0	5.4	5.3
P4	1.2	4.3	5.6	4.5
m1	2.0	5.7	5.0	6.5
m2	—	.1	.5	1.0
Lower:				
I2	3.2	3.5	3.7	4.1
I3	4.1	5.0	5.0	5.6
C	3.9	.1	1.6	2.8
p1	3.8	4.2	4.3	4.2
P2	3.6	5.9	6.0	6.3
P3	2.7	5.3	6.2	6.0
P4	.9	2.5	3.0	3.9
m1	.2	2.6	1.0	1.7
Total tooth height	54.4	72.9	79.1	88.4
Specimen data				
Age	Days?	73 days	66 days	103 days.
Date	Aug. 15	Sept. 9	Sept. 2	Oct. 9.
Body length, cm		72	69	80.
Body weight, kg		7.4	7.9	11.6.
Percent MNW		137	146	215.

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Table 10.—*Gingival height of permanent teeth in the pup, female*

Teeth	Specimen catalog number [1]				
	26-6-60 A	15-8-60 C	23-8-60 B	15-8-60 B	23-8-60 C
	Gingival height (mm) [2]				
Upper:					
I1	2.7	5.0	4.0	3.5	3.5
I2	3.3	5.0	4.4	3.6	3.8
I3	5.0	7.2	6.2	6.3	7.0
C	.2	—	3.1	6.0	4.8
p1	3.6	5.5	4.2	5.5	5.1
P2	2.0	3.3	3.2	4.4	4.4
P3	.1	3.2	2.0	2.9	3.2
P4	—	1.6	1.9	.2	2.6
m1	—	2.0	3.6	3.5	4.8
m2	—	—	—	—	—
Lower:					
I2	2.3	2.7	3.2	3.0	2.9
I3	2.7	3.7	4.3	3.8	3.7
C	3.0	—	2.7	5.3	5.6
p1	2.8	4.0	4.3	3.5	3.5
P2	2.9	4.4	4.1	4.4	4.4
P3	2.5	4.2	3.5	4.1	4.4
P4	—	1.4	1.3	1.5	3.0
m1	—	—	.1	—	1.9
Total tooth heights	33.1	53.2	56.1	61.5	68.6
	Specimen data				
Age	Newborn	Days?	Days?	Days?	Days?
Date	June 26	Aug. 15	Aug. 23	Aug. 15	Aug. 23
Body length, cm	65				
Body weight, kg	4.4				
Percent MNW	92				

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Teeth	Specimen catalog number [1]			
	D6 62	D1 62	D5 62	D4 62
	Gingival height (mm) [2]			
Upper:				
I1	4.5	3.6	4.0	4.1
I2	5.0	3.8	4.1	4.1
I3	8.3	6.5	6.8	6.4
C	3.0	7.2	6.4	9.5
p1	6.5	5.7	6.6	7.0
P2	4.3	5.7	6.6	6.8
P3	4.2	5.0	7.0	6.2
P4	4.2	4.0	6.0	6.0
m1	6.0	5.2	5.5	7.0
m2	—	—	—	.5
Lower:				
I2	3.6	3.7	3.9	4.0
I3	4.8	3.8	4.5	4.2
C	2.0	7.4	7.0	9.0
p1	4.7	3.9	5.0	4.8
P2	5.9	4.0	5.5	5.0
P3	5.0	4.8	5.0	5.5
P4	3.3	3.0	3.7	4.3
m1	.6	.5	3.2	3.3
Total tooth heights	75.9	77.8	90.8	97.7
	Specimen data			
Age	92 days	66 days	83 days	73 days.
Date	Sept. 28	Sept. 2	Sept. 19	Sept. 9.
Body lenght, cm	67	73	73	73.
Body weight, kg	8.4	6.8	8.0	8.5.
Percent MNW	175	142	167	177.

[1] Specimens are listed by increasing total tooth heights.
[2] A dash indicates an unerupted tooth.

Table 11.—*Gingival height of permanent teeth in the adult*

Teeth	Five males, age 10 years or older			Five females ages 6 to 15 years (mean 11)		
	Gingival height (mm)			Gingival height (mm)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Upper:						
I1	3.0	4.8	3.94	2.7	4.3	3.54
I2	3.7	6.0	5.18	2.8	4.8	3.96
I3	7.7	13.4	10.24	6.0	8.3	7.20
C	27.0	36.0	30.60	13.0	20.5	16.88
p1	6.2	7.2	6.66	4.4	8.2	6.68
P2	5.8	8.6	6.72	3.8	7.3	5.90
P3	4.1	7.1	5.66	4.0	6.9	5.58
P4	4.5	7.2	5.98	4.0	6.7	5.20
m1	4.0	10.5	6.58	2.0	[1] 6.5	4.45
m2	4.2	[1] 7.5	5.43	2.4	[1] 4.0	2.85
Lower:						
I2	.5	4.1	3.00	2.7	4.0	3.22
I3	1.0	6.7	4.64	3.0	4.8	4.06
C	22.0	27.0	25.00	9.0	17.3	13.94
p1	4.2	9.0	6.42	3.7	5.3	4.84
P2	5.0	7.8	6.14	4.5	6.1	5.42
P3	5.4	9.6	7.20	5.6	6.9	6.36
P4	4.9	9.0	7.02	4.9	6.7	6.04
m1	5.8	9.3	7.10	3.9	7.7	5.94

[1] Sample of four specimens only.

Table 12.—*Estimated sequence of gingival eruption of permanent teeth in the male*

Teeth	N [1]	Mean gingival height of tooth (mm)		Maturation percent [4]	Estimated sequence	
		In pups [2]	In adults [3]		A [5]	B [6]
Upper:						
I1	6	3.30	3.94	84	2	2
I2	6	3.43	5.18	66	4	4
I3	5	4.32	10.24	42	6	7
C	2	.58	30.60	2	16	16
p1	5	3.20	6.66	48	5	6
P2	5	1.33	6.72	20	9	9
P3	2	.78	5.66	14	11	12
P4	2	.45	5.98	7	14	14
m1	2	.67	6.58	10	12	13
m2	0	.00	5.43	0	18	18
Lower:						
I2	6	2.80	3.00	93	1	1
I3	6	3.82	4.64	82	3	3
C	2	.90	25.00	4	15	15
p1	6	2.65	6.42	41	7	5
P2	5	1.78	6.14	29	8	8
P3	5	1.32	7.20	18	10	10
P4	3	.58	7.02	8	13	11
m1	1	.03	7.10	1	17	17

[1] Number of specimens, out of six, in which the tooth has erupted.
[2] Mean gingival height of tooth in six pups (the first-listed in table 9).
[3] Mean gingival height of five adults (table 11).
[4] 100 (column 2/column 3).
[5] Sequence estimated from percent height only (see page 304).
[6] Sequence estimated from percent height and number of specimens in which the tooth has erupted.

It is clear that, within a tooth group, such as the upper incisors, eruption proceeds in an anteroposterior direction. It is not so clear, and is perhaps only a small-sample effect, that teeth in a mandibular group erupt earlier than those in the corresponding maxillary group. (It will be recalled that calcification is earlier in lower than in upper teeth.) The largest teeth, the canines, are 15th and 16th in order or eruption; only the posterior molars erupt later, 17th and 18th. For about 6 weeks, while the permanent canines are erupting, the deciduous canines are functioning in their stead.

At birth, in each upper quadrant, from 2 to 7 of the 10 permanent teeth may have cut the gum (plate 4). Those which are consistently absent from the oral cavities of five newborn specimens are P4, m1, and m2. In each lower quadrant, from four to six of the eight permanent teeth may have cut the gum. Only m1 is consistently absent from the oral cavities of five newborn specimens. Upper C has erupted in one out of five specimens; lower C in two out of five. During a brief perinatal period, the pup may have no posterior teeth at all, when the three deciduous molars above and below have exfoliated and only p1 above and below have cut the gums. During this period, the posterior one-third of each gum line is dark pinkish gray, from congestion of blood at the sites of teeth about to erupt.

We conclude, from extrapolation of the evidence of tables 9 and 10, that the first permanent tooth (lower I3) to erupt from the fetal gum does so in the fetus of 4.0 kg. (80 percent MNW, about 29 weeks implanted age), in early June, about 5 weeks before birth. The last tooth (upper m2) to erupt does so 6 to 13 weeks after birth, in August to October. It is nearly erupted in a specimen of known-age 39 days; it is barely erupted in a specimen of 103 days. Permanent teeth in situ in the gums of a yearling are shown in plate 12.

There is some evidence that supernumerary teeth are late in eruption. In the right upper quadrant of a pup several weeks old, an extra premolar is just cutting the gum between p1 and P2. The normal premolars are already in place, their tips 3 mm. beyond the gum line.

An earlier statement by Scheffer (1950, p. 309) is inexact. "When the fur seal is born in midsummer the canines, as well as most of the other permanent teeth, have erupted." In fact, while the canines may have erupted, the well-formed and functional teeth which are usually visible in each canine locus are the deciduous set. The permanent canines cut the gum before age 10 weeks (tables 9 and 10, plate 13, A).

In the skulls of five males, age 10 years or older, the tips of the teeth are highest above the gum in an adult, but not an old, individual, age 14 years (table 12). In the skulls of five females, ages 6 to 15 years, the teeth are highest in a 13-year-old (table 12).

Growth and Maturation of Permanent Teeth

Closure of the root.—As dentin is gradually deposited within the root canal of the permanent tooth, the diameter of the canal decreases. Eventually, the canal is filled and its blood vessels and nerves are pinched off (plate 13, B). The timing of root closure, by individual tooth and by sex, is shown in tables 13 and 14. Teeth such as lower

TABLE 13.—*Root closure in the permanent teeth, male*

Teeth	Age of specimen in months or years								
	9 mo.	14 mo.	14 mo.	2 yr.	2 yr.	3 yr.	3 yr.	4 yr.	4 yr.
	Stage of root closure [1]								
Upper:									
I1	—	o	—	x	x	x	x	x	x
I2	—	o	—	x	o	x	x	x	x
I3	closes in 7th to 10th year								
C	closes after 20th (?) year								
p1	—	—	—	—	—	—	—	o	—
P2	—	—	—	—	—	o	—	x	x
P3	—	—	—	—	—	x	—	x	x
P4	—	—	—	—	—	x	o	x	x
m1	—	—	—	x	o	x	x	x	x
m2	—	—	—	x	o	—	o	x	x
Lower:									
I2	—	x	x	x	x	x	x	x	x
I3	—	x	x	x	x	x	x	x	x
C	closes after 12th (?) year								
p1	—	—	—	x	o	x	o	x	x
P2	—	—	—	x	o	x	o	x	x
P3	—	—	—	o	—	x	o	x	x
P4	—	—	—	—	—	x	—	x	x
m1	—	—	—	o	—	x	o	x	x

[1] Symbols: Dash (—)=root canal open; o=root canal nearly closed; x=root canal closed.

TABLE 14.—*Root closure in the permanent teeth, female*

Teeth	Age of specimen in months or years					
	3 mo.	7 mo.	15 mo.	2 yr.	3 yr. [1]	3 yr. [2]
	Stage of root closure [3]					
Upper:						
I1	—	—	o	x	x	x
I2	—	—	o	x	x	x
I3	—	—	—	—	—	x
C	closes after 15th year					
p1	—	—	—	—	—	x
P2	—	—	—	—	—	x
P3	—	—	—	x	o	x
P4	—	—	—	o	o	x
m1	—	—	o	x	o	x
m2	—	—	—	—	o	x
Lower:						
I2	x	x	x	x	x	x
I3	o	o	x	x	x	x
C	closes in 7th or 8th year					
p1	—	—	—	o	o	x
P2	—	—	—	x	x	x
P3	—	—	—	—	o	x
P4	—	—	—	—	o	x
m1	—	—	—	—	o	x

[1] Slightly younger than 3 years on April 12.
[2] Slightly older than 3 years on September 11.
[3] Symbols: Dash (—)=root canal open; o=root canal nearly closed; x=root canal closed.

TABLE 15.—*Length of root of the permanent right upper canine with increasing age* [1]

Age	Males			Females		
	Length of root			Length of root		
	Number	Range	Mean	Number	Range	Mean
Years		*Mm.*	*Mm.*		*Mm.*	*Mm.*
0 [2]	4	0.3–0.7	0.5			
½ [3]	7	3.2–5.5	4.5			
1	2	9.1–9.2	9.1	3		8.9
2	25	9.5–13.0	11.6	8	10.0–13.6	12.1
3	8	12.3–15.5	13.6	20	11.9–17.2	13.7
4	17	13.8–17.7	16.2	20	12.2–17.0	14.7
5	2	17.0–17.1	17.1	20	13.7–18.0	14.9
6	1		21.8	20	13.7–20.6	16.7
7	2	22.3–24.1	23.2	20	16.5–20.2	18.5
8	1		33.1	18	15.6–20.9	18.3
9				5	15.7–19.8	18.3
10	3	28.4–33.2	30.3	21	17.6–23.9	19.8
11				13	18.9–23.4	20.3
12				2	17.0–23.0	19.6
Old [4]				9	19.1–24.3	21.6

[1] Unless otherwise noted, data are from known-age (marked) seals recovered on the Pribilof Islands in summer.
[2] Full-term fetal, July 6, 1957.
[3] "Yearlings" about 6 to 7 months old, found dead or dying on Oregon beaches after a storm, late January to early February 1950.
[4] Nine canines with crown worn and root canal closed, or nearly closed, selected from 100 unmarked females killed on a breeding ground, October 3, 1950.

incisors, with slender roots, close earlier than teeth, such as canines, with larger roots.

Evidence on the maximum age of root closure in male teeth is poor (table 13). The oldest known-age skull in the collection is a 14-year-old. In three 10-year-olds, the diameter of the right upper canine root canal is 6, 8, and 8 mm., respectively—far from closed. In an 11-year-old, it is 8 mm., while the diameter of the lower canine canal is 0.3 mm. In the 14-year-old it is 7 mm., and the canals of the lower canines are closed. In a very old individual of undetermined age, with worn and polished teeth, the root of the left upper canine still has a canal 0.6 mm. in diameter, whereas the root of the left lower canine has long since closed. We tentatively conclude that upper canines in the male close after the 20th year (or in some individuals never?); lower canines after the 12th.

Evidence on the maximum age of root closure in female teeth is more conclusive (table 14). In the upper canines of 44 females (23 ten-year-olds, 15 eleven-year-olds, 4 twelve-year-olds, and 2 fifteen-year-olds), the diameter of the root canal varies from 0.1 to 1.5 mm., average about 0.5 mm. In the two 15-year-olds, the diameter of the canal is 0.2 mm. In a 21-year-old, the canal is closed. We conclude that the female upper canine closes after the 15th year.

Growth of the root.—Increase in size of the growing root has been studied for the right upper canine. This tooth was selected in 1949 as the one which would be used, in future Pribilof seal studies, as an indication of age. Length of root by age and sex is given in table 15. Changes in the root are illustrated in plates 14 and 15. At birth, when the upper canine is largely hidden within the bony alveolus, the root is less than 1 mm. in length. On the evidence of its size and shape, the root grows rather uniformly during the 3- to 4-month period when the pup is nursing. At time of weaning, when the pup learns to feed for itself, growth of the root declines. The evidence is a faint "first-autumn depression" or valley circling the root. Some teeth show it plainly (plate 15), others do not. At completion of the first year of life, a "second-autumn depression" is formed around the root. Another depression is formed in the third autumn, and in each successive autumn until the seal approaches an age of 10 to 15 years. Then each depression tends to become shallow and narrow and to be hidden by a deposit of cementum (plate 16).

As long as the root canal remains open, dentin is deposited on the walls of the root cavity, the deposit being thicker and more opaque in winter, spring, and summer; thinner and more translucent in fall. As a result of this unequal deposition, each annual layer is visible on a longitudinally sectioned tooth as a discrete cone slightly smaller than, and nesting within, the cone of the previous year (plate 17). Meanwhile, a thin but fairly distinct layer of cementum is being laid down annually on the outside of the root. The source of the cementum is the connective tissue surrounding the root, not the pulp of the tooth. Cementum layers continue to be laid down after the root canal closes. Zander and Hürzeler (1958) measured cementum thickness on 233 single-rooted human teeth and found that it showed a straightline increase with age. Thickness tripled between ages 11 and 76 years. This was "surprising in view of the fact that growth processes usually decrease with advancing age" (p. 1043).

Kubota et al. (1961) described growth layers near the level of the cementoenamel junction. These are, from outside inward: cementum, prenatal dentin (opaque), neonatal line (translucent), postnatal dentin consisting of (a) interglobular dentin mixed with the granular layer of Tomes and (b) a translucent layer which is formed in spring. When the root canal closes, dentin ceases to form in regular conical layers. While stratified deposits of some tooth substance continue to form at the base of the root, they tend to be thin and irregular, and we do not know what to call them. We sliced longitudinally and polished all of the right teeth of a known-age 13-year-old female. The smallest tooth, the 1st lower incisor, whose root canal probably closed within the 1st year of life, shows no distinct layers in the dentin. The lower canine, where the root canal probably closed in the 7th or 8th year, shows seven conical layers of dentin. The upper canine, where the root canal is still open, shows 13 layers.

Annual growth lines in the teeth of the seal develop in both sexes, and in captive as well as wild individuals. Growth of the root is always slower in autumn. We suggest that the period of slow growth is related to the annual molt of the pelage which takes place in autumn in seals of all classes (Scheffer, 1962). A male seal was captured on the Pribilof Islands on October 17, 1948 and was delivered to the San Diego Zoo a few days later. It died on May 18, 1953, after almost 5 years in captivity. The root of its right upper canine is of normal size (length 22.6 mm.); the growth ridges are somewhat confused (plate 18). Nevertheless, two experienced biologists (C. E. Abegglen and A. Y. Roppel) estimated correctly and independently the age of the seal as 5 years. Mansfield and Fisher (1960) counted 18 to 20 layers on the tooth of a harbor seal *Phoca* that had been brought as a pup to the Seattle Zoo and died there at age 19½ years.

The relative importance of the various environmental factors which contribute to the formation of growth ridges cannot now be evaluated. It seems possible both that molt in autumn may cause a decrease in deposition of root substance and that heavy feeding in spring may cause an increase. There is ancillary evidence that most of the annual body weight increment is added in spring.

From the evidence of certain teeth (plate 19, B and C), the accretion of root substance may suddenly accelerate or decelerate. Ridges on the surface of the growing root, finer than annuli and spaced between them, are thought to originate in individual periods of intensive feeding. Plate 19, A reproduces a gelatin impression of the surface of a yearling male canine tooth. The seal was killed on September 13, at estimated age 14 months. Around the root one can count about 25 fine ridges, more or less distinct, arranged in a near-rhythmic pattern.

Typical postcanine roots in situ in a middle-aged seal are illustrated in plate 8. Other roots, somewhat atypical as a result of bone resorption, are shown in plate 20, A.

Crown.—The crowns of the permanent teeth become streaked and stained dark brown soon after birth. In a specimen a few days old taken on June 26, (female, 4.4 kg., 92 percent MNW) the teeth are already moderately stained. The pigment is heaviest on the posterior series of teeth and on buccal, as opposed to lingual, surfaces. The chemistry of the pigment is not known.

Tooth crowns of the fur seal do not suffer wear to the same extent as do crowns of land carnivores like wolf and bear. Where the dentin of the seal tooth has been exposed, its surface becomes polished and shiny (plate 20, B).

For each canine showing crown-tip wear, we have estimated its height, had there been no wear (tables 7 and 8). Tip wear is insignificant in 1-, 2-, and 3-year-olds. On the upper canines of 6- and 7-year-olds, it may reach 1 mm. in males and 0.7 in females; on the lower canines, a little less.

GROWTH CHANGES IN SKULL AND JAWS

In both sexes, the halves of the mandible remain separate through life, as in the dog but not in man. They are united by tough connective tissue and cannot easily be pulled apart. Right and left molariform tooth rows are nearly parallel. They may diverge posteriorly up to 5 degrees. Each approaches a straight line, though it may be slightly convex or, rarely, concave. The shape of the tooth row does not vary appreciably with age or sex (plates 21 and 22).

A useful indication of physiological age or maturity of the individual is the size of the skull. We have measured condylobasal length and cranial width for 76 skulls (34 males and 42 females), and have compared them with measurements of the upper and lower postcanine series (tables 16 and 17 and figures 3 and 4). The results are summarized on page 310.

Male

Condylobasal lengths in two newborn males are 121 and 122 mm.; in three old adults they are

TABLE 16.—*Skull size and length of the permanent postcanine series, by age, male*

Age	Specimens	Condylobasal length	Cranial width	Length of postcanine series	
				Upper	Lower
	Number	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Percent MNW[1]					
25	1	72	55	19	21
33	1	81	58	20	18
33	1	85	61	20	20
42	1	90	67	22	21
Newborn	2	121	85	33	29
Weeks, 1–2	1	129	86	33	32
Ca. 9 months	1	143	91	35	30
Ca. 14 months	2	165	95	[2] 39	35
Years:					
2	2	173	93	40	33
3	3	180	98	43	36
4	2	191	95	44	36
5	3	200	102	47	38
6	2	213	107	49	40
7	2	213	106	[3] 45	38
8	[4] 3	241	133	[2] 53	43
9	1	232	126	[2] 52	43
10	3	230	122	50	41
10+	3	241	132	54	43
Total	34				

[1] Fetus, 25 percent of mean newborn weight.
[2] One skull has an extra pair of upper premolars.
[3] One skull lacks a pair of upper premolars.
[4] For one broken skull, measurements of skull size are lacking.

TABLE 17.—*Skull size and length of the permanent postcanine series, by age, female*

Age	Specimens	Condylobasal length	Cranial width	Length of postcanine series	
				Upper	Lower
	Number	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Percent MNW[1]					
28	1	79	59	21	19
33	1	84	64	21	20
38	1	85	63	21	22
56	1	99	76	24	22
Newborn	2	122	84	33	27
Ca. 3 months	1			33	29
Ca. 7 months	1	140	88	33	28
Ca. 8 months	1	145	89	35	31
Ca. 15 months	2	159	95	38	35
Years:					
2	3	163	93	40	32
3	2	173	94	39	32
4	4	172	93	42	33
5	7	174	91	41	34
6	2	185	93	48	37
7	2	183	98	44	37
8	2	180	92	43	33
9	3	183	95	44	35
10	1	180	91	42	33
10+	5	190	96	46	36
Total	42				

[1] Fetus, 28 percent of mean newborn weight.

237, 242, and 243 mm. The difference represents a mean increase through life of 98 percent over newborn size. Cranial widths in two newborn males are 85 and 86 mm.; in three old adults they are 131, 131, and 135 mm. The difference represents a mean increase through life of 55 percent. The skull of a male at age 8 or 9 is about as large as it ever will be, though length and width increase slightly after age 9 as a result of bony growth of the premaxillary and mastoid processes.

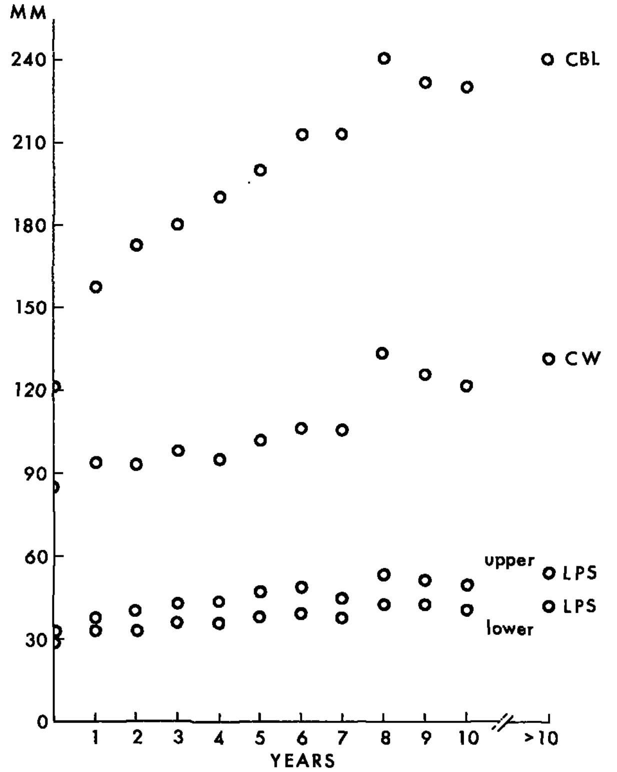

FIGURE 3.—Condylobasal length, cranial width, and length of permanent postcanine series, by age, male. (From table 16, based on 30 specimens.)

In estimating the age at which skull growth reaches a plateau, we have also referred to published data on condylobasal length and mastoid width of 108 fur seal skulls (Scheffer and Wilke, 1953).

Lengths of upper postcanine series in two newborn males are 32 and 33 mm.; in three old adults, 53, 55, and 55 mm. The difference represents a mean increase of 67 percent. The upper jaw does not increase in length after age 8 or 9.

Lengths of lower postcanine series in two newborn males are 29 and 29 mm.; in two old adults, 43 and 43 mm. The difference represents a mean increase of 48 percent. The lower jaw does not increase in length after age 8 or 9. Growth changes in the lower jaw of the male are illustrated in plate 23. In the sample illustrated, the length of the jaw increased by 54 percent in the period from birth to age 3 (the age of sexual maturity in some males). It increased 53 percent between age 3 and adulthood. This growth spurt in postpubertal life, observed in the male only, is related to the fact that the fur seal is polygynous. To the adult male attempting to hold his place in a fiercely competitive social order, strong jaws and teeth have survival value. In the same sample, the ratio of length of jaw to length of postcanine series is 2.4:1 for the full-term fetus and 3.9:1 for the old adult. The postcanine tooth-row grows slower than the mandibular corpus posterior to it. The postcanine tooth-row itself increased 45 percent (29 to 42 mm.). As the tooth row lengthens, the diameter of each socket increases; the spatial arrangement of the tooth row remains fairly constant.

Female

Condylobasal lengths in two newborn females are 121 and 123 mm.; in five old adults they are 185, 189, 191, 191, and 196 mm. The difference represents a mean increase through life of 56 percent. Cranial widths in two newborn females are 82 and 96 mm.; in five old adults they are 95, 96, 96, 96, and 99 mm. The difference represents a mean increase through life of 15 percent. The skull of the female does not appear to grow in length or width after age 5 or 6. With respect to skull size, the female reaches maturity about 3 years before the male.

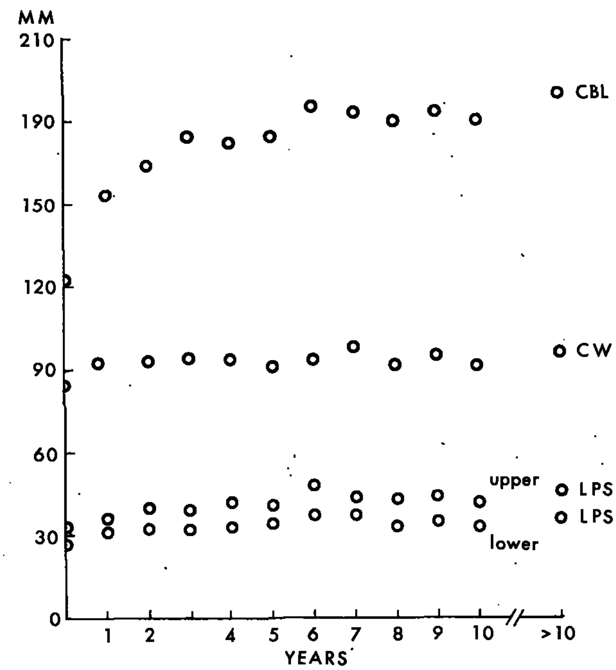

FIGURE 4.—Condylobasal length, cranial width, and length of permanent postcanine series, by age, female. (From table 17, based on 38 specimens.)

Length of upper postcanine series in two newborn females are 32 and 33 mm.; in five old adults 45, 45, 46, 46, and 49 mm. The difference represents a mean increase of 42 percent. The upper jaw continues to grow in length until age 5 or 6.

Lengths of lower postcanine series in two newborn females are 26 and 28 mm.; in five old adults 34, 35, 36, 37, and 37 mm. The difference represents a mean increase of 33 percent. The lower jaw continues to increase in length until age 5 or 6.

ANOMALIES

Prenatal

In a sample of 123 skulls of both sexes, 14 (or 11 percent) show anomalies of the dentition. Four have extra teeth. Ten lack one or two teeth, and apparently did not have them at time of birth.

Of the four skulls with extra teeth, three have extra premolars in the upper middle series and one has extra premolars in the lower middle series (plate 24). The skull with extra lower premolars is remarkable for having 45 teeth—9 extra! It has three extra upper incisors lingual to, and similar to, I1 and 2; four extra lower incisors lingual to I2 and 3; and a pair of extra lower premolars between P2 and 3.

In the dog, when supernumerary teeth are present, they are incisors or premolars, usually unilateral and in the upper jaw (Miller, 1952). In the fur seal (as noted in three out of four cases), extra premolars in the upper jaw are more common than in the lower.

Of the 10 skulls with teeth prenatally lost, 4 lack one and 6 lack both upper m2. This posterior tooth, which is unopposed, is small and weak. It quite certainly has the least function of any of the teeth. Where there is unilateral absence, the remaining one may be unusually small, or be broken off at the alveolar rim. We suspect that m2 can be lost in early postnatal life when the maxillary bone is still growing actively and is able to fill in the bony alveolus without trace. Thus, one cannot always distinguish, in an adult skull, between prenatal and postnatal loss of m2. According to Simpson (1961, p. 100) "a tooth . . . that no longer occludes or that is in the process of reduction and loss of essential function (like the human wisdom teeth) is demonstrably exceptionally variable in both structure and size."

In addition to the random sample of 123 skulls utilized in this report, 4 selected "freaks" were

TABLE 18.—*Beginning events in the dental development to age 12 weeks* [1]

Body weight	Approximate percent mean newborn weight	Approximate month	Deciduous teeth					Permanent teeth			
Kg											
0.05	1	December									
.10	2	January	*CC*								
.15	3	January	*CC*					*CC*			
.20	4	January		*AE*				*CC*			
.25	5	January		*AE*				*CC*			
.30	6	February		*AE*				*CC*			
.35	7	February		*AE*				*CC*			
.40	8	February		*AE*				*CC*			
.45	9	February						*CC*			
.5	10	February						*CC*			
1.0	20	March				*RC*		*CC*			
1.5	30	March			*GE*	*RC*		*CC*			
2.0	40	April			*GE*	*RC*		*CC*			
2.5	50	April			*GE*	*RC*	*EX*	*CC*	*AE*		
3.0	60	May			*GE*	*RC*	*EX*	*CC*	*AE*		
3.5	70	May				*RC*	*EX*	*CC*	*AE*		
4.0	80	June				*RC*	*EX*		*AE*	*GE*	
4.5	90	June				*RC*	*EX*		*AE*	*GE*	
5.0	100	July (birth)				*RC*	*EX*		*AE*	*GE*	
8.0	160	August (age 6 weeks)					*EX*			*GE*	
13.0	260	October (age 12 weeks)									*RC*

[1] These events are beginning in one or more teeth: *CC*=crown calcification, *AE*=alveolar eruption, *GE*=gingival eruption, *RC*=root closure, and *EX*=exfoliation.

observed: (1) a skull with an extra pair of upper premolars between P2 and 3, (2) a skull with supernumerary upper canines, (3) a skull with seven extra teeth in the upper and lower series of incisors and anterior premolars, and (4) a skull with an extra pair of lower molars. The last was figured by Scheffer (1958). It is remarkable in that it represents the only known specimen having an extra tooth at the posterior end of a tooth row.

Postnatal

Damage represented by empty sockets, or teeth broken off, is apparent in both sexes and in both upper and lower jaws. In the lower jaw of a 7-year-old female, P3 is deformed and blackened (plate 25, A). Evidently the crown was accidentally broken; then an abscess formed around the root and the bone of the socket eroded. In a young male, about 6 years old, that died in the Seattle Zoo, right upper C is greatly deformed (plate 25, B). Here also a root abscess is the cause. From the left mandible of an old female, the four premolars have been lost and the bone itself has undergone extensive change (plate 26, A). The bony alveoli of a male raised in captivity have a spongy, eroded appearance (plate 26, B).

We have seen no evidence of caries in seal teeth. Hall (1940) examined the skulls of 3,761 land carnivores and found caries in 2 percent of 360 bears (*Ursus* and *Euarctos*), but in no other carnivores.

SUMMARY AND CONCLUSIONS

The dentitions of 167 specimens of *Callorhinus ursinus* ranging from early fetal life to adulthood have been studied. Crown and root morphology of deciduous and permanent teeth are described. A terminology is presented for the kinds of teeth, their topographic relationships, their developmental stages, and their measurements. The time sequence is shown for calcification, alveolar eruption, gingival eruption, root closure, and exfoliation (table 18). Formulas are presented for deciduous, mixed, and permanent dentitions (fig. 5). Increase with age is shown for skull length and width, and for length of upper and lower postcanine series. Certain prenatal and postnatal anomalies, especially supernumerary and absent teeth, are described. The following observations and conclusions are believed to be new or worthy of emphasis:

1. Calcification is initiated in all deciduous teeth between implanted ages 7 and 9 weeks, when the fetus has attained 2 or 3 percent of its estimated newborn weight. Initial calcification in the permanent teeth overlaps that in the deciduous teeth, though it is still in progress up to about implanted age 27 weeks and 70 percent estimated newborn weight. The very early development of the permanent teeth enables the young seal, at age 3 or 4 months, to convert abruptly from a diet of milk to one of fish and squid.

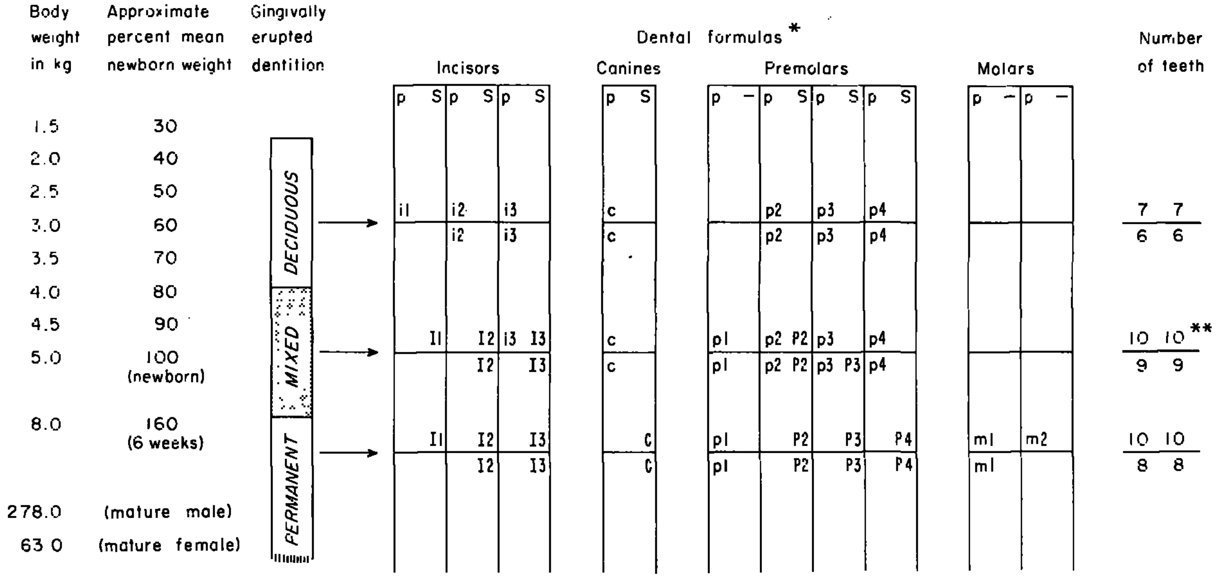

FIGURE 5.—Dental formulas at three stages of development.

*Primary teeth are in small letters; secondary teeth in large. Maxillary teeth are shown above the bar, mandibular teeth below.

**The mixed (successional) dentition is highly variable. Shown here are teeth which have usually erupted in the perinatal period.

2. With the exception of the canines, the deciduous teeth are nonfunctional. The smaller ones (incisors) exfoliate during fetal life; the premolars exfoliate during perinatal life; one or another of the canines may persist for 13 weeks after birth. With the exception of the canines, which cut the gums early, the sequence of gingival eruption is random, or nondirectional, in the tooth rows.

3. At birth, the crown tips of all of the permanent teeth are at, or above, the bony alveolar rims. From two to seven teeth in each upper quadrant, and from four to six in each lower quadrant, may have cut the gums. Variability in the neonatal (mixed) dentition has apparently little significance for survival. The last permanent tooth (upper m2) erupts at age 6 to 13 weeks. Directionally, the sequence of gingival eruption is anterior to posterior, except in the canines.

4. If a "lower 1st incisor" was present in ancestral seals, it has left no embryological trace. In each upper quadrant the 1st premolar (1st postcanine) and the 1st and 2d molars (5th and 6th postcanines) are, on embryological evidence, primary permanent teeth. Similarly, in each lower quadrant the 1st premolar and the 1st molar are primary permanent teeth.

5. The lower medial incisors (I2) and the upper and lower premolars (P2, P3, and P4) usually have anterior and posterior cusplets, suggesting an origin in distinctly tricuspid, perhaps triconodont, teeth. Upper m2 is nearly always double-rooted; certain other posterior teeth are occasionally so. The percentage of consistently double-rooted teeth in the deciduous dentition is 23.1; in the permanent dentition 5.5, suggesting that there has been an evolutionary trend toward a single root.

6. The roots of the permanent teeth continue to grow through life, more slowly after the root canal closes. It closes at age 3 months in small teeth, and at some time after 20 years in large teeth. Annual discontinuities (ridges and layers) occur outside and inside the root; up to 27 have been counted.

7. Skull size and length of postcanine series increase very little after age 8 or 9 years in the male and age 5 or 6 years in the female.

8. In a sample of 123 skulls, the dentitions of 14 (or 11 percent) are anomalous. Four have supernumerary teeth and ten have prenatally absent teeth. Supernumerary teeth have been found in the molar series only once: in lower m1 locus. Upper m2 has no antagonist and, when present, is quite variable in size.

9. Among the problems remaining unsolved are the sequence of calcification of the upper deciduous teeth and the mechanism of gingival eruption of

the deciduous teeth. The frequency distribution of deciduous and permanent teeth in the neonatal (mixed) dentition is known to be highly variable. A more precise understanding of the variability could be obtained by collecting more specimens of newborn pups.

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PLATES

The numbers in parentheses following a caption are photo-catalog numbers in the VBS series, the Marine Mammal Biological Laboratory.

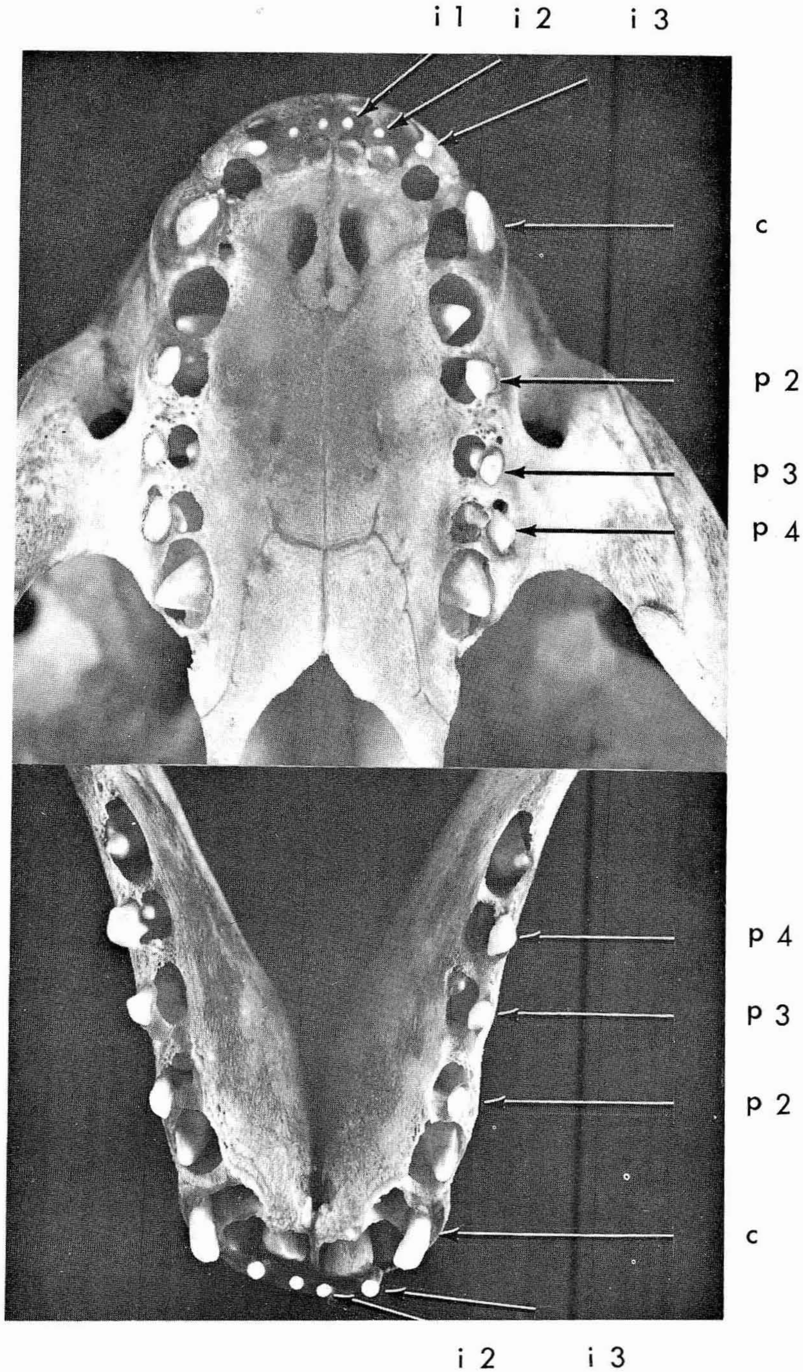

PLATE 1.—Complete deciduous dentition of a fetal female of 1.59 kg., 33 percent MNW. (For terminology of teeth see p. 296.) (4348, 4349)

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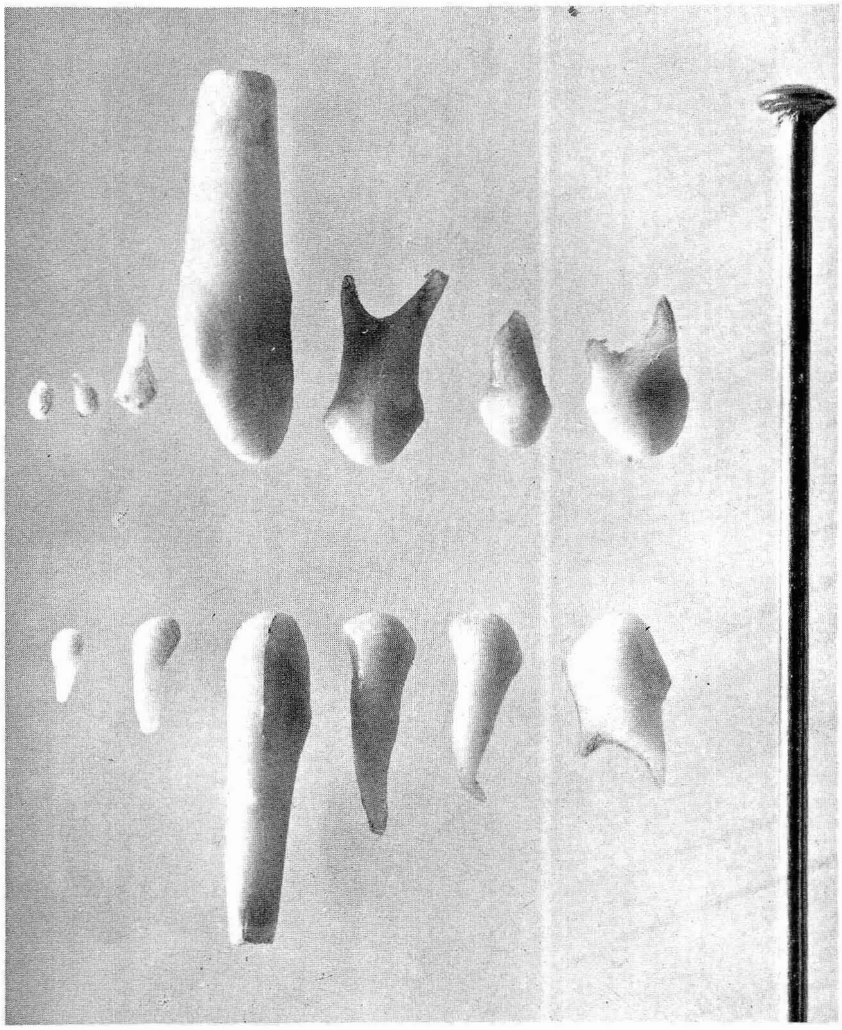

PLATE 2.—Deciduous teeth of the fetal female illustrated in plate 1; left teeth, labial or buccal surfaces; common pin at right. (4385)

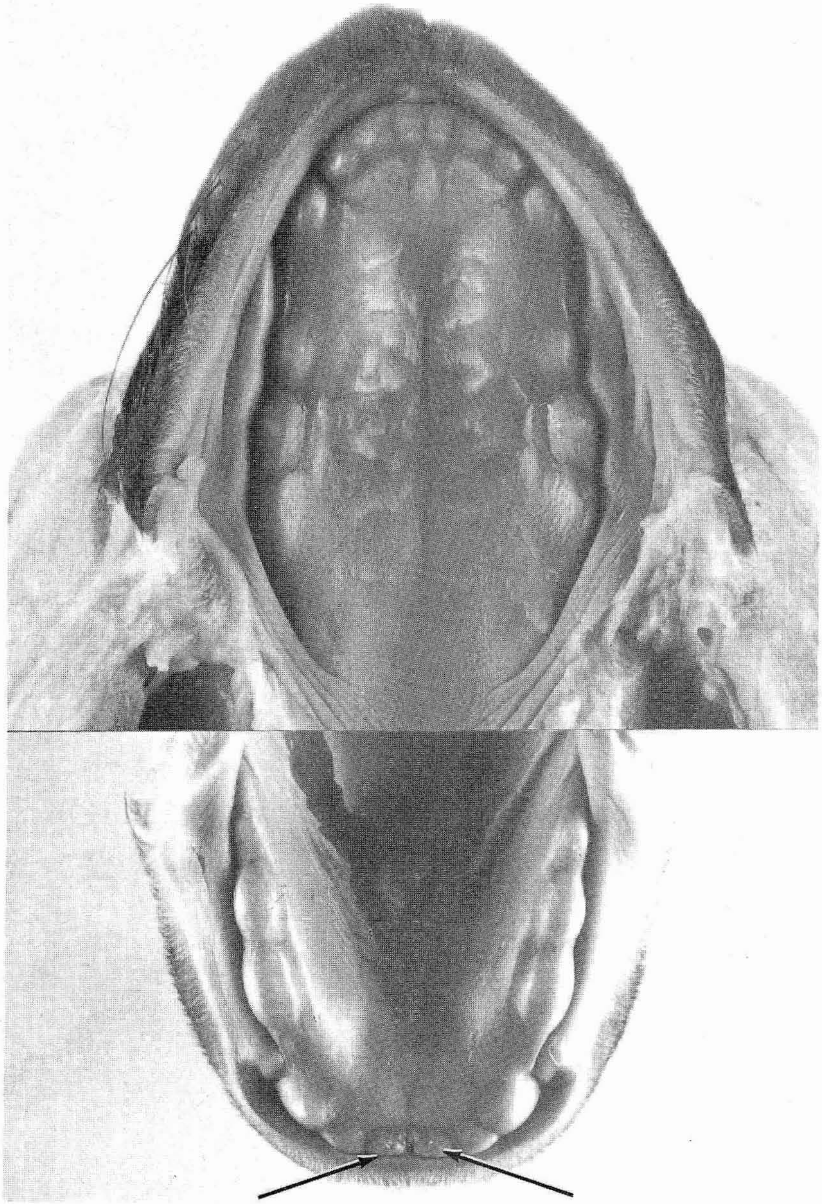

PLATE 3.—Deciduous dentition of a fetal female of 1.70 kg., 34 percent MNW, at onset of gingival eruption. Only lower right and left i2 (arrows) have started to erupt. (4388, 4389)

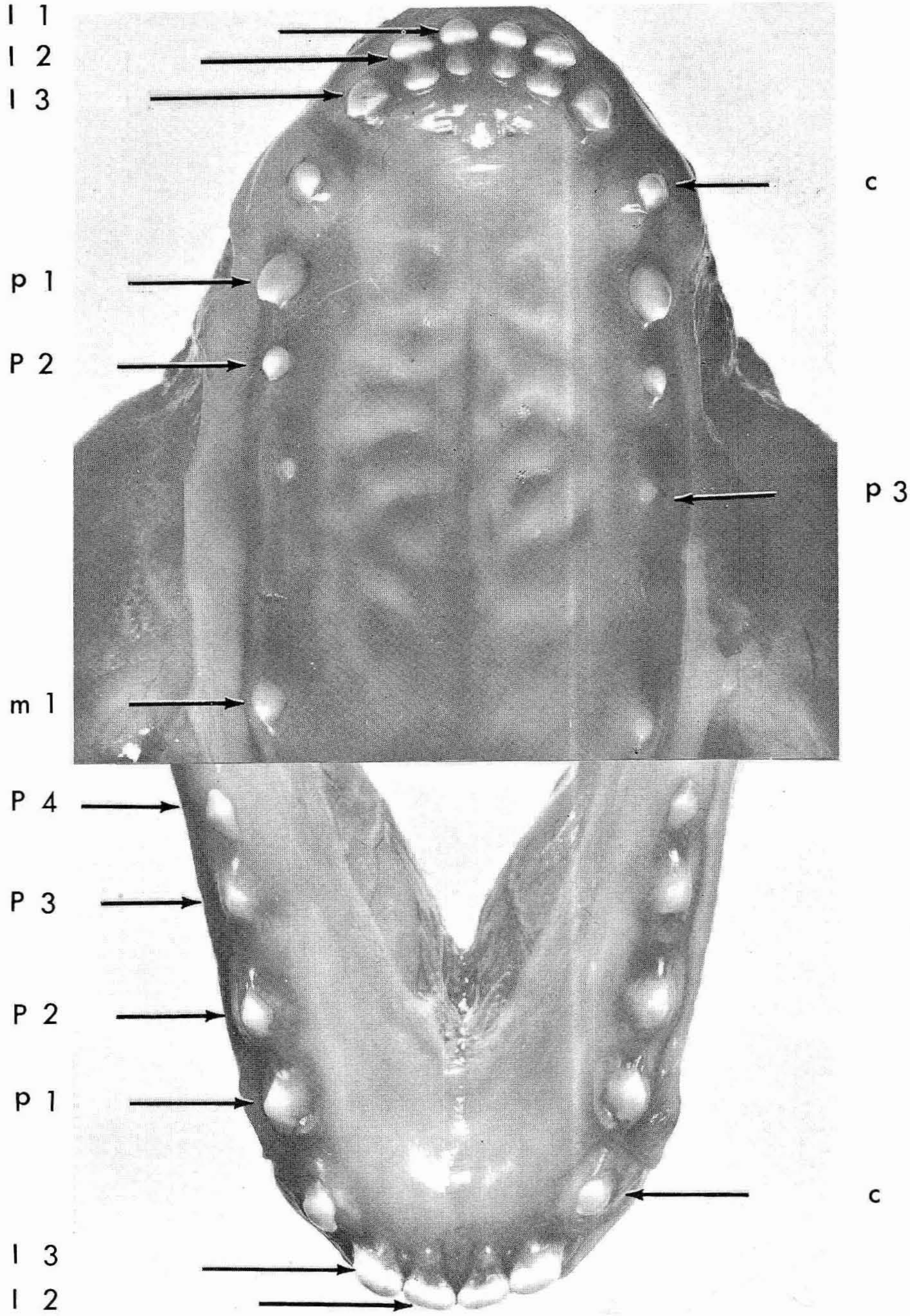

PLATE 4.—Deciduous dentition (arrows at right) and permanent dentition (arrows at left) of a full-term fetal male of 4.3 kg., 89 percent MNW. (2078, 2079)

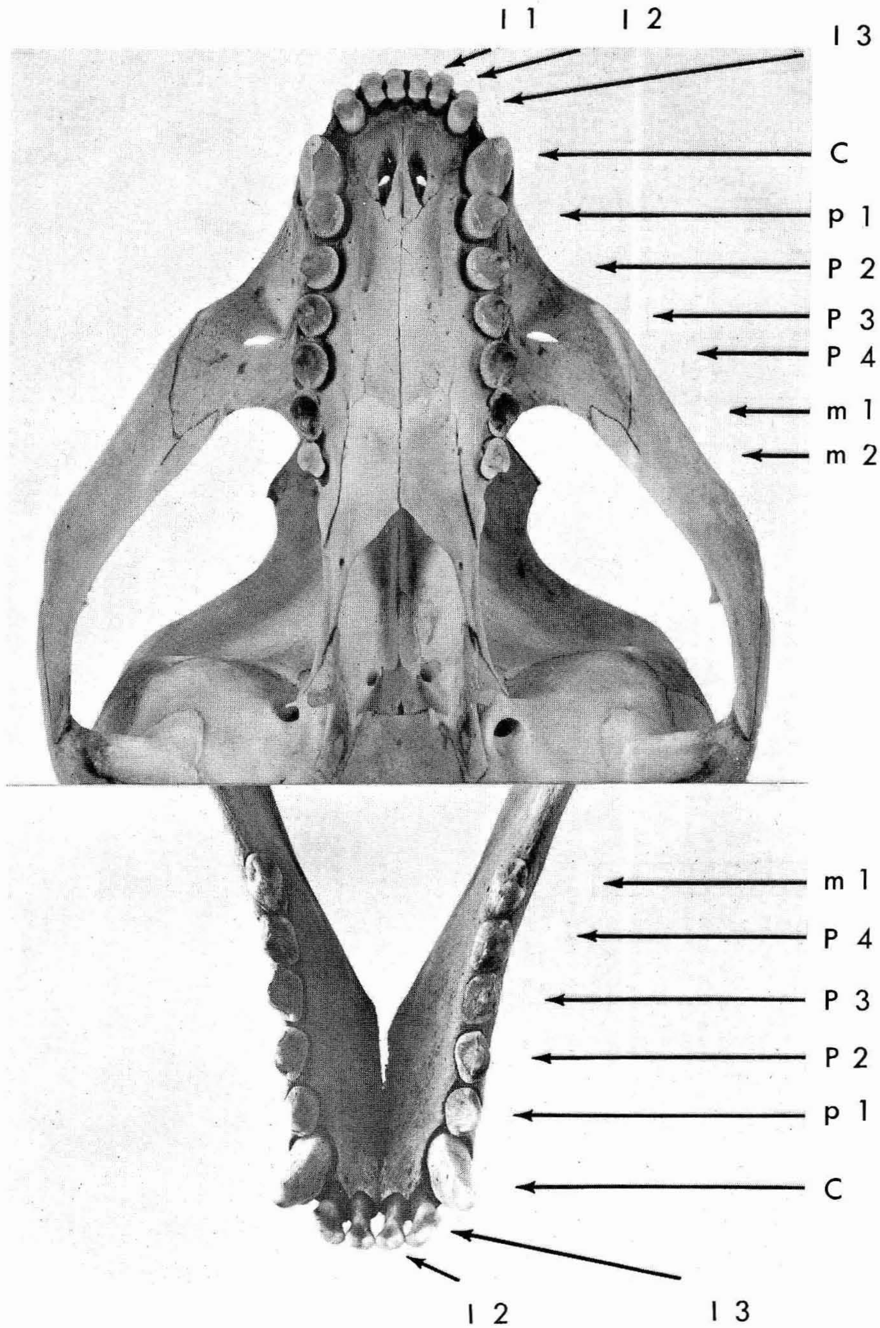

PLATE 5.—Complete dentition of a female about 7 months old, occlusal aspect. (3041, 4311)

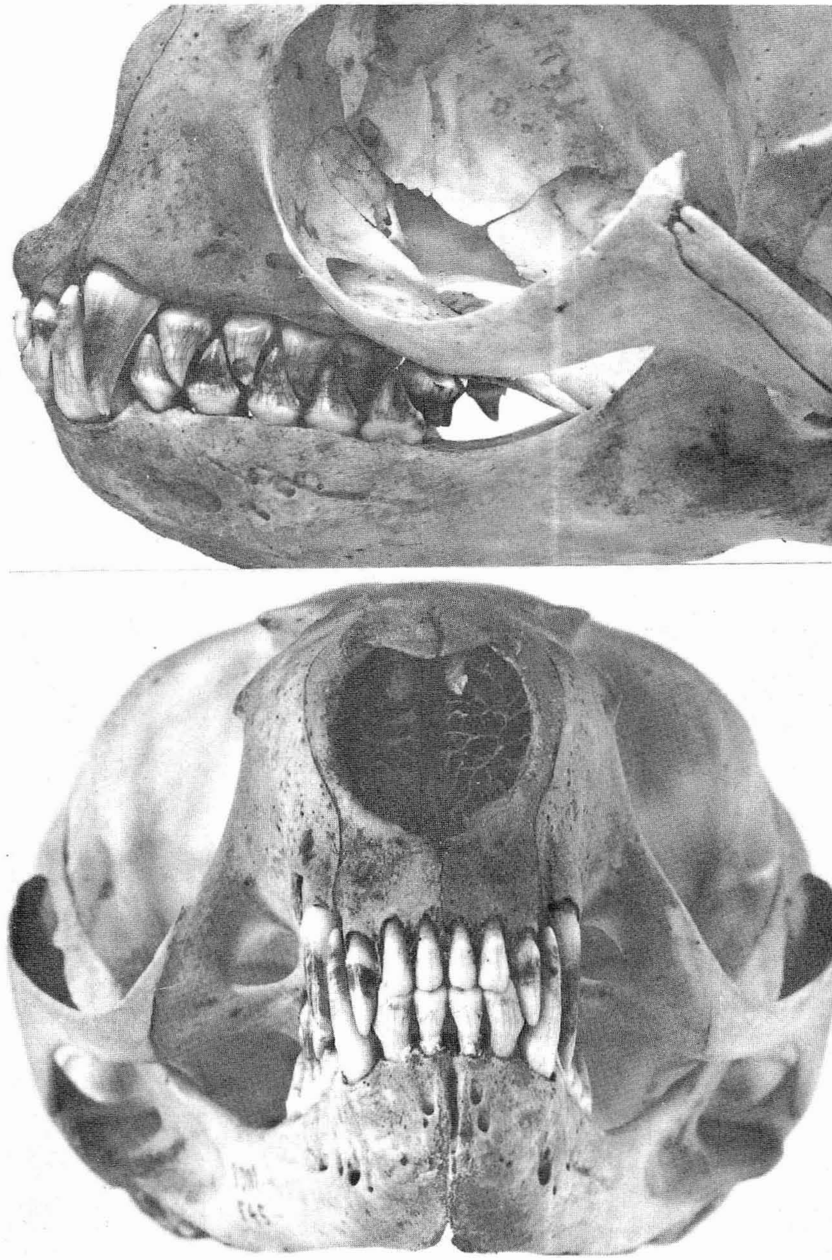

Plate 6.—Complete permanent dentition of a female about 7 months old, lateral and anterior aspects. (Same skull as shown in plate 5.) (4310, 4309)

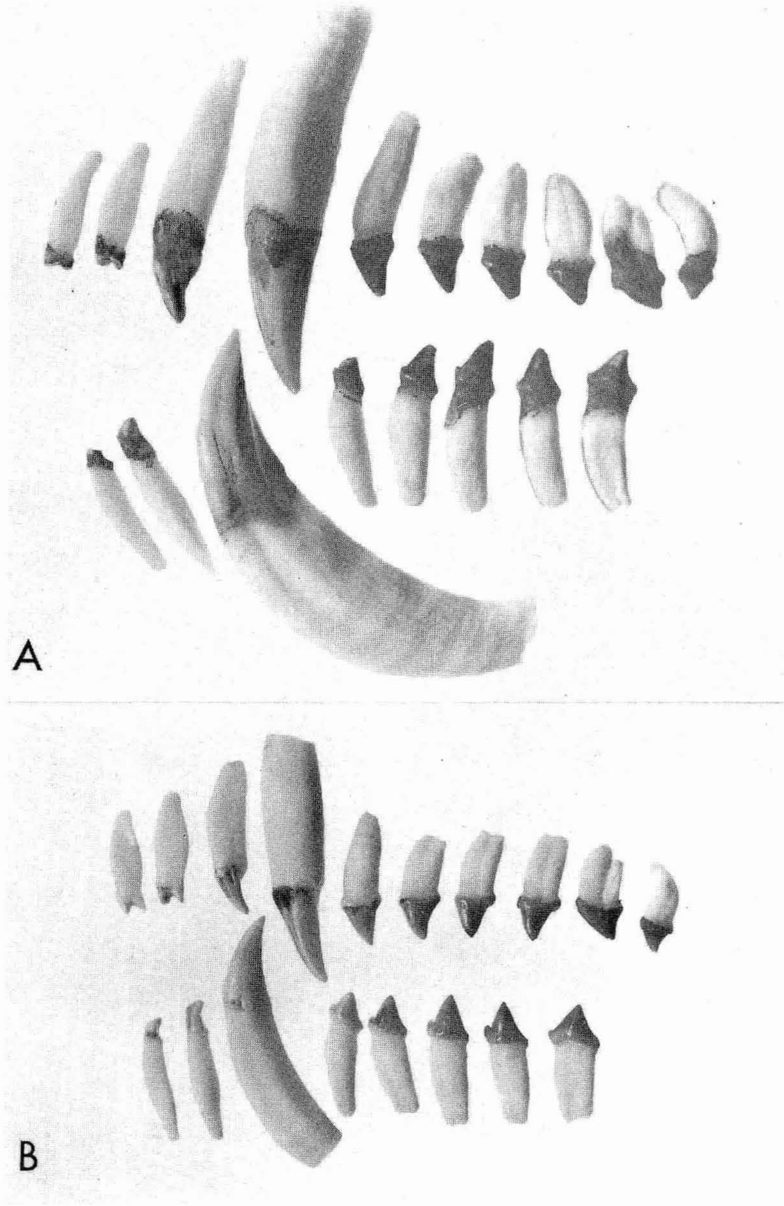

PLATE 7.—Permanent teeth of adults. Left teeth; distal surface of incisors, buccal surface of canines and postcanines; natural size. (A) Male, 10 or 11 years. (B) Female about 6 years. (2430, 2429)

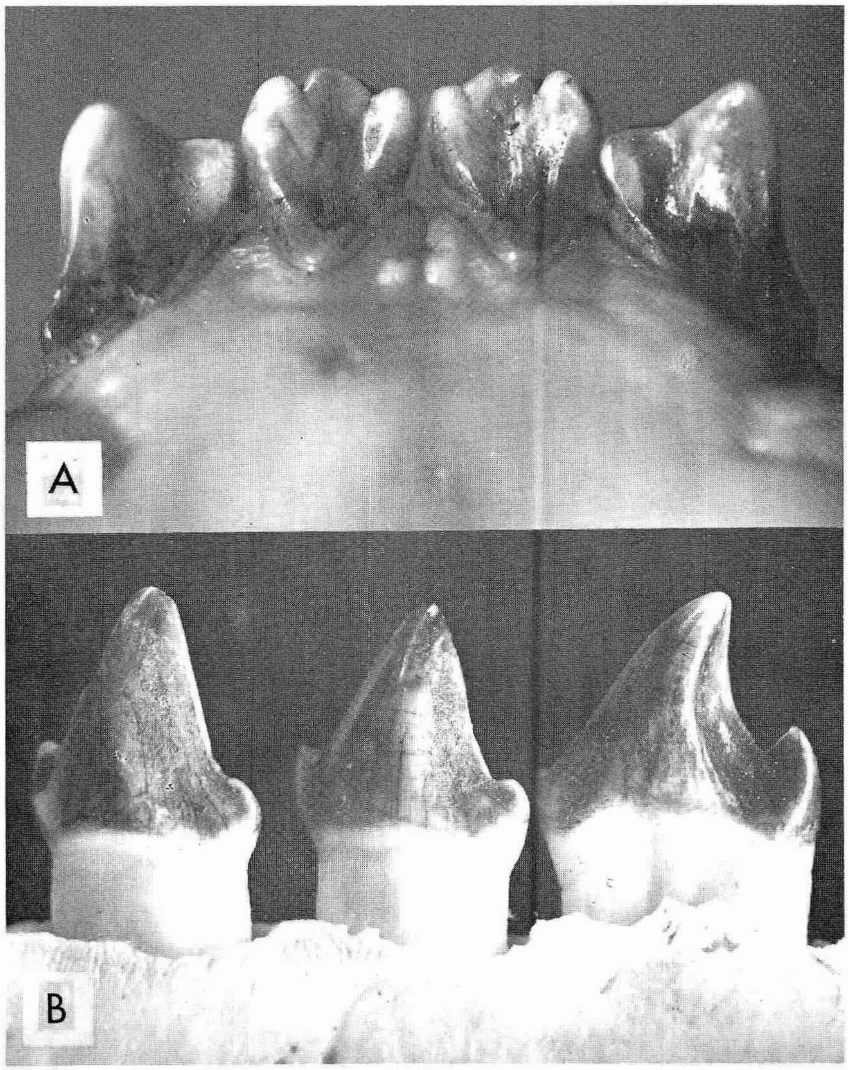

PLATE 8.—Shape of cusps of permanent teeth. (A) Lower incisors of 1-month female; lingual surface. (B) Three lower molariform teeth—left P3, P4, and m1—of 7-year female; buccal surface. (4428, 4375)

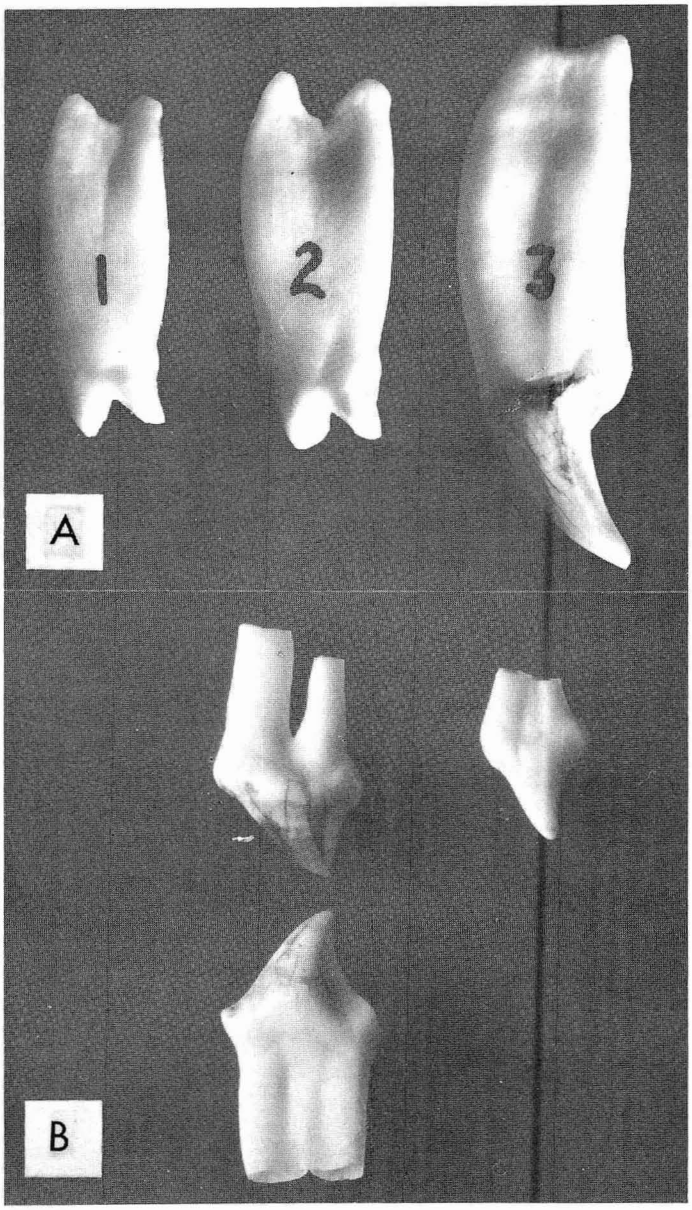

PLATE 9.—Shape of roots of permanent teeth. (A) Left upper incisors of 7-year female; distal surface. (B) Roots of left upper m1 and m2, and lower m1, of 3-month female; buccal surface. (4406, 4396)

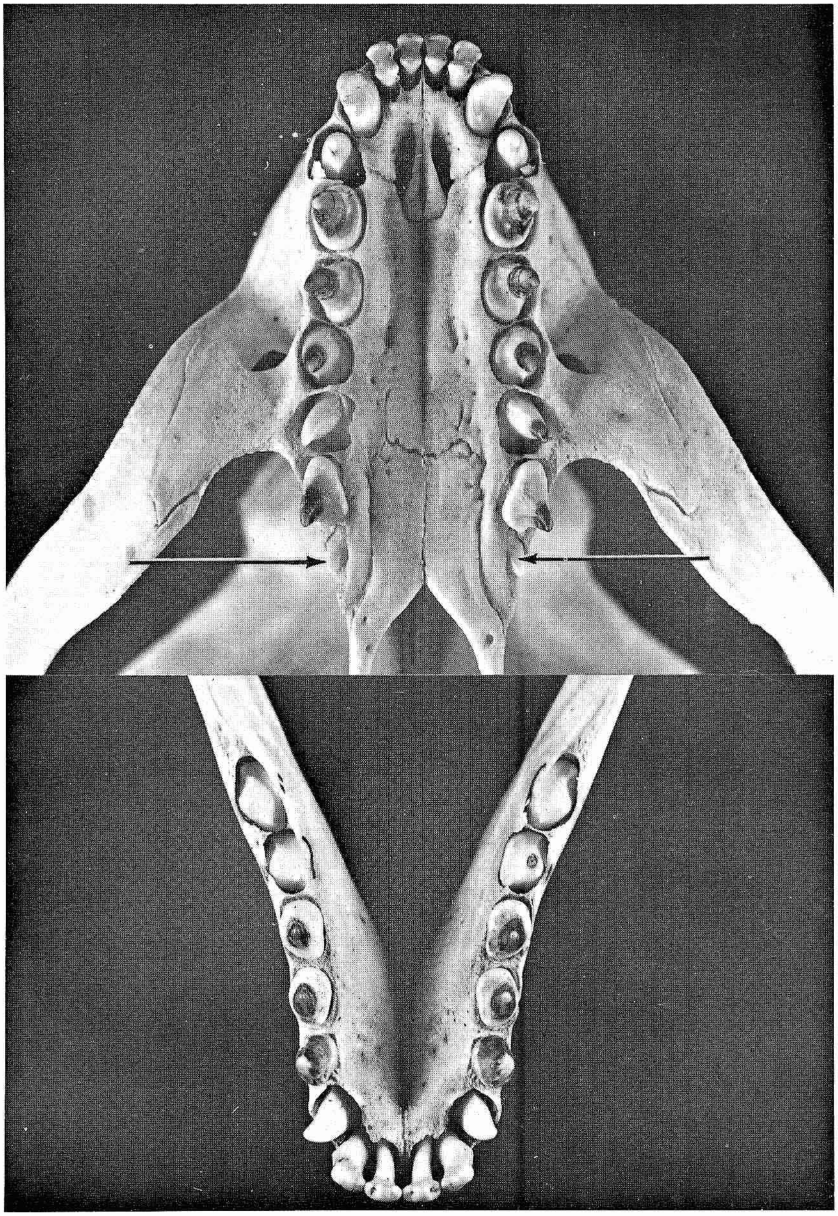

PLATE 10.—Permanent dentition, after alveolar eruption, of a female several days old; upper m2 on each side (arrow) has barely erupted; all deciduous teeth have exfoliated. (4339, 4340)

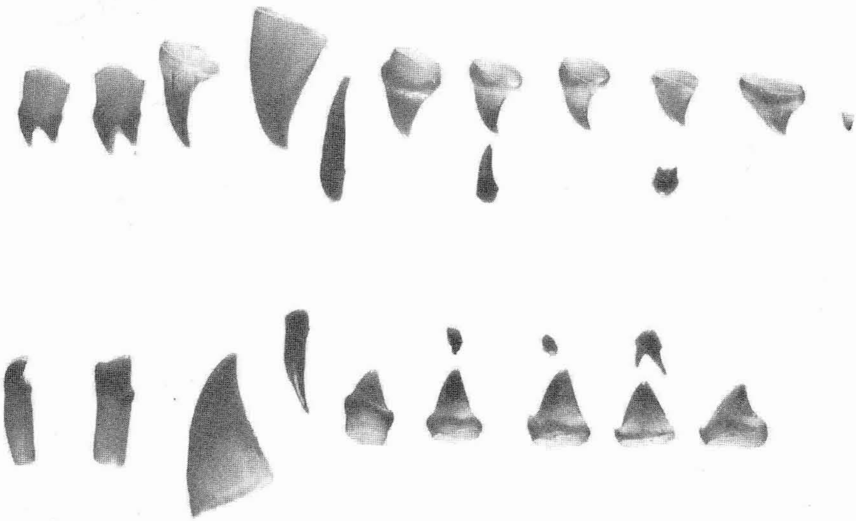

PLATE 11.—Permanent teeth and persistent deciduous teeth of a newborn male. Left teeth; distal surface of incisors, buccal surface of canines and postcanines. Seven deciduous teeth persist; upper p3 and all incisors have disappeared. (Lower i3 was present in the right mandible.) (2814A)

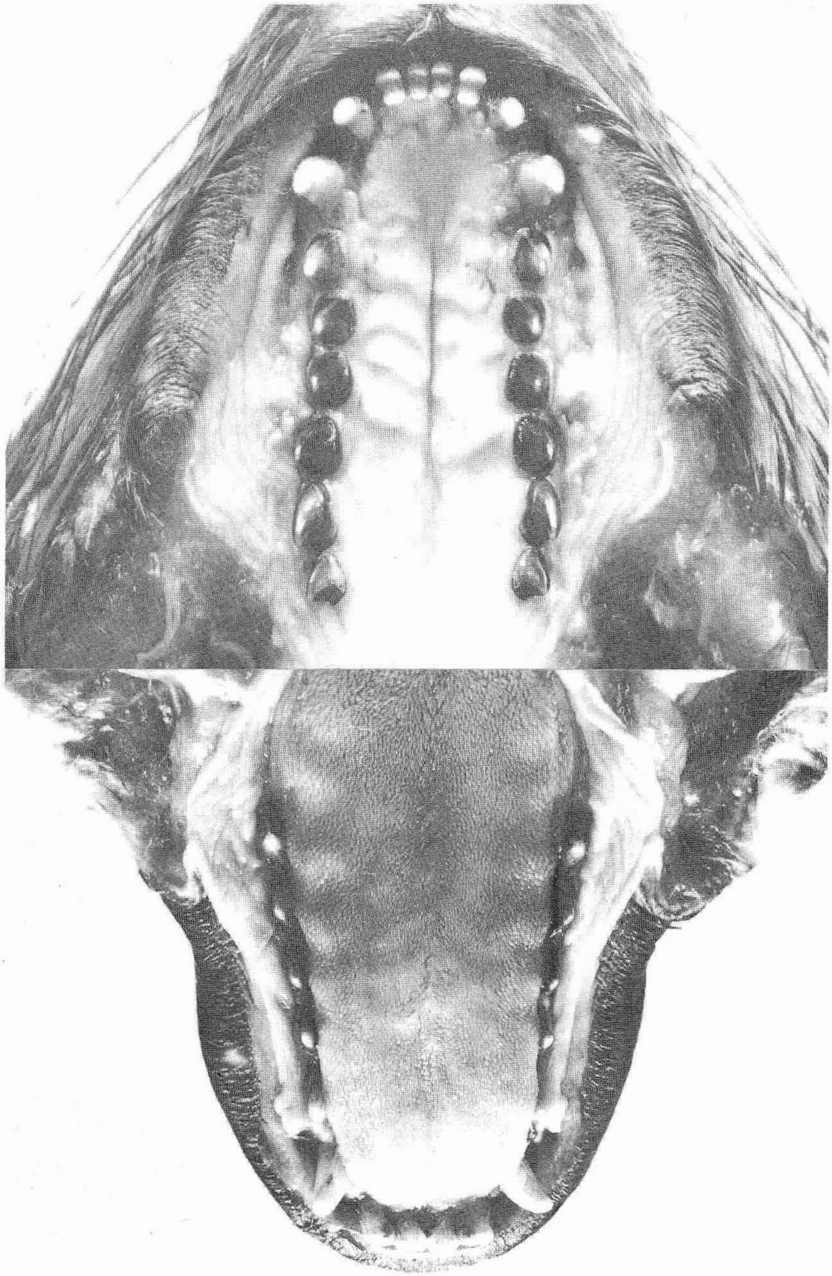

PLATE 12.—Permanent dentition, after gingival eruption, of an 8-month female, March 10, 1960. (4364, 4365)

PLATE 13.—(A) Upper canines in a mixed dentition stage; arrow indicates left permanent canine erupting along mesiolingual side of deciduous canine, in 1-month female. (B) Closure of root canal in an upper canine of a 12-year female. (4429, 4405)

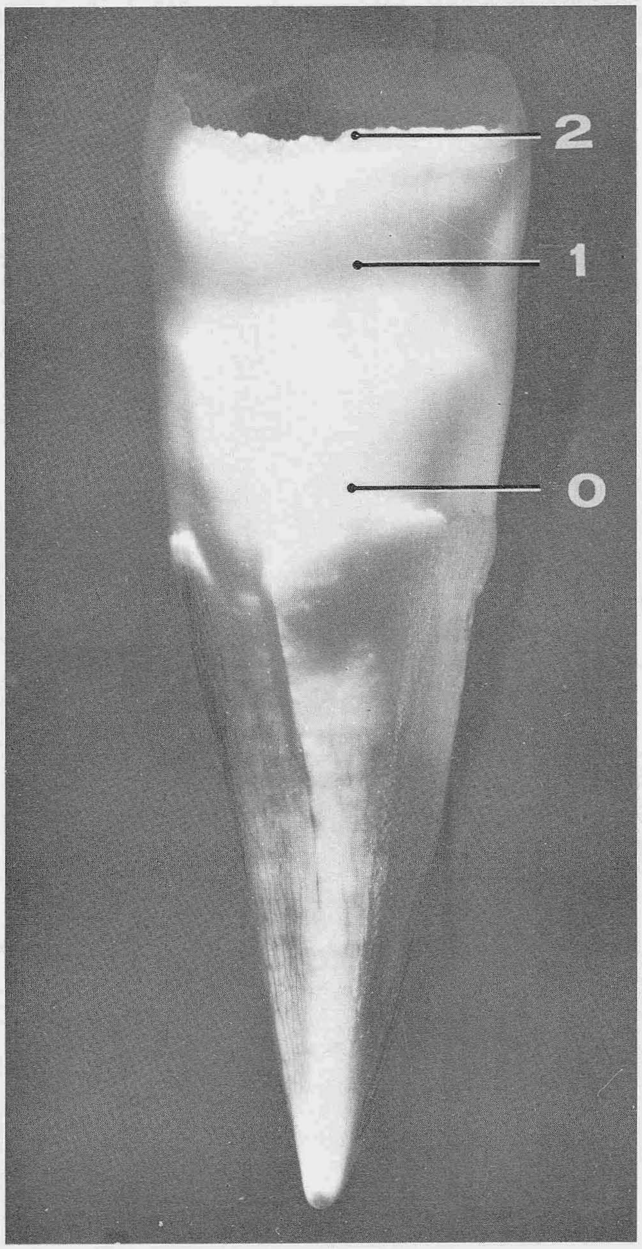

PLATE 14.—Annuli on right upper canine of a 2-year male, July 17, 1949; distal surface; ×5. Numbers show approximate position of root base at ages 0 (birth), 1 and 2 years. (2697)

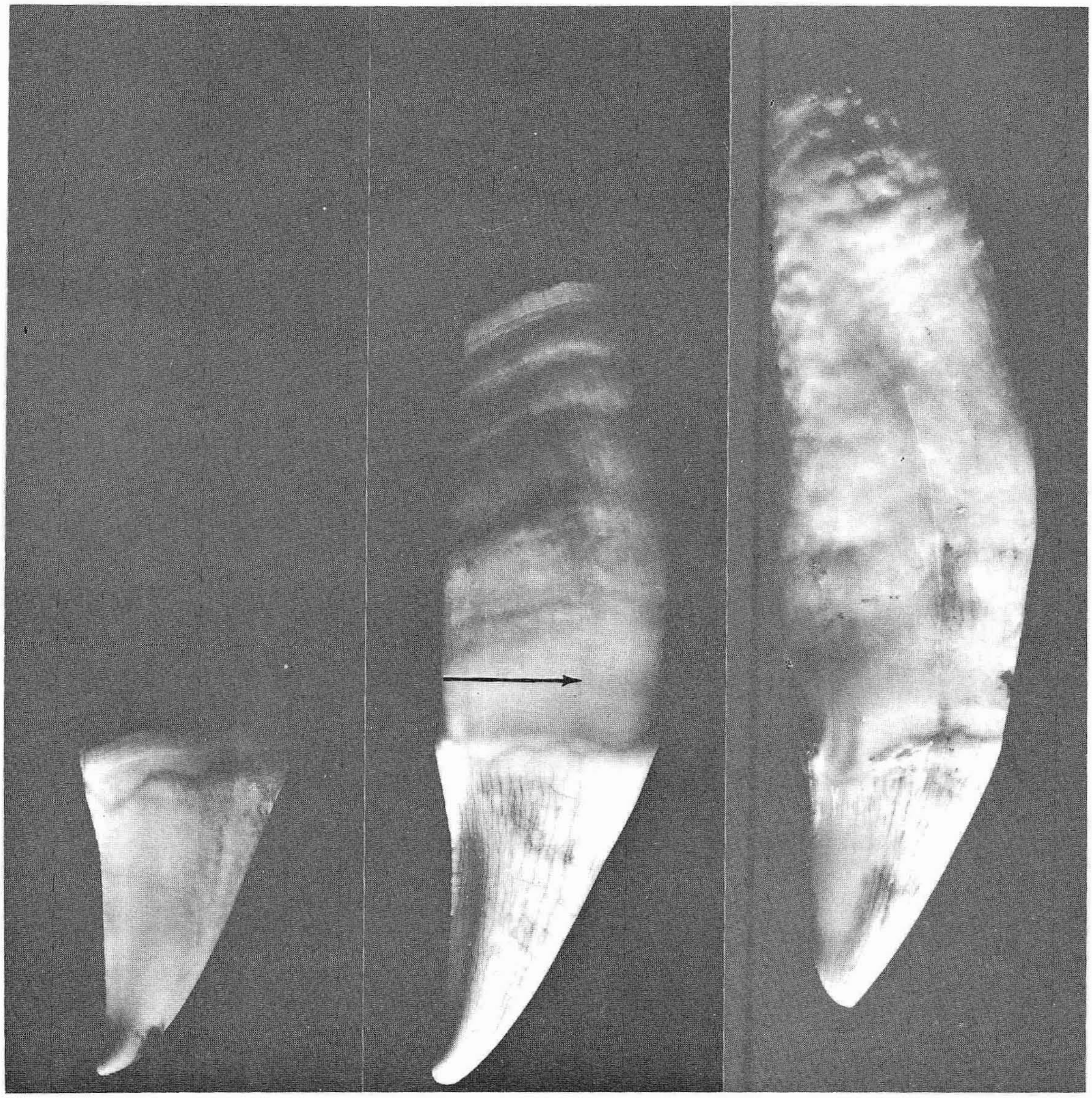

PLATE 15.—Annuli on right upper canines of males of three ages; buccal surface. (Left to right) pup several weeks old, killed on 8 August; 6-year-old (tagged), killed on June 17, (arrow points to first-autumn depression); 14-year-old (tagged), killed on July 16. (2701, 2703, 5295)

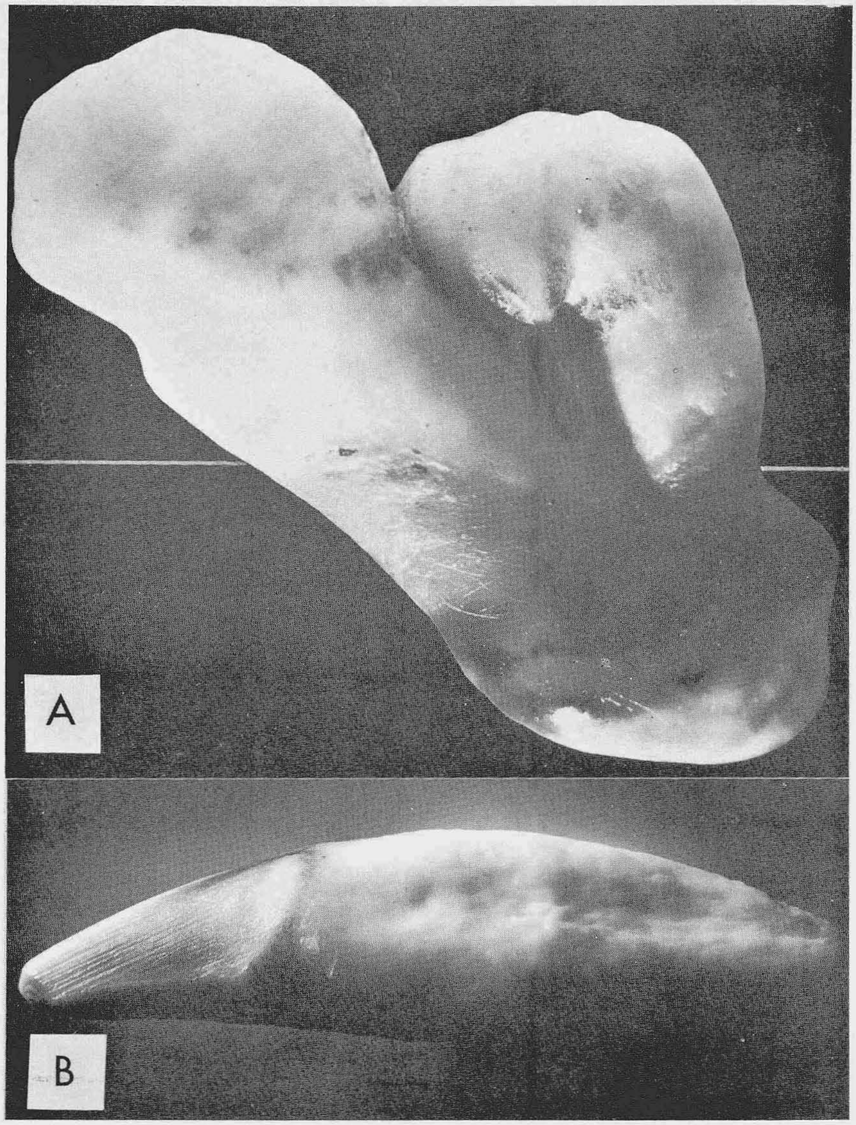

PLATE 16.—Cementum on teeth of old adults. (A) Left upper 1st molar of male; buccal surface; white line indicates gum level. (B) Right upper canine of 19-year (tagged) female; lingual surface; crown at left. (4423, 4488)

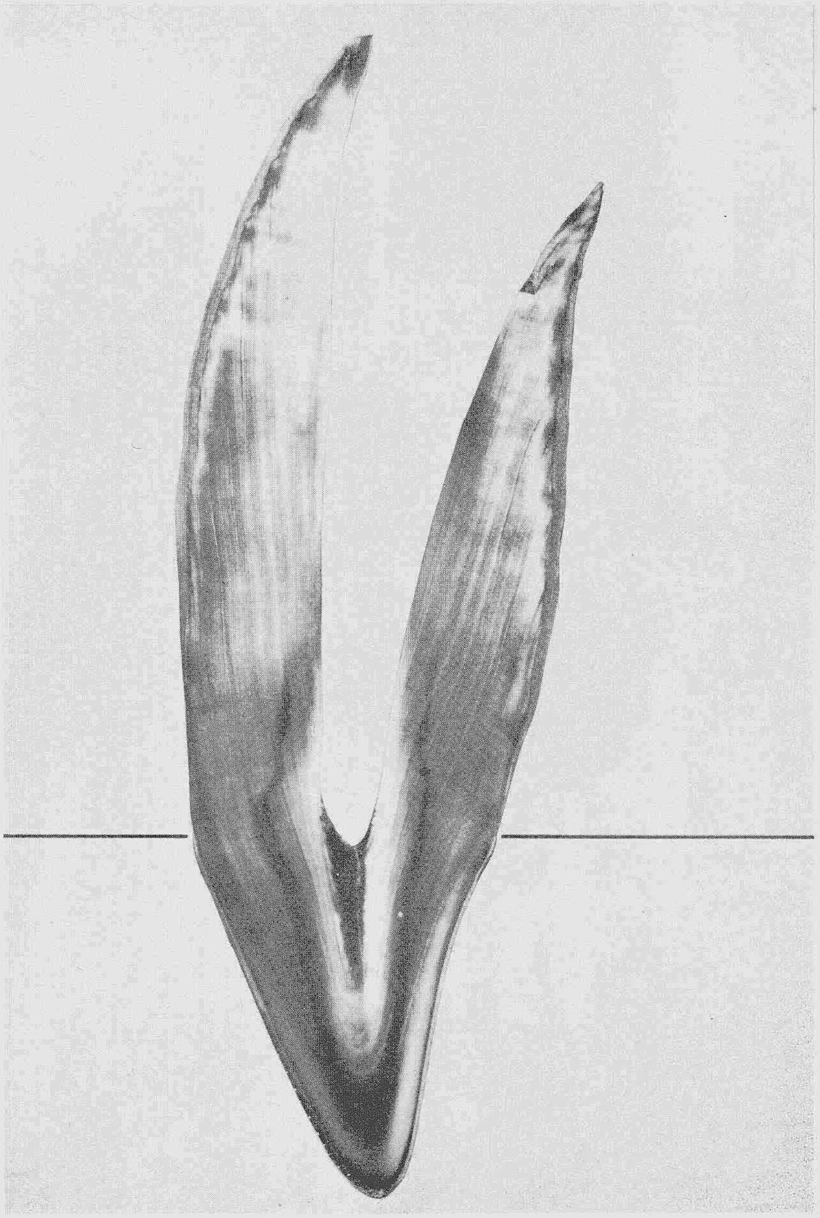

PLATE 17.—Internal structure of right upper canine, showing annuli; median section; 9-year (tagged) male; photographed by UV-excited fluorescence; lingual aspect; line indicates cementoenamel junction. (US 58–737, Mrs. Marion P. Kumpula.)

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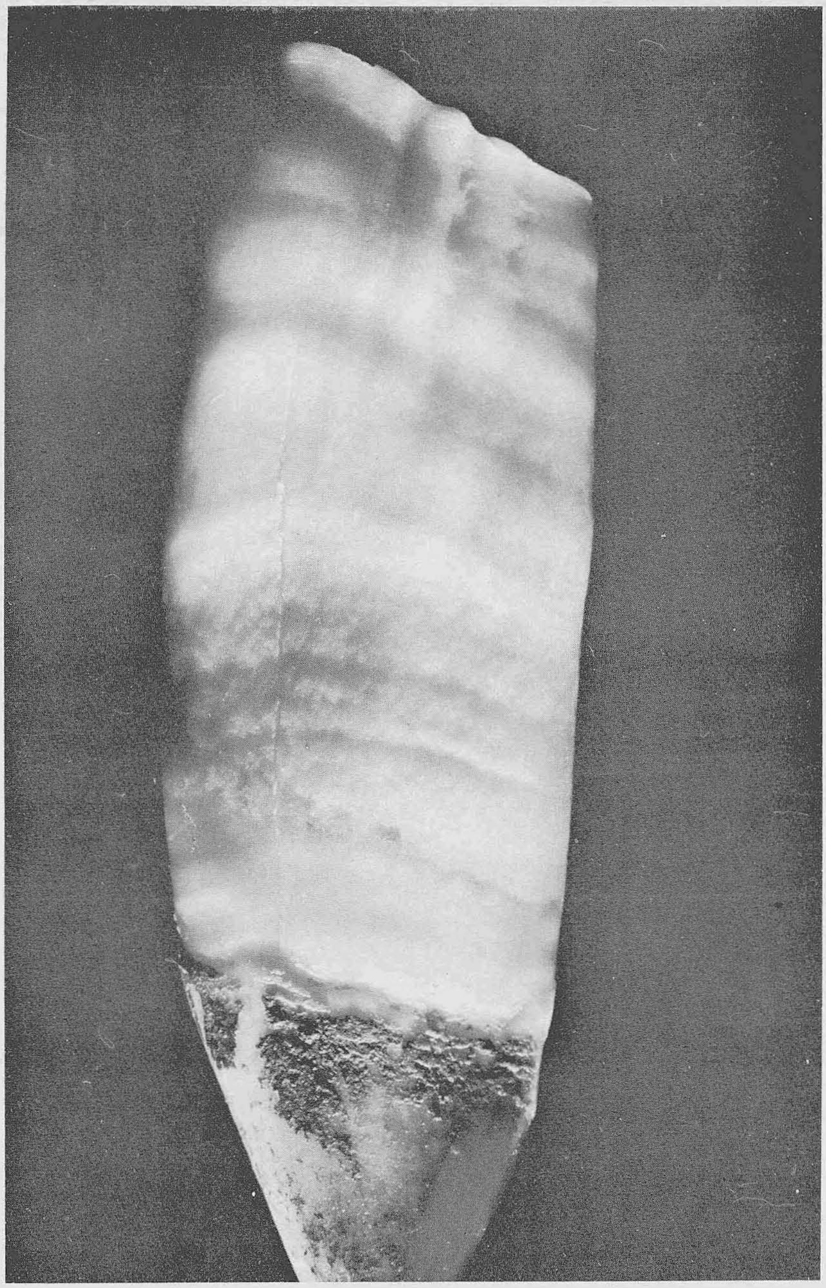

PLATE 18.—Annuli on right upper canine of a seal raised in captivity; known age 5-year male; lingual surface. (4487)

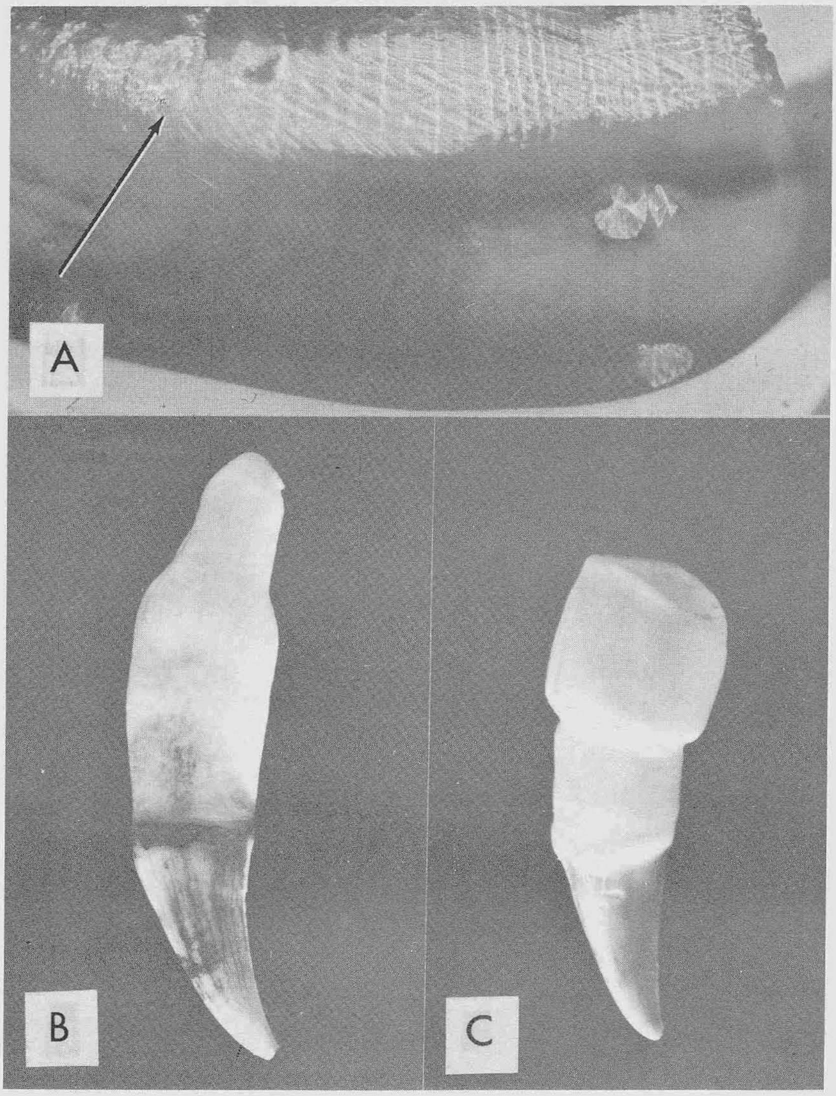

Plate 19.—Differential growth of the root. (A) Gelatin impression of fine ridges on left lower canine of yearling male; labial surface; cementoenamel junction at arrow; root at right. (B) Left upper canine of female over 10 years old; labial surface. (C) Right upper canine of female, estimated age 4 years; lingual surface. (4409A, 4402, 4403)

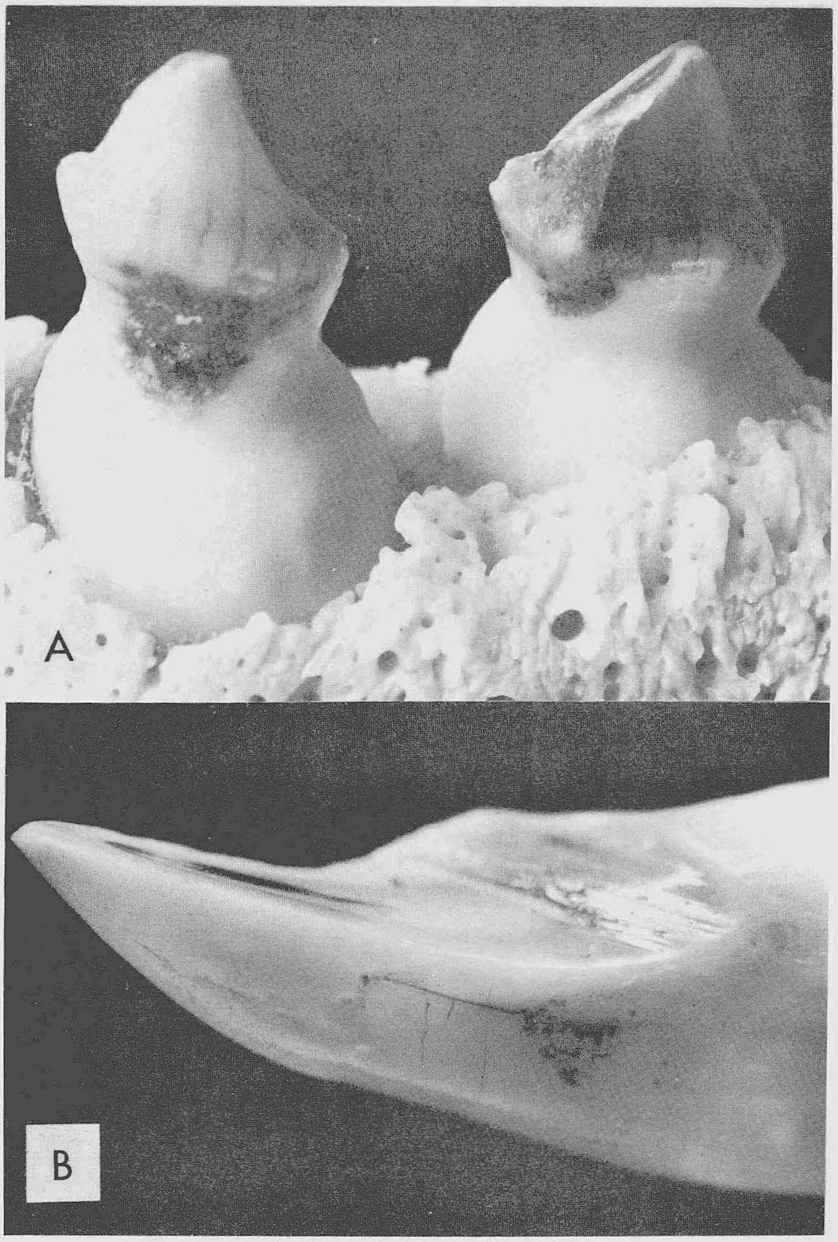

PLATE 20.—(A) Appearance in situ of premolars of an 8-year (tagged) male; lower left 1st and 2d; buccal surface. (B) Wear on the crown of the left lower canine of a female over 10 years old; labial surface. (4380, 4404)

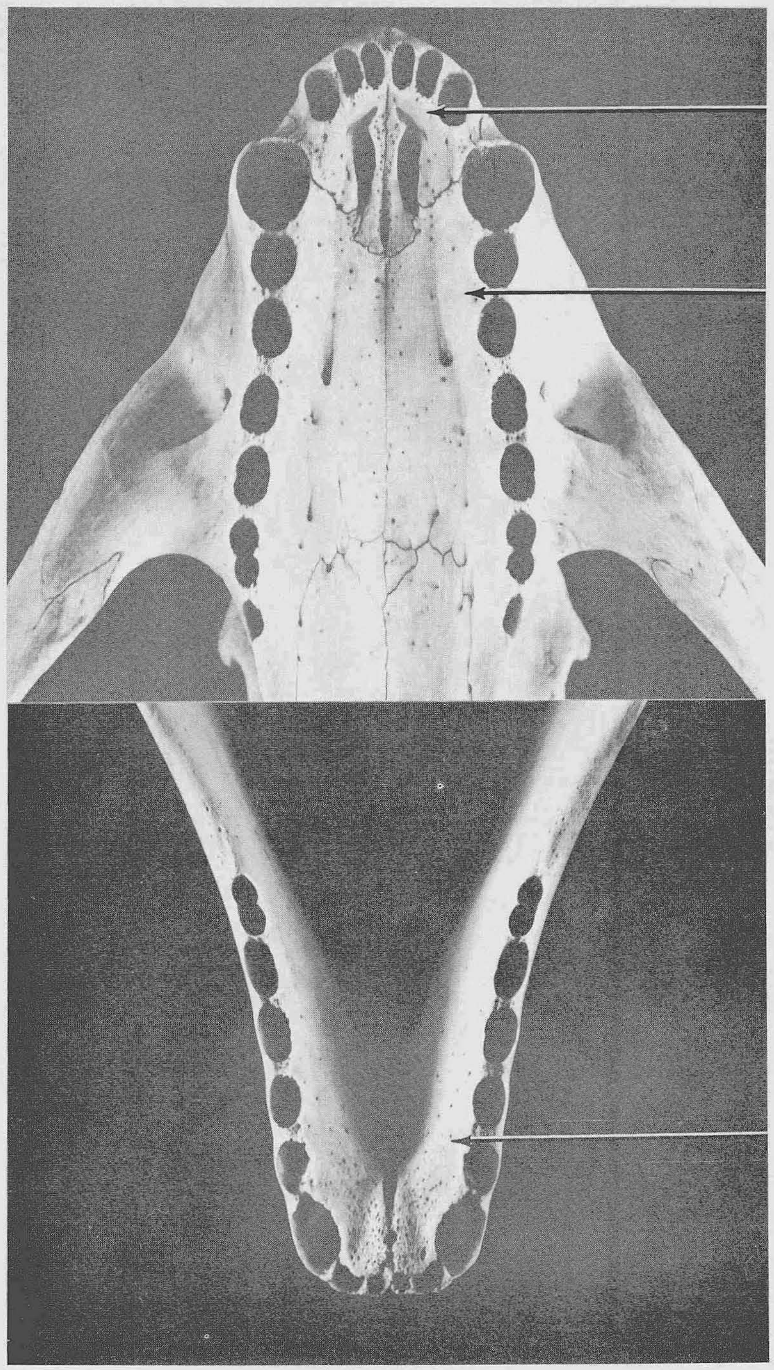

PLATE 21.—Jaw bones of a female, estimated age 5 years. Arrows show (top to bottom) premaxilla, maxilla, and mandible. (4410, 4411)

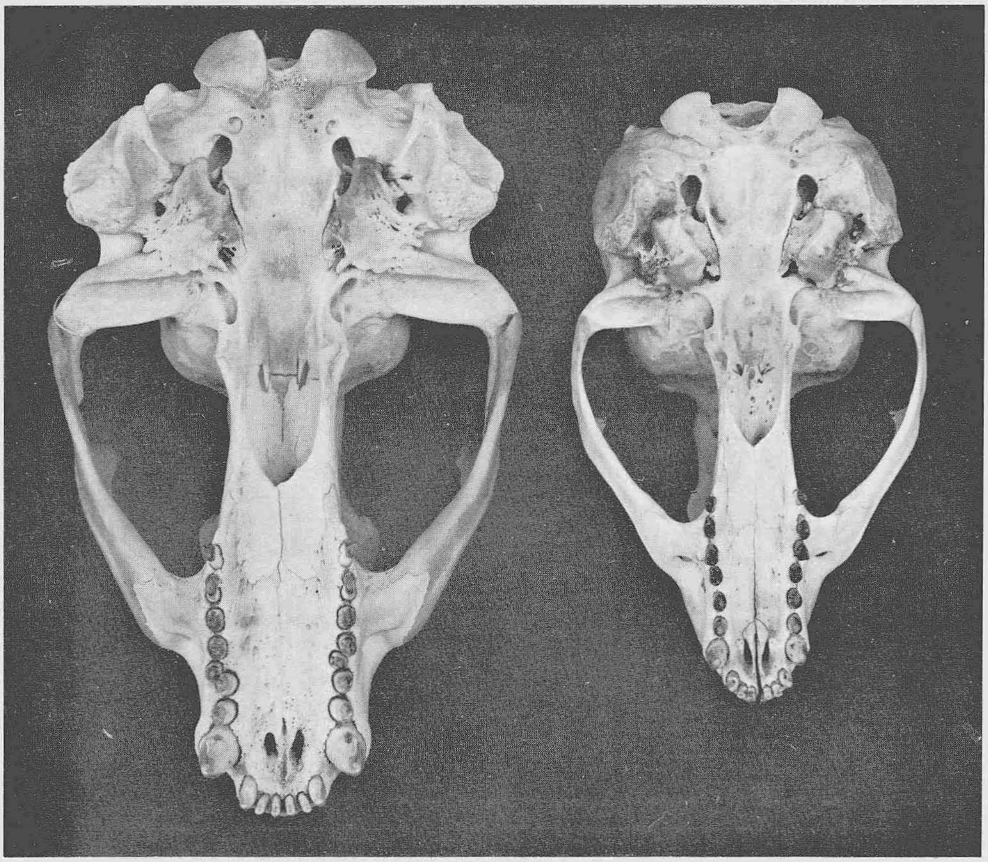

PLATE 22.—Skulls of 8-year male and female (both tagged); male (left) condylobasal length 235 mm., female 184 mm. (4494)

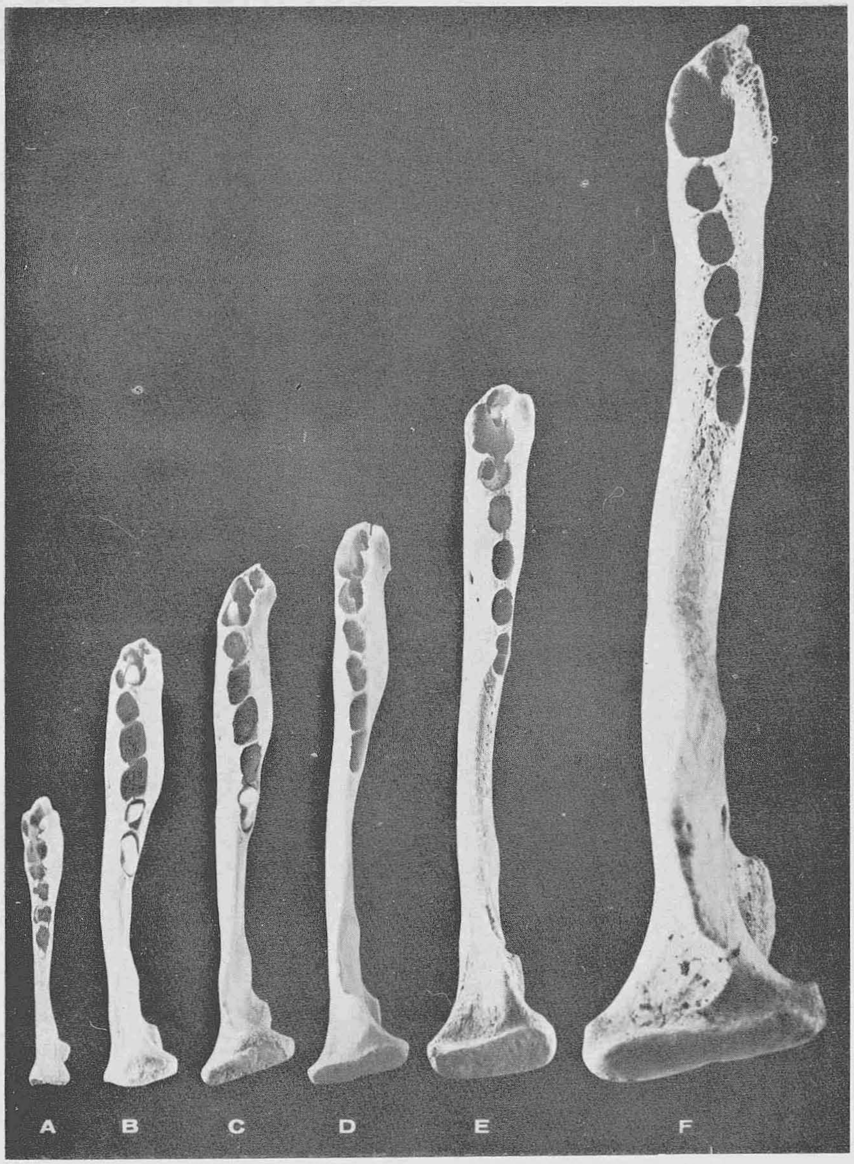

PLATE 23.—Left mandibles of six males, illustrating growth changes with age, natural size. (A) Fetus of 1.36 kg., 25 percent MNW. (B) Fetus of 6.0 kg., 111 percent MNW. (C) Pup 1–2 weeks old. (D) Yearling about 9 months old. (E) Three-year-old (tagged). (F) Old adult. (4426)

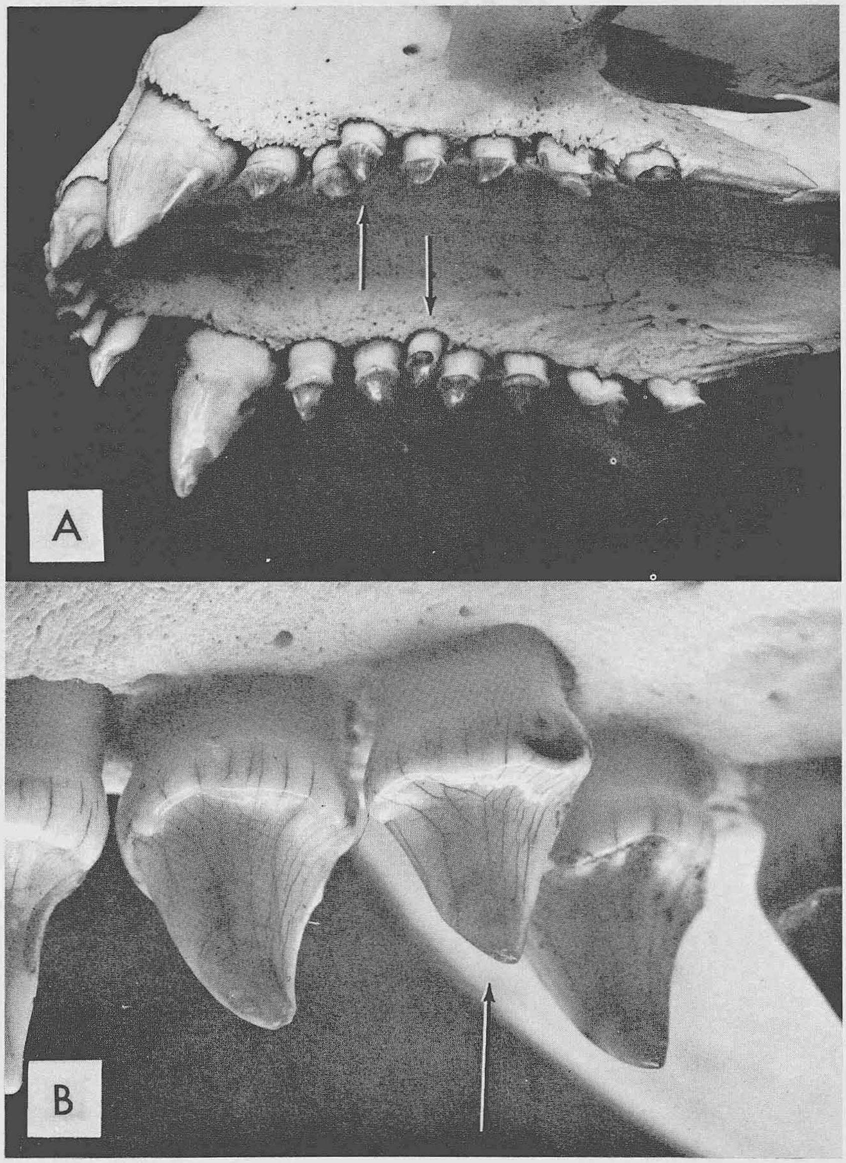

PLATE 24.—Extra premolars in two males. (A) Pair between upper P2 and 3 in an 8-year-old (tagged). (B) One of a pair between upper P2 and 3 in a yearling; right jaw; lingual surface. (4374, 4377)

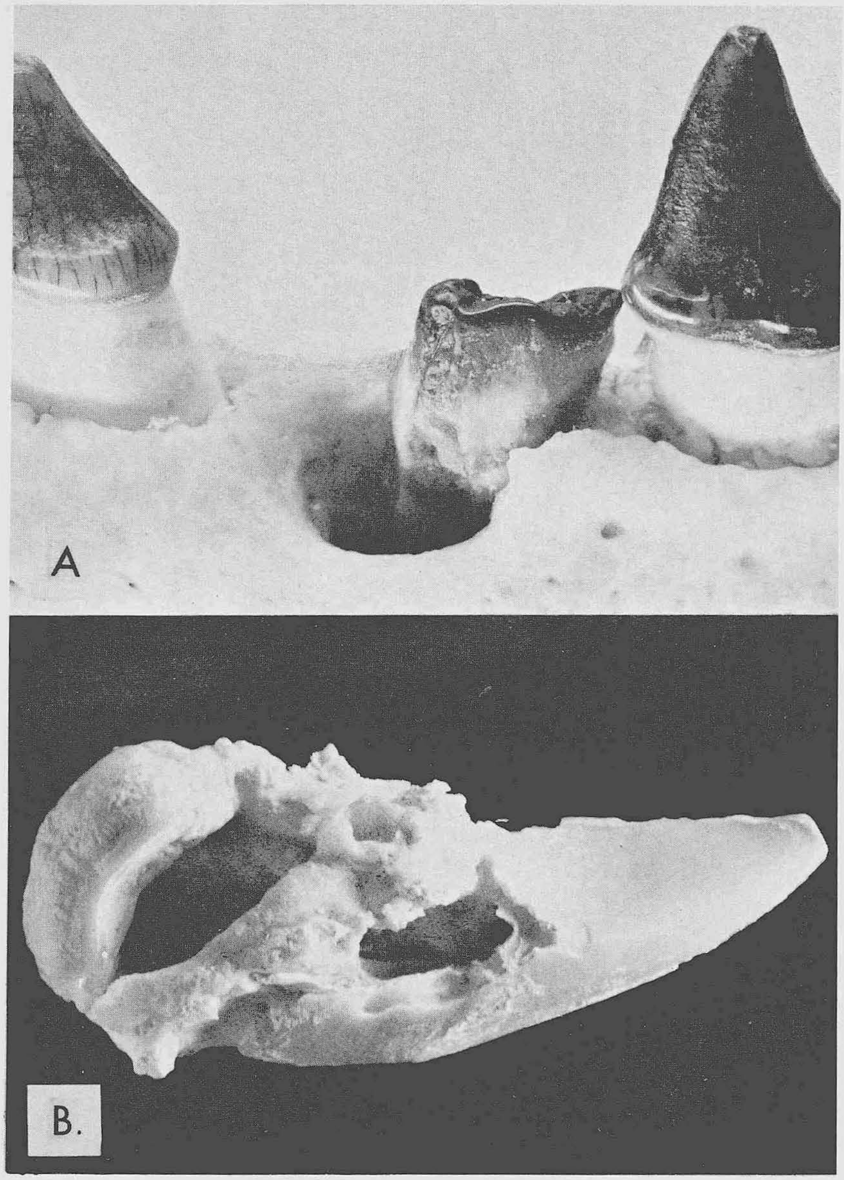

Plate 25.—Effect of root abscesses on tooth and jaw. (A) Lower right P3 of a 7-year (tagged) female; lingual surface. (B) Upper right canine of a known-age 6-year male raised in captivity; lingual surface. (4378, 4401)

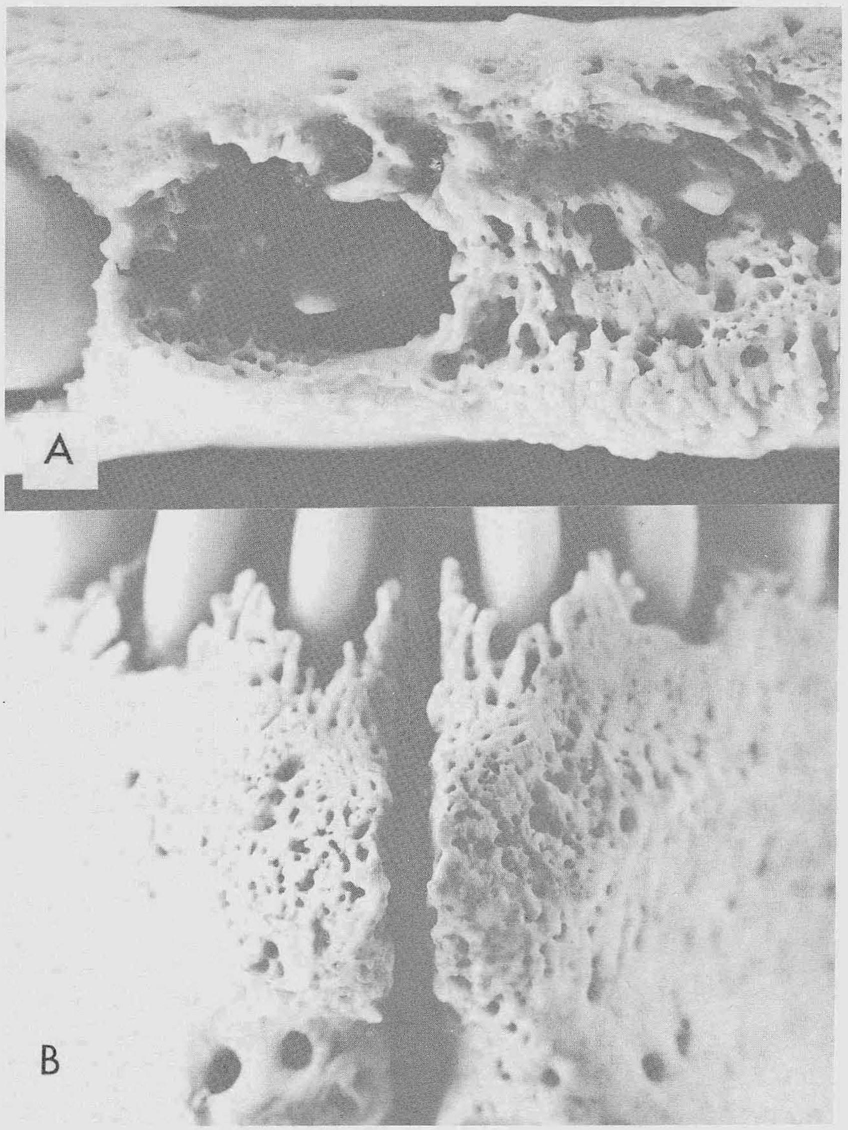

PLATE 26.—Spongy bone of the jaw. (A) Left mandible of female over 10 years old; canine at left; all premolars missing; occlusal surface. (B) Mesial end of mandible of 5-year male raised in captivity. (4373, 4376)