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The Dentition Of The Walrus (Odoberus Obesus)

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THE DENTITION OF THE WALRUS (ODOBENUS OBESUS).

By W. MONTAGUE COBB, M.D., Ph.D.

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The Dentition of the Walrus, *Odobenus obesus* *.

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(Plates I.–VI. ‡; Text-figures 1–8.)

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INTRODUCTION.

Previous descriptions of walrus teeth appear to be confined almost entirely to the Atlantic animal, *Odobenus rosmarus*, between which and the Pacific

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† Communicated by Sir ARTHUR KEITH, F.R.S., F.Z.S.

‡ For explanation of the Plates, see p. 667.

species, *Odobenus divergens* (*obesus*), no essential dental differences have been discovered. More or less detailed discussions of the dentition of *Odobenus rosmarus* may be found in the writings of Rapp (1828), von Baer (1838), Macgillivray (1838), Wiegmann (1838), Stannius (1842), Jaeger (1844), Owen (1853), Malmgren (1863), Flower (1869), Huxley (1872), and many others. A thorough abstract of the contributions of these workers is available in Allen's excellent monograph on the history of North American Pinnipedia (**6**). Kellogg (1922) (**7**) has shed light on certain morphological features from the evolutionary standpoint.

The observations and interpretations reported here originated in the examination of two hundred and nineteen miscellaneous teeth picked up at random on different shore-localities, three mounted upper jaws with tusks, and one mandible in the Hamann Museum of Western Reserve University, collected by Dr. I. Lester Furnas during a visit to Alaska in 1931. These observations, however, could not have been developed and amplified without an examination of the thirty-two skulls in the National Museum, for the opportunity to examine which I am indebted to the kindness and courtesy of Mr. Gerrit S. Miller, Jr. The author is deeply beholden to Prof. T. Wingate Todd for the inspiration and facilities which caused the investigation to be undertaken and for the kind offices which made possible its continuance.

The Dental Formula.

This subject has at various times received the attention of anatomists from three standpoints—namely, the nature of the first tooth in the upper and lower rows of the crushing battery, the teeth represented in the deciduous and successional dentitions, and the homology of the cheek-teeth.

Identification of the Anterior Crushers.*

It is not difficult to recognize that the anterior permanent tooth in the upper jaw of an adult animal, though molariform, is the third or outer incisor. Goethe (**6**), is credited with earliest recognition of this fact. The fœtal specimens of Rapp (1828), and Malmgren (1863), and the young skull of Jaeger (1844) very clearly demonstrated this tooth in its typical mammalian position in the premaxilla (Pl. I.). Macgillivray (1838) pointed out that in older specimens the rim of the alveolus may be partially formed by the maxilla although the socket itself would be found in the intermaxillary.

The anterior member in the lower jaw is not so easy of identification. It has been termed variously an incisor, a canine, and a premolar before being definitely established as a canine. Rudolphi, in 1802, first advanced the correct view. It is interesting to note that early observers relied for evidence upon adult morphological features, condensed by Rapp into four characters, as follows :—(*a*) The canine is further removed from the rest than they are from each other. (*b*) It has greater length and thickness in the adult. (*c*) It stands close to the temporary or milk-incisors and occludes against the outermost of the upper incisors †. (*d*) It lacks the transverse depression seen on the inner side of the crown of the cheek-teeth ‡. Again, descriptions of fœtal and young

* We have substituted the term "crushers" for the "grinders" of older authors in referring to the functional teeth other than the tusks, because it expresses more accurately the actual mode of action, no lateral motion being possible in this carnivorous jaw.

† Frequently the canine is close against $Pm._1$.

‡ The reference is evidently to an inconstant pattern of wear, and considered normal because of an insufficient number of specimens.

specimens furnished the decisive evidence of identity, first by Rapp and later by Jaeger and Malmgren. In each of these specimens three incisor sockets were present with the canine close to the outer incisor and with four crushing teeth behind it. These are plainly visible on Pl. I.

The Successive Dentitions.

The problem of the teeth represented in the milk and permanent dentitions has been indeed a puzzling one, for it involves factors of phylogenetic heritage, retrogression, and specialization. As confirmed by our own observations three formulæ are presented for the deciduous, successional, and functional sets respectively:—

Deciduous .... i. $\frac{3}{3}$, c. $\frac{1}{1}$, m. $\frac{3}{3}$ =28.

Successional .... I. $\frac{2}{0}$, C. $\frac{1}{1}$, P. $\frac{4}{3}$, M. $\frac{1}{1}$ =26.

Functional .... I. $\frac{1}{0}$, C. $\frac{1}{1}$, P. $\frac{3}{3}$ =18.

The Deciduous Dentition.

The commonly accepted formula for the milk dentition, i. $\frac{3}{3}$, c. $\frac{1}{1}$, m. $\frac{4}{4}$ =32, was first established by Malmgren in 1863, and subsequently adopted by Allen (1880). The formulæ of Rapp in 1828 and Flower in 1869 were but slightly different. Rapp did not find in his specimen a fourth lower crusher, a tooth which we have considered belongs to the successional set, and Flower, even after a careful review of Malmgren's work, concluded that there were but two incisors in each jaw. The National Museum specimen has both of these questionable teeth. Although this skull has suffered the loss of several of the small teeth through maceration, vestiges of the sockets for the missing teeth remain. The deciduous dentition, therefore, is clearly represented in the upper jaw by three incisors, a canine, and three molars. No observer has reported a predecessor for the first premolar, a phenomenon long recognized in other remotely related animals (4). In the lower jaw there occur three incisors, a canine, and three molars (Pl. I.).

All the deciduous teeth are small, conical in shape, and apparently functionless. In both jaws the medial or first incisor is very small, the second and third progressively larger, and the molars are larger still. The first and second molars are subequal in size; the third upper molar is the largest of all the deciduous teeth, and the canines are intermediate in size between the second and third molars.

In Malmgren's and the somewhat younger National Museum specimens the roots apparently are fully formed before the teeth are shed, which is said to occur shortly after birth. Flower (4) thought that often these teeth may be absorbed without cutting the gum while in other specimens they may persist to adult life. Without doubt all three variants occur. Of these post-natal shedding is probably the most frequent. An example of absorption without eruption is displayed in the left upper jaw of the fœtal skull in Pl. I., where the two posterior cheek-teeth have been absorbed. Persistence to adult life can happen only in the case of the third upper milk-molar when it has no successor, and the upper and lower " permanent " molars, because the location of these teeth in the rear of the jaw, away from the seat of greatest functional activity, together with the protection afforded by the gums, gives them a chance to survive. No milk-incisor in its exposed position is sufficiently robust to withstand the abrasive effects of the molluscan diet, and the roots of the second molars in our specimen already are half absorbed by the pressure of their functional successors.

The Successional Dentition.

The formula for the successional set has been given as I. $\frac{2}{0}$, C. $\frac{1}{1}$, P. $\frac{4}{3}$, M. $\frac{1}{1}$ =26. It differs from that generally accepted in the inclusion of a second upper incisor, in definitely acknowledging the existence of a successional tooth to the third upper milk-molar, and in regarding the last upper and lower rudimentary cheek-teeth as molars of the successional set.

Pl. I. offers indubitable evidence that there is a successor to the second upper milk-incisor. Both are obviously in place. Pl. II., *a*, shows the adult tooth firmly lodged in the premaxilla. Its flattened worn surface proves unmistakably its functional capacity as well as the toughness of the underlying gum in the lower jaw. This tooth was found in two other adult skulls, though smaller and more conical in shape, but in neither of these did it appear to have functional value. Its alveolus was noted in one other of the National Museum skulls.

It is much to be regretted that we have no specimens which show in a similar way the successional fourth upper premolar replacing the third milk-molar, but must rely on indirect evidence for its existence. The evidence, nevertheless very convincing, comprises two facts, (1) the small size of the milk-set as a whole, and especially of the third upper milk molar, and (2) the large size of the fourth upper premolar and of its alveolus in adult skulls (Table I.).

TABLE I.—Dimensions of Alveoli behind Pm. ^{3}.

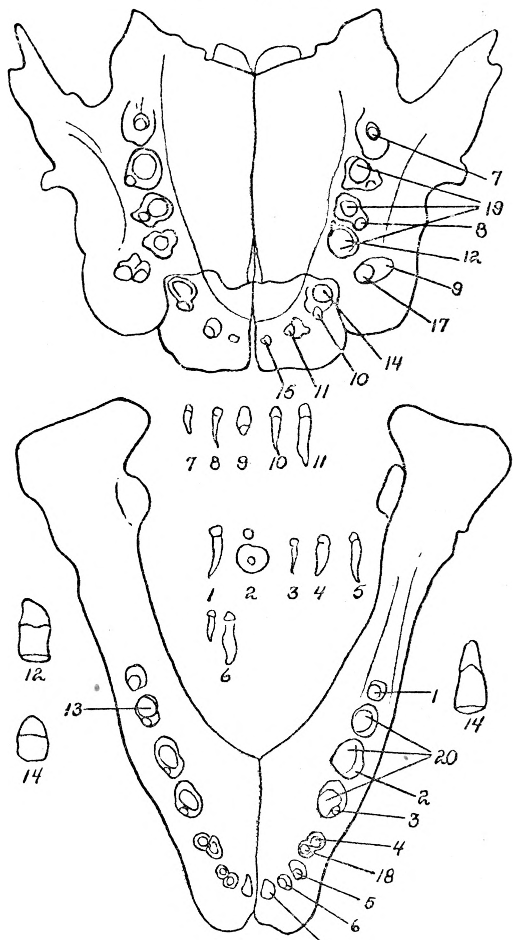
			Right.			Left.		
No.	Cat. No.	Tooth-socket.	Dist. behind next. ant. tooth.	AP.	T.	Dist. behind next ant. tooth.	AP.	T.
1.	35683.	Pm.^{4}	3·7	12·1	10·5	6·1	8·7	9·1
2.	11746.	Pm.^{4}	10·7	5·7	6·8	10·6	6·8	5·4
3.	21103.	Pm.^{4}	3·6	10·3	11·6	2·7	10·7	13·2
4.	21103.	M.^{1}	C.	6·6	7·5	Not present.		
5.	7889.	Pm.^{4}	16·3	4·6	4.5	11·6	7·5	8·4
6.	84868.	Pm.^{4}	14·2	10·1	7·3	17·2	7·0	6·6
7.	16448	Pm.^{4}	9·7	6·7	6·3	7·9	9·0	6·0
8.	16448.	M.^{1}	C.	5·3	4·7	C.	5·1	4·1
9.	14396.	Pm.^{4}	8·1	5·4	10·0	6·7	6·9	10·8
10.	14396.	M.^{1}	6·5	4·2	2·6	6·3	3·2	2·4
11.	21104.	Pm.^{4}	Not present.			10·8	3·2	3·7

All measurements in millimetres.
C. = confluent with Pm.^{4}.

Malmgren's figures show that in his fœtal skull the milk-molars are fully formed and very minute (text-fig. 1). These are similarly represented in Flower's diagram of 1869 (text-fig. 2 *a*). The National Museum skull is present confirmation of the fact. The root of its third upper milk-molar was approaching completion. The diameter of the cross-section at no point of any of the small teeth exceeded two and a half millimetres, yet all had attained the proportions of full growth.

On the other hand, in three adult skulls illustrated by the example in Pl. III. fourth upper premolars in position were of much larger size (near

Text-figure 1.



Malmgren's fœtal skull, 1863.

that of Pm. 3) and similar in colour to their fellows of the set*. These actual specimens and the measurements of the alveolus for this tooth made on eight other jaws † demonstrate that usually when this tooth is found in the adult, it is unquestionably larger than the fully grown milk-molars of the fœtal skulls, and is certainly too large to permit inclusion in the milk-dentition. This tooth

* The milk-teeth are whiter than their successors in the fœtal skull, Nat. Mus. No. 217913.
† Pm.[4] is absent on one side in two of the eight specimens.

must be identified as successional even though an erupting permanent tooth with its milk predecessor still in place has not yet been recorded.

Although this successional tooth does occur it is not always present. Further, there is one specimen, No. 21104 (Table I.), in which the alveoli are small enough to have lodged a milk-tooth. From the study of these and other specimens it was impossible to determine whether these alveoli had originally been larger but become reduced in size through encroachments of bone behind a wearing dental rudiment, or whether they represented the actual size of the tooth originally contained therein. The shallowness of these alveoli made the former explanation seem more probable, but does not exclude the latter. The known inconstancy of the successor suggests that this milk-tooth may occasionally, as Flower believed, persist to adult life, in some animals perhaps never cutting the gum.

A fœtal or very young individual ordinarily exhibits behind the third milk-molar in each jaw one rudimentary tooth which, though erupting with the milk-set, must be designated "permanent" molars for reasons given in the discussion of homologies. The lower "permanent" molar is somewhat larger than any of the milk-teeth, but the upper approximates the anterior milk-molars in size. Both of these teeth are usually shed early, but occasionally may survive to adult life as previously mentioned.

In the formulæ of earlier workers the first or medial deciduous incisors or the single molars of the successional set, both upper and lower, have always appeared as erratic in occurrence, regardless of the names applied to them. The National Museum fœtal specimen has both the upper third milk-molar and the single successional molar already absent on the left side, a shallow depression alone remaining to mark their former site. Variability in the occurrence of these teeth, coupled with their rudimentary size, must be taken as an indication of retrogression tending toward ultimate disappearance.

The Functional Dentition.

While the erratic occurrence of the "superfluous" successional teeth has given rise to much confusion in description, the stability in the number of truly "functional" teeth in the adult walrus has permitted almost unanimous agreement to the formula I. $\frac{1}{0}$, C. $\frac{1}{1}$, P. $\frac{3}{3}=18$. It is this functional remnant of the successional dentition which is usually called "permanent" in text-books, since the majority of adult animals have already lost medial and second incisor, fourth upper premolar, and upper and lower successional molars.

Tooth Eruption.

The slender evidence given by the material at our disposal indicates that both milk and permanent dentitions erupt practically as units. This specialization is probably associated with the diet. In the milk-teeth of the fœtal specimen, Nat. Mus. No. 217913, the outer incisor with completely formed root is erupted more fully than the hinder molars, the roots of which are not quite completed. The root of the second upper milk-molar already is half absorbed from the pressure of the growing permanent tooth beneath it.

As gauged by the distance of their tips from the alveolar margins in the same specimen the order of eruption of the successional teeth appears to be :—*Upper Jaw.* Molar, with the milk set ; Outer Incisor ; First Premolar ; Second Incisor (when present) ; Third Premolar ; Second Premolar. All of these teeth seem to erupt practically together. The canine erupts distinctly later than the other successional teeth. It must, however, be noted that Stannius in 1842 and Jaeger in 1844, in their studies on young skulls, recorded the second "molar," meaning second upper premolar, as the largest and most worn of the series, as though one should infer that it is the first successional tooth to erupt. *Lower Jaw.* Molar, apparently just after eruption of the milk-set; Second Premolar; First Premolar; Third Premolar. The Canine, as in the upper jaw, erupts definitely later than the other teeth.

The fourth upper premolar, when it does occur, is very probably the last of the successional series to erupt.

Homology of the Cheek-teeth.

The problem of the cheek-teeth as it confronted the early investigators was twofold, first, whether the rudimentary elements sometimes found in the adult belonged to milk or permanent dentition, and, second, following in a way upon the first, which teeth were molars and which premolars.

Flower discussed the question at some length in 1869, and left it unsettled (**4**). Other authors, with apparent diffidence, have used the complex "PmM" for the permanent cheek-teeth.

Evidence has been presented above to show that the original incisors and rudimentary cheek-teeth (excepting the hindmost tooth of upper and lower jaws) are of the milk-dentition, and that successors may or may not follow the upper second incisor and third molar.

The fourth upper rudimentary cheek-tooth must be designated a molar of the successional set even though it erupts and is shed with the milk-teeth, because there is no direct evidence to the contrary and because any other assumption would require the explanation of either five premolars in a carnivore or a predecessor to a molar tooth. The latter alternative may appear tenable when the beast is compared with the Cetacea, which have an extremely large number of retrogressive conical teeth, but which have also a supernumerary rudimentary milk-dentition. However, it is more difficult to allow the appearance of additional milk-teeth in the walrus, which is losing teeth, than in the Cetacea, which have gained them.

The lower posterior rudimentary cheek-tooth is considered a "permanent" molar, because there is no evidence of a successor in the material at our command. This leaves but three premolars and postulates the complete loss on one premolar and its predecessor. This would not be an unusual circumstance in a carnivore (*cf.* Ursidæ and Canidæ), and may easily have occurred before our pinnipede had completed its aquatic adaptation. Since there is still an unlikely possibility that a successor to this tooth might be discovered eventually, a larger series of fœtal and young skulls will be necessary to confirm this conclusion.

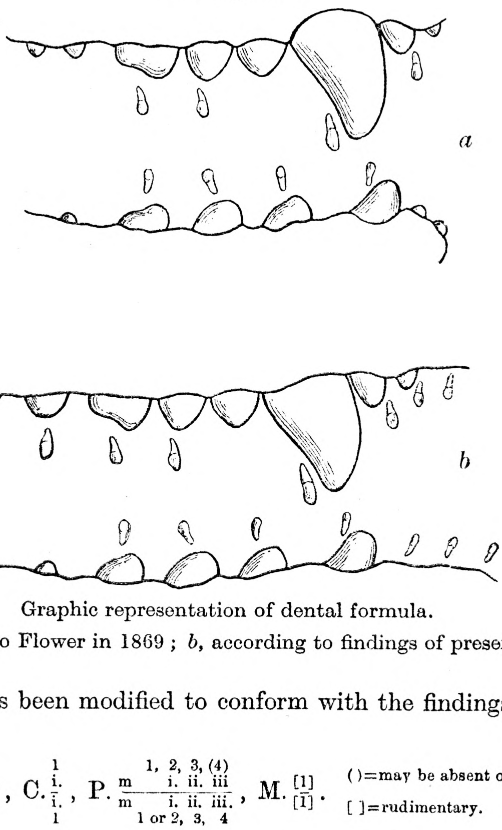
Summary of the Dentitions.

The deciduous dentition of the walrus, represented by the formula i. $\frac{3}{3}$, c. $\frac{1}{1}$, m. $\frac{3}{3}=28$, is rudimentary and quite non-functional. These teeth commonly disappear before birth or are shed soon thereafter; in exceptional instances the third upper milk-molar may persist into adult life.

The successional dentition, I. $\frac{2}{0}$, C. $\frac{1}{1}$, P. $\frac{4}{3}$, M. $\frac{1}{1}=26$, includes four inconstant and unstable members, the second upper incisor, the fourth upper premolar, and the upper and lower molars. The incisor may become functional, aided by the hardness of the underlying gum. The single upper molar almost invariably is lost early, though it may persist. The fourth upper premolar and single lower molar are lost before middle life according to Allen (**6**), but the National Museum skulls show that the fourth upper premolar may survive to a riper age. The molars are rudimentary, and usually erupt, and are shed with the milk-teeth.

The remaining teeth, I. $\frac{1}{0}$, C. $\frac{1}{1}$, P. $\frac{3}{3}=18$, constitute the functional dentition usually seen in museum specimens. The complete dental equipment of the walrus is given in the following formula, and from it the animal's dental life-history may be traced. This is shown graphically in text-fig. 2, *b*, where Flower's

Text-figure 2.



Graphic representation of dental formula.

a, according to Flower in 1869 ; *b*, according to findings of present study.

diagram of 1869 has been modified to conform with the findings of the present study.

$$\text{I.}\,\frac{\overset{(2),\ 3}{\text{i. ii. iii.}}}{\text{i. ii. iii.}},\ \text{C.}\,\frac{\overset{1}{\text{i.}}}{\underset{1}{\text{i.}}},\ \text{P.}\,\frac{\text{m}\quad\overset{1,\ 2,\ 3,\ (4)}{\text{i. ii. iii}}}{\text{m}\quad\underset{1\text{ or }2,\ 3,\ 4}{\text{i. ii. iii.}}},\ \text{M.}\,\frac{[1]}{[1]}.$$

( )=may be absent or reduced.

[ ]=rudimentary.

GROWTH-CHANGES IN THE ALVEOLI AND PALATE.

There is a dearth of data on the progress of growth in the walrus. External characters, such as body-size and the condition of the skin, are useful solely for approximate estimates of age and development. The tusks are very variable. Allen gives Lamont's estimates of the age of the tusks as "first year, no tusks, second year, about the size of a lion's canine, and third year, about six inches." Somewhat different figures are given by a few other authors, but the standards must be regarded as not yet satisfactory. At this time it is possible only to indicate three other regions in the dental area where marked growth-changes occur, all resulting from the specialization of the canines, which may be found suitable for studies of growth when a sufficient series of skulls is available. These are, antero-posterior extension of the canine alveolus, deepening of the palate, and growth at the base of the alveolar arch.

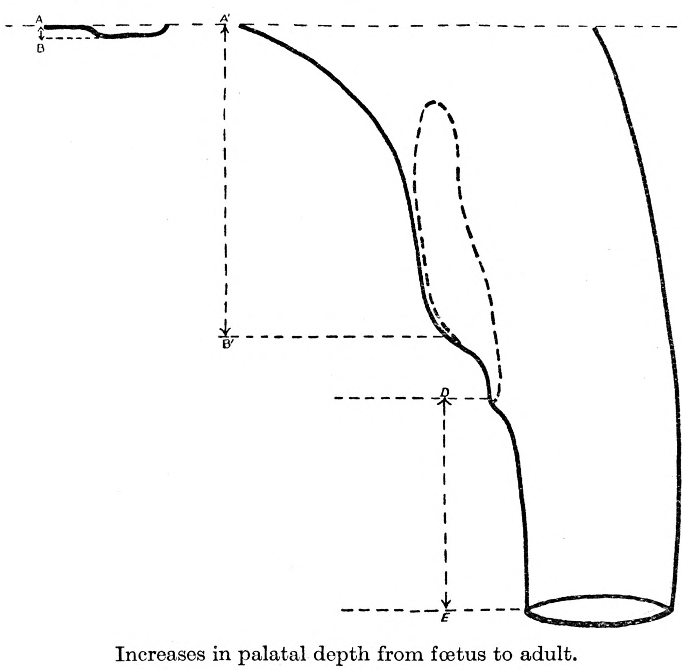
Antero-posterior Extension of the Canine Alveolus.

Comparison of Pls. I. & II. shows that in the fœtal skull the antero-posterior limits of the canine alveolus lie between those of the incisor and first premolar, somewhat nearer the latter, these three teeth forming a triangle of which the canine is the apex. Yet in the adult the whole dental battery is overshadowed by the alveolus of the tusk. Here the antero-posterior dimension of the lateral margin of the bony alveolus is approximately equal to the extent of the row of upper cheek-teeth, including the molariform incisors. The tooth-row gives the impression of having been pushed back slightly in the palate : the incisor is not quite abreast of the anterior margin of the alveolus, while the third premolar projects a trifle behind its posterior limit. The extension therefore is chiefly in the posterior direction.

Deepening of the Palate.

Proceeding with this dimensional increase is another in the height of the palate, shown by text-fig. 3. In the fœtal skull, where the teeth are just

Text-figure 3.



Increases in palatal depth from fœtus to adult.

about to erupt, the alveolar bone of the crushers and tusks is but little lower than the palatal roof. However, in the adult there have been two tremendous increases in palatal height due to the deposit of alveolar bone, one to accommodate the cheek-teeth, A′–B′, the second to provide for the tusk, D–E. The effect of this growth on the angle of tooth implantation will be discussed below.

Growth at the Base of the Alveolar Arch.

Still another site of palatal growth may be observed in the separation of alveoli for the upper third and fourth premolars. In young skulls the two are closely adjacent, but in the adult they are separated by considerable distances, given in Table I.

In two of the three skulls where a molar was present behind the last premolar (Table I.) the alveoli of the two are confluent; in the third there is a small separation. This means that there is anterior palatal extension through inter-alveolar bone-growth in front of the fourth premolar, but practically none behind it. If this extension is not paralleled in the rostrum above it may be one of the means by which the upward tilting of the face cited by Kellogg (**8**) is accentuated. It is certainly not necessary for the accommodation of teeth.

One other fact which sheds interesting light upon the subject of growth in the odobenid face is that the animal suckles for two years. When fœtal and adult skulls are compared it is perfectly clear that the head has to grow tremendously to house the functional teeth. We know also from the nature of the animal's diet that when it begins to feed it must have efficient crushing organs. The inference therefore is that during the long period of mammary feeding the walrus is preparing for a successful future by growing a face that will be large and strong enough to lodge an adequate dental armament. The unique way in which the teeth themselves adjust to this palatal growth and the increased demand upon them is described in the discussion of the patterns of wear and age.

INTER-RELATIONS OF TUSKS, DENTAL FORM, AND DIET.

A very brief inspection of a walrus skull is ample to demonstrate that it owes its peculiarities almost entirely to the development of its huge tusks. According to the best evidence available at present the walruses, or Odobenidæ, are derived from the eared seals, or Otaridæ. Kellogg (**8**) states that a marked increase in the size of the tusks was, without question, one of the earliest steps in the modification of the Otarid skull into the Odobenid type. If this surmise be true, the ancestral walrus must have found its growing tusks a handicap to predaceous feeding but convenient for a diet of bottom-dwelling molluscs.

Thus two distinct lines of specialization can be traced in the Odobenid skull, the one consisting of modification for the support of the huge canines and the other of adaptations to a special diet. Upon the efficacy of the second type of course the survival of the animal depended.

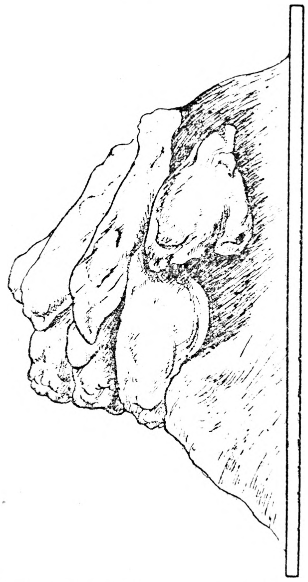
Kellogg has further pointed out that the shortening of the rostrum and the upturning of the facial skeleton are undoubtedly the result of the enormous increase in size of the upper canines, while, in turn, the effect of their increasing abrasive action has been a constriction at the symphysis in the mandible. The massiveness of the skull as a whole is correlated with the type of dental battery and a bottom-feeding habit. Let us now examine the relations of tusks, dental battery, and diet in some detail.

Modifications in Dento-facial Form induced by Tusk Development.

In the first place mechanical interference with biting has been responsible for the loss of function and disappearance of all the lower incisors as well as the medial and often the second incisor in the upper jaw, and also, coincidentally, for the alignment of outer upper incisor and the lower canine with the cheek-teeth.

The other modifications might be termed environmental. Looking down upon the cheek-teeth from the tip of a well-developed tusk one can observe the striking manner in which its alveolus dominates the palato-alveolar architecture. It will be recalled that the teeth of the walrus are probably secondarily simple and retrogressive * and that the young unworn tooth is a simple conical structure growing out rather perpendicularly from each jaw. In the adult maxilla, although the alveoli of the crushers have grown proportionately

Text-figure 4.



Text-figure 5.

Fig. 4.—Outward displacement of the angle of implantation of upper teeth (lateral view). U.S. Nat. Mus. No. 35518.

Fig. 5.—Same feature (medial view). U.S. Nat. Mus. No. 16437.

with the teeth, the alveolus of the canine has extended considerably both downward and backward to form a perpendicular bony wall lateral to the crushing row. In so doing it has formed niches which enshrine the buccal surface of the conical extremities of the teeth. This surface is secondarily covered with cementum, and only the lingual flattened side of the original conical extremity is left exposed beyond the gum.

Accompanying this growth there has been a lateral extension of the canine alveolus, as a glance at the muzzle will show. This carries outward the occlusal extremities of the cheek-teeth, swinging their angle of implantation into a more oblique position (text-figs. 4 & 5). It is more marked in the premolars and cannot be of great importance for in large and old specimens the angle of

* Since the oldest known ancestral odobenid had simple protodont teeth, retrogression from a tuberculo-sectorial form cannot be proved, but is assumed as probable because of the numerous definitely carnivorous characters of the skull.

implantation of the incisors may be turned lingually, which, however, is due chiefly to inward compression from thickening alveolar bone.

As the incisor and third premolar lie at the extremes of the canine alveolus the wall of the latter is somewhat more distant from and has greater slope opposite them ; the full effect of the support of this outer wall is best manifested in the first and second premolars.

Another interesting and easily observed feature is the inclination of the long axes of the roots of the upper premolars, because their occlusal extremities have been carried forward slightly by the tusks. In the skull from which text-fig. 4 was drawn the tusks emerged more anteriorly directed than in that represented by text-fig. 5, where they are more vertical. Consequently the adjacent teeth shown in Pls. IV. & VI. reflect the difference. It will be noted that the slope of the incisor, because of its position in the premaxilla, is less influenced than the premolar slope.

An insight into the arrangement of teeth in relation to functional characters of the maxilla is furnished by the contour-pattern of the roots when viewed from the side. A contour of the set resembles an irregular arc, highest and with greatest curvature posteriorly. The first premolar is always curved, so as to present a convexity anteriorly, while that of the third premolar is posteriorly directed. The second premolar is curved in whichever direction best fits the pattern. In Pl. IV. the convexity of $Pm.^2$ is backward, while in Pl. VI. it is forward. It will be noticed that here also the incisor is more independent of the general pattern than any other member. The reasons for this are to be sought in its situation and in its great variability in size.

Features of Dento-facial Form related to Diet.

A discussion of the significance of a diet in morphological structure of jaws may very properly begin with a description of the food. Our account is adapted in greatest part from Lydekker (**7**). The walrus mainly subsists on the bivalved molluscs *Mya truncata* and *Saxicava rugosa*, commonly known as gapers. These it is said to rake up from the sea-bottom with its tusks. In addition it also consumes fishes and crustaceans, and with its animal food swallows, perhaps unintentionally, large quantities of sea-weed (*Fuci*). When feeding on bivalves the hard shells are crushed with the admirably adapted blunt-crowned cheek-teeth. The shells are rejected before the soft parts are swallowed, and when the latter are taken from the stomach they are quite uninjured if recently swallowed, the siphon, lobes of the mantle, etc. being found in perfect condition. This indicates that the molluscs cannot be ground up by the blunt cheek teeth as has been asserted, but that the shells are removed in some other way, probably by the action of the lips. Off Greenland, at any rate, the walrus consumes large quantities of the small shrimp known as *Gammarus locusta*, of which the males are about an inch in length and the females still smaller. Of these crustaceans the chitinous covering is removed before the creature is swallowed. How this is accomplished is difficult to imagine. Among the occasional articles of diet are eider ducks, Arctic fulmars, portions of dead whale, porpoise, or seal, and, more rarely, live cetaceans and seals. How they proceed about these operations we are not told.

The findings of the present study are in no way fitted to answer from first-hand observation the questions arising in the preceding paragraph. The inference to be drawn from the dental anatomy seems to be that the shells *are* taken into the mouth, first, because of the concentration of crushing force in the front of the mouth, second, because certain basins in the alveolar bone next the occlusal surfaces may be thus accounted for, as well as the large non-carious cavity found in the second upper premolar of two specimens, and third, because of the highly polished exposed bevelled surfaces of the teeth which do not obtrude upon the occlusal area.

In considering the concentration of crushing force in the anterior region of the mouth, Kellogg's reference to the general massiveness of structure in bottom feeders is recalled, particularly concerning the anterior portion of the mandible. Looking at Pls. V. & VI. we may see this influence expressed in the dental architecture. In the mandible there is a marked diminution in size of the hinder teeth. The first tooth, the canine, lodged in the thickest part of the bone at the point where most effective leverage is obtainable, is the largest tooth, while the first premolar just behind approaches it in size. The decrease is well marked in the second premolar, and in the third it amounts to four-fifths the bulk of the canine. It is easy to understand under these circumstances how the posterior premolar and the molars have tended to disappear in the walrus, situated as they are in a smaller portion of the jaw where even with greater size they could not exert much leverage on the shell-food.

If Pl. II., *a*, be examined carefully basin-like excavations may be seen lateral to the posterior part of the first and second premolars. In one specimen these bowls were of sufficient size to contain a small marble. Since they are in the bone of the canine alveolus they probably represent responses to pressure of a fairly continuous nature while the latter was growing. Such pressure would most naturally be supplied by a hard substance in the food.

In two specimens of the upper second premolar, one at Western Reserve University and the other at the National Museum, a somewhat cone-shaped non-carious cavity was observed. These probably started from a slight defect in the softer secondary dentine in which calcareous or mineral matter became embedded, the cavity being worn by repeated pounding.

The third point mentioned, the highly polished lingual exposed surface of the teeth which is not on the occlusal area was thus described by Macgillivray, the Scots naturalist, in 1838 (2, p. 221):—

"A circumstance that seems to me very singular and for which I cannot account, is, that although the grinders are so placed as to meet at the points only, the outer surface of the lower not falling within the line of the upper so as to meet their inner surface, nor the reverse in any possible case, the jaw having no lateral motion, which is rendered impossible both by its articulation and by the barriers formed by the tusks, yet the inner surface of *both* upper and lower grinders is obliquely worn, in old individuals in a very remarkable degree and more or less in younger. Sometimes the grinders are, moreover, flattened at the points and frequently they are worn down to the level of the jaw. The mastication of fuci on which the walrus feeds could hardly produce these effects."

The reader will have noted that Macgillivray's observations are essentially accurate but that his erroneous information on the diet of the walrus is responsible for his failure to give an interpretation of the curious oblique surface. In addition, he did not seem to draw a clear distinction between the occlusal surface and the area under discussion, to which it bears a great resemblance. We have already accounted for the exposure of this area as the palatal or lingual side of the original conical tooth. There remains to be shown the manner in which the polish is acquired. The early writer was quite right in concluding that the mastication of fuci could hardly produce these effects; but the crunching of hard substance, such as shells, might. Although we cannot explain the details of the process the deduction appears inescapable. This polished non-occluding surface will be referred to subsequently as the "abrasive" surface, as distinguished from the true occlusal area.

The Individual Teeth.

On surveying the assembled teeth collected by Dr. Furnas, sorted into the proper groups, one is impressed both with the tremendous range of variability shown by each separate member of the dentition, the specimens being from animals of various ages and sizes, and, on the other hand, with the relative constancy of certain general characteristics of the collection as a whole and of the distinguishing features of the various teeth as groups.

One general characteristic, not previously mentioned though seldom absent, is the convexity of the palatal and lingual surfaces respectively of the roots in both jaws, while the buccal surfaces are more vertical or even concave. This is exactly the opposite of the condition in the toothed whales.

The plane of the polished abrasive surface of the teeth shows great variation, though usually forming an acute bevel at the exposure of its gingival border. The causes for this variation are chiefly differences in the proximity, direction, and size of the tusks, as well as in the age and size of the animal.

The foregoing pages have related how the walrus tooth as originally formed is simple and conical, with a tendency to transverse flattening in the lower jaw, and how this shape is later modified to give the differentiated areas seen in the adult specimen. Text-fig. 6 recapitulates these features diagrammatically. We have seen already how the enamel is early worn away, and, how in the upper jaw the buccal side of the crown, because of the juxtaposition of the growing canine alveolus, is secondarily covered with cementum, and finally, how in both jaws the abrasive surface of the dentinal crowns very early acquires a high polish from the hard substances masticated, probably through movement of the tongue. Thus the upper functional crowns are surfaces but slightly elevated from the gum, while in the lower teeth they are chisel-shaped, being bevelled at the expense of the abrasive surface.

The Functional Crowns.

Throughout our treatment of the subject the importance of structural pattern and its significance has been repeatedly emphasized. Pls. II., III., & VI. show the pattern formed by the exposed dental surfaces in the adult. Morphologically these are portions of the roots, but they function as crowns, and are so designated.

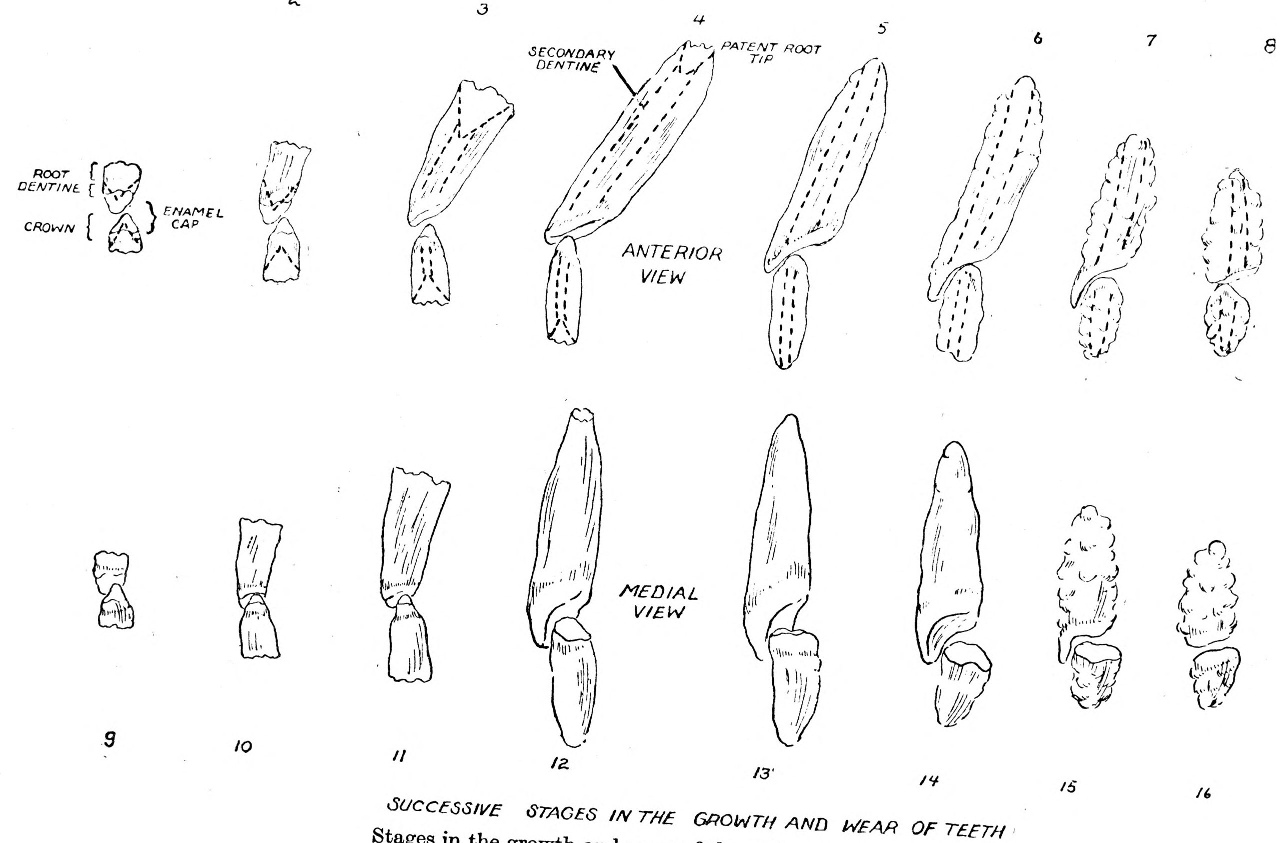
Upper Jaw.

In the upper jaw the three premolars appear as a definite unit slightly separated from the incisor.

The largest premolar is the second, the third is the smallest, and the first generally intermediate in size. The incisor is the most variable tooth in the row, being in some animals larger than the second premolar and in others less in size than the first. It is most frequently intermediate in size between the first and second.

In the shape of the crowns there are characteristic distinctions. The incisor tends to be rounded or in some animals flattened transversely, the latter form appearing most frequently in specimens with very large tusks. The premolar group is generally slightly flattened obliquely. The obliquity of the greatest diameter is directed from behind and lingually, forward and buccally. The first premolar is the most compressed of the trio, its greatest diameter being nearly transverse in many specimens. The second is the most rounded, sometimes having even a squared outline, but with a tendency to elliptical obliquity. The last premolar is often ovoid, and its long diameter has greater forward inclination than that of any other member.

Text-figure 6.



Stages in the growth and wear of the walrus tooth.

Table II.—Dimensions of Functional Crowns.

			UPPER.								LOWER.							
			Right.				Left.				Right.				Left.			
No.	Cat. No.		I.	Pm. 1.	Pm. 2.	Pm. 3.	I.	Pm. 1.	Pm. 2.	Pm. 3.	C.	Pm. 1.	Pm. 2.	Pm. 3.	C.	Pm. 1.	Pm. 2.	Pm. 3.
1.	11746.	AP.	26·1	18·8	22·4	20·5	24·6	19·0	23·0	20·0	**24·1**	21·8	20·3	17·3	21·7	**18·5**	20·4	15·3
		T.	20·9	23·6	25·3	22·1	23·3	25·0	29·0	27·0	**23·0**	18·3	16·7	11·7	17·5	**17·3**	17·7	12·1
2.	14397.	AP.	29·2	16·8	22·7	22·0	28·2	19·0	28·2	18·1	23·5	21·7	**19·6**	**12·3**	23·7	21·9	**19·2**	**11·4**
		T.	16·7	15·2	21·0	18·7	18·0	16·1	19·4	17·3	19·9	16·0	**15·3**	**11·7**	19·5	16·5	**15·6**	**11·0**
3.	16437.	AP.	30·6	17·9	27·0	27·0	31·3	20·0	26·9	25·4	27·5	25·8	22·6	12·8	27·5	27·1	24·6	..
		T.	21·6	15·2	26·0	26·4	23·2	19·1	27·1	24·0	22·3	19·0	17·0	11·7	21·3	18·8	17·0	..
4.	16446.	AP.	21·3	21·5	28·5	16·4	21·0	21·2	31·5	18·6	23·8	24·0	20·8	12·2	24·7	22·7	20·7	14·2
		T.	17·8	22·2	24·0	20·1	17·4	20·0	26·3	20·4	19·0	18·2	18·5	12·7	20·3	17·0	17·4	14·2
5.	16757.	AP.	17·8	13·2	19·5	19·7	18·2	14·4	19·5	20·4	15·2	17·2	14·8	10·5	17·4	16·9	15·3	11·1
		T.	14·8	14·4	17·1	15·0	17·2	13·3	18·2	17·4	11·7	13·2	12·7	9·0	14·2	12·7	13·9	9·0
6.	144995.	AP.	13·6	15·6	20·6	16·9	14·4	15·4	22·1	**16·6**	13·2	18·8	**14·9**	12·3	14·9	15·9	14·1	9·5
		T.	12·6	14·1	20·5	19·5	12·4	14·3	20·5	**16·3**	14·1	10·9	**9·5**	7·8	12·3	10·3	9·7	8·3
7.	220151.	AP.	26·6	16·9	24·8	21·9	27·2	18·6	24·2	25·1	27·4	22·2	19·8	14·3	22·6	16·9	18·6	13·3
		T.	21·2	18·6	20·2	24·7	26·1	17·8	19·3	26·5	28·7	22·7	21·0	16·9	22·4	17·8	17·1	15·3
8.	22200.	AP.	20·5	18·5	27·5	17·8	22·3	18·7	31·5	17·5	23·1	22·9	20·7	10·7	22·8	24·0	19·5	12·3
		T.	10·5	17·9	21·0	15·7	17·5	16·9	22·2	15·3	20·0	15·5	14·5	9·7	19·3	16·1	15·3	11·6

Measurements in millimetres. Clarendon figures indicate alveolus was measured instead of tooth, which was missing.

Lower Jaw.

Here again the three premolars appear as a unit from which the canine is separated by a somewhat wider diastema.

The teeth show progressive diminution in size posteriorly. The canine is definitely the largest tooth and the third premolar is much the smallest. Premolars 1 and 2 are subequal in size and only slightly smaller than the canine.

The outline of the canine has a pronounced tendency to be rounded, while the premolars show antero-posterior elongation. The last premolar, because of its small size, may appear rounded.

The Roots.

The adult walrus tooth is mostly root. In the discussion on the effects of the tusks and diet the pattern of the roots has been described for both jaws. Pls. IV. & V. show the relative independence of the incisor from the premolar series.

Upper Jaw.

As suggested by its appearance *in situ* the second premolar has the longest and largest root. Its backward tilting is usually the sharpest. The root of the first premolar is generally relatively slender and but little shorter than that of the second. The third is quite the stocky dwarf of the group, though it may exceed the first in thickness. Its posterior curvature is so marked in many specimens that its silhouette resembles an inverted comma. The variability of the incisors is excellently illustrated by Pls. IV. & V. In Pl. V. the incisor has the characteristic features described and is somewhat smaller than the first premolar, while in Pl. V. it is easily the largest tooth in the head.

The large type of incisor shown in Pl. V. we believe should be considered the more advanced, since there seems to be a concentration of pounding force forward, evidenced by increase of size and weight in bone and tooth, evolving in the walrus jaws as shown above, the specialization being practically complete in the mandible. If this be so, the size of the second upper premolar represents either the present limit of a genetic trend toward progressive diminution from behind forward, in the size of the members of the dental battery, or an enlargement compensatory for the first premolar, which might have greater area were it not in the most cramped position in the jaw. The latter explanation, however, seems improbable and unnecessarily teleological.

So in the most specialized types the incisor is the largest tooth in the upper jaw and the canine the largest in the lower. This pattern is more constant in the lower jaw, where we have seen no exceptions, than in the upper jaw, where exceptions are frequent.

The incisor is of particular interest because it has undergone three distinct modifications in this specialization—first, alignment with the premolars and assumption of molar form and function, second, retrogression along with all its fellows to a simple conical shape, and, finally, secondary enlargement, which provides greater crushing force in the anterior region of the jaws.

Lower Jaw.

These teeth have been reviewed in the preceding incidental references. The relationship as to size shown by the functional crowns holds also for the roots, as these too progressively decrease in size posteriorly. The canine and first premolar have a convex anterior border and the second and third a convex posterior border.

Comparison of Upper and Lower Dental Rows.

In Section III. we have seen how the vertical or outwardly inclining lower teeth, with their shorter thicker roots, occlude with the longer upper teeth, which, with their longer and more slender roots, rest like the sides of a steep gable roof upon their counterparts below (text-figs. 4 & 5).

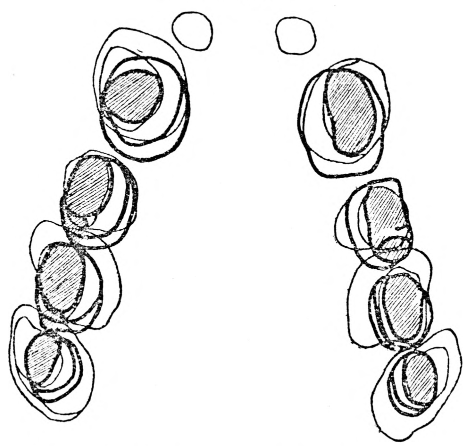
The lower row is shorter than the upper, the difference being due chiefly to the third lower premolar, which is the smallest tooth in the head. The lower canine and second premolar have occlusal surfaces, but slightly less than those of the upper incisor and second premolar; the lower first premolar, however, is decidedly longer than the corresponding upper tooth as regards occlusal surface (text-figs. 7 & 8).

The Occlusion.

The Types of Occlusion.

The ordinary occlusion is exhibited in Pls. IV. & V. The lower canine occludes with the upper incisor and first premolar, the first lower premolar with the first and second upper, the second lower with second and third upper,

Text-figure 7.



"End-to-end" type of occlusion. U.S. Nat. Mus. No. 220151.
Upper teeth, light line; lower teeth, heavy line; occlusal area, hatched.

and the third lower with the third upper. This may be regarded as a generalized primitive mammalian alternate occlusion, as each lower tooth but the last occludes with two uppers.

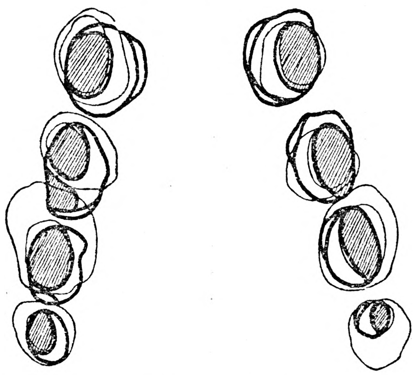
Pls. II., V., & VI. show a more advanced type in different degrees, where a given lower tooth occludes only with its corresponding upper. All gradations between these two forms of occlusion are found.

The Sites of Occlusion.

From text-figs. 7 & 8 it is clear that the narrow lower teeth impinge upon their wider upper fellows near the buccal side of the latter and toward their posterior portion, thus leaving above a more or less broad strip of unoccluded surface anteriorly. On to the latter the hinder region of the next lower tooth in front will extend in the primitive type, while it will be unabraded in a fully advanced type (Pls. II., III., & VI.).

In the lower teeth (Pls. V. & VI.) there is a small eminence toward the buccal side which results from the alternate occlusion with two upper teeth. In the most nearly alternate occlusion this eminence will be large and prominent and near the anterior end of the tooth. As progression toward end-to-end occlusion continues this projection is reduced in size and forced posteriorly until it is about to be lost as in Pl. II., where an almost perfect end-to-end occlusion is seen to have developed.

Text-figure 8.



Mixed types of occlusion. U.S. Nat. Mus. No. 22200.
Upper teeth, light line ; lower teeth, heavy line ; occlusal area, hatched.

Pl. VI. shows an ideal demonstration specimen. On the right is a completely end-to-end occlusion in the second premolars. On the left the corresponding teeth are in primitive alternate occlusion. The most striking features, however, are found in the first two pairs of the battery of the right side, where the upper tooth pattern is impressed by wear upon the lowers and the uppers have been worn to resemble lowers (text-fig. 8). This in all likelihood is due simply to an early malocclusion in which the right lowers were inclined outwardly so as to strike nearer the buccal side of the upper teeth than usually happens. Why this should have occurred is not clear, because the alveoli of the two sides are in satisfactory alignment.

The Patterns of Wear and Age.

The Tooth at Different Ages.

Text-fig. 6 tells the story of the walrus tooth from infancy to old age. Specimen No. 1 is adapted from Malmgren's fœtal skull, all the others are from the group gathered by Dr. Furnas.

We see from the unerupted tooth of the fœtal skull that when first formed it has the normal proportions of a mammalian tooth, for the crown has then a nearly complete cap of enamel with a lower girdle of apparently exposed dentine. This size of tooth is adjusted to the space available at that period. We have already mentioned that the animal is nursed for the long period of about two years, during which time, owing to the rigid requirements of the Odobenid diet, he must be developing a face and dental armament sufficient for the crushing of shells. During this period the walrus sheds his useless milk-teeth and replaces them by the permanent set, although even at the end of two years his face cannot have reached adult dimensions.

TABLE III.—Number of Teeth in National Museum Specimens.

No.	Cat. No.	Species.	Upper.	Lower.
1.	7889.	*divergens.*	7	
2.	9475.	,,	6	1
3.	11746.	,,	0	0
4.	14396.	,,	9	
5.	14397.	,,	8	
6.	16437.	,,	8	8
7.	16447.	,,	..	0
8.	16446.	,,	..	0
9.	16447.	,,	6	
10.	16448.	,,	4	
11.	16756.	,,	8	
12.	16757.	,,	8	8
13.	21101.	,,	0	
14.	21102.	*rosmarus.*	0	
15.	21103.	*divergens.*	0	
16.	21104.	*rosmarus.*	0	
17.	22014.	,,	4	0
18.	35518.	*divergens.*	8	8
19.	35683.	,,	..	8
20.	63302.	,,	0	
21.	84868.	,,	1	
22.	121177.	*rosmarus.*	6	1
23.	144995.	*divergens.*	..	0
24.	151712.	,,	8	
25.	199528.	*rosmarus.*	3	
26.	200336.	*divergens.*	6	1
27.	217913.	,, (fœtal).	23	14
28.	218365.	,,	0	
29.	220151.	,,	10	8
30.	22200.	,,	8	
31.	256002.	,,	6	
32.	21045.	,, (young).	17	12
		Total..	164	69

Total, both jaws 233
Total, Furnas Collection 219

Total number of teeth examined 452

To meet this requirement a simple specialization has been developed which makes it appear on comparing adolescent and fully adult skulls that the teeth must increase in girth after eruption. The mechanism is merely that the roots continue to grow as cones (text-fig. 6, Nos. 2 & 3), thus increasing their circumference proximally until the full adult size is reached. Then the growth energy slackens and the apical foramen is formed in the tapering root.

While the jaws are growing the teeth are being worn down, and as the occlusal surfaces thus become progressively larger the dental battery constantly keeps pace with the size of the jaws from early life, when the face is very small, to adulthood, when it is exceedingly large.

The National Museum has but one young skull, No. 21045, intermediate between the fœtus and the young adult. This belongs to an animal of nearly two years according to Lamont's standard. It serves, however, to confirm deductions which already had been made from the conical shape and open roots of several functional teeth in the Furnas collection—namely, that adjustment of the functional set to the growing face is accomplished by circumferential expansion of the growing extremity of a root. In this particular specimen very little wear has occurred. The roots of all the teeth are open, but only that of the second upper premolar exhibits an apical extremity which was apparently increasing in diameter. This seems to indicate that increase in root-diameter of the several teeth occurs at different periods in growth. This renders a series of skulls of progressive age necessary for a full understanding of this phenomenon.

Estimating from the length of specimen No. 3, which seems to have reached its maximum diameter, the longest teeth in the head grow as much as their full adult length before the conical end ceases to expand. The whole life-story

TABLE IV.—Classification of Teeth in Furnas Collection.

	RIGHT.				LEFT.				Total.		Young.	On Exh.	
	I.	Pm. 1.	Pm. 2.	Pm. 3.	I.	Pm. 1.	Pm. 2.	Pm. 3.	R.	L.			
Upper .	7	28	15	11	18	26	14	7	61	65			
Lower .	6	6	8	4	2	7	4	2	24	15			
Total. .	13	34	23	15	20	33	18	9	85	80	7	47	219

I. For lower teeth should be read "canine."

of such a tooth may, perhaps, be represented by a vertical spindle, one half of which is completed during the period of facial growth to full adult size. During this period the tooth is worn down to the site of maximum diameter without disturbance of adjustment between the size of the tooth and facial dimensions. Beginning with adult life, the other half of the spindle is gradually worn down until, in very old animals, the tooth may be lost completely. As all the teeth are not of the same length some of them wear out before others. The posterior lower teeth are usually the first to be used up and shed.

In the National Museum there is one specimen of a toothless mandible in which all the sockets are clearly outlined but too shallow to have supported teeth.

Deposit of Secondary Dentine.

In text-fig. 6 the broken lines outline the root-canal and the extent to which the pulp-cavity is filled by secondary dentine. This process ultimately results in the formation of a solid cylinder which has functional advantages. The secondary, dentine demands further investigation ; it is darker in colour than the primary, and as the tooth is worn it is continually visible as a brownish inner core surrounded by the whiter primary dentine. It presents ordinarily in cross-section a lamelliform structure seemingly continuous with that of the primary layers, but in some cases it has an amorphous appearance. Mr. Miller tells me that walrus teeth are often carved as charms to simulate elks' canines, and that the dark inner " core " of the walrus tooth is a very reliable guide to the true origin of a charm in which it is present.

The Pattern of Wear.

In text-fig. 6, Nos. 1–4 and 9–12 show the change in the angle formed by the upper and lower teeth in occlusion caused by the shift in the angle of implantation of the upper teeth between the fœtus and the adult. Beginning with No. 5, the pattern of wear, as it proceeds in adult life, is easily followed.

The walrus, being a carnivore, still preserves the carnivore form of the tempero-mandibular joint. A study of the wear-pattern is therefore facilitated by the restriction of biting movement to the vertical type alone.

Since the narrower lower teeth occlude against the broader upper teeth concavities or basins of wear are formed on the uppers and convexities are formed on the lowers. Wear results in simple abrasion of dentinal substance at points of contact. In the primitive type of occlusion the interdigitating areas have no contact, at least until wear is well advanced, and consequently remain as eminences on the teeth (Pls. IV. & VI.). The circumstances controlling the position of these areas have been described in the section on occlusion.

Studying text-fig. 6, Nos. 5–8 and 13–16, we see that the lower crusher pounds a hollow in the upper, the outer side of which becomes a flange, which with continuous wear is itself worn off, the process beginning posteriorly. The portion of the lower tooth which wears the flange is itself smoothed into an occlusal surface at the expense of the buccal side. When the flange has been worn off this surface is again out of occlusion, though it is being constantly shortened by the uninterrupted end-to-end wear. (When an upper occludes with two lowers a double flange may be produced which will be worn off from either end.)

The polished bevelled surface which, according to evidence cited, is produced by abrasion of shell-fragments, is continually extended on to new areas as the wear involves more of the dental column. Partly because of the greater obliquity in position of the upper teeth their bevelled surface has larger area than that of the lower teeth, particularly in the third premolar. The gingival boundary of this polished surface in the lower teeth often has a characteristic curve, due to the fact that the gum extends nearer the occlusal surface anteriorly than behind. This curve is well marked in small teeth, and is especially useful for identification purposes. It characterizes also the secondary occlusal surface produced on the buccal side of the lower teeth by their abrasion against the flanges ground out upon the uppers, though it is best marked in large teeth.

The Appearance of Hypercementosis.

Still another feature which deserves comment is the hypercementosis seen about the roots of old teeth, both upper and lower. Our specimens show that the hyperplastic deposit begins at the root-tip and extends to the occlusal margin. It probably takes several years for complete envelopment to be accomplished.

The most logical explanation which suggests itself for this phenomenon is that it is a response to the irritative action of the functional pounding to which the teeth are subjected.

Summary.

1. The dental peculiarities of the walrus, *Odobenus obesus*, may be ascribed in their entirety to the structural modifications induced by the huge size of the canine tusks and to the diet which the animal has adopted.

2. The dental succession is best represented by the formulæ : Deciduous i. $\frac{3}{3}$, c. $\frac{1}{1}$, m. $\frac{3}{3}$=28 ; Successional I. $\frac{2}{0}$, C. $\frac{1}{1}$, P. $\frac{4}{3}$, M. $\frac{1}{1}$=26 ; Functional I. $\frac{1}{0}$, C. $\frac{1}{1}$, P. $\frac{3}{3}$=18. The last of these is well known. The first differs from previous interpretations in recognizing but three milk-molars, and the second is devised to acknowledge definitely the existence of a successional upper second incisor and fourth premolar and to designate as true molars the upper and lower posterior rudimentary teeth.

3. The enlargement of the upper canines has caused the loss of the medial incisors, the alignment of the outer upper incisor and lower canine with the cheek-teeth, and an antero-lateral shift in the angle of implantation of the upper teeth.

4. The diet, composed chiefly of hard-shelled molluscs, has required a concentration of force in the anterior portion of the mouth. This has been accomplished by the production of massive jaw-bones and heavy solid dental columns.

5. The necessity for an adequate dental armament at an early age has been met (*a*) by a long period of suckling, while the face and teeth were growing ; (*b*) by the nearly simultaneous eruption of the entire dental battery ; and (*c*) by the expanding cones of the growing roots, which made it possible for dental equipment to keep pace with facial development without additional teeth, a mechanism not noted in any other mammal.

6. The details of the processes of structural modification, growth, wear, and senescence related to the dentition have been recited according to the evidence available.

7. By the application of the principles set forth in this discussion miscellaneous specimens of teeth may be identified with reasonable accuracy.

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EXPLANATION OF THE PLATES.

Plate I.

Fœtal skull and mandible : milk and successional dentitions. Fœtal, palatal, and alveolar structure. U.S. Nat. Mus. No. 217913.

Plate II.

Adult skull (*a*), with mandible (*b*): full functional dentition; well-developed permanent second upper incisor. Nearly complete "end-to-end" occlusion. Slight excavation of bone lateral to second upper premolars. U.S. Nat. Mus. No. 220151.

Plate III.

Young adult skull: successional fourth upper premolar in position. Teeth but slightly worn, leaving conical shape clearly discernible. U.S. Nat. Mus. No. 14396.

Plate IV.

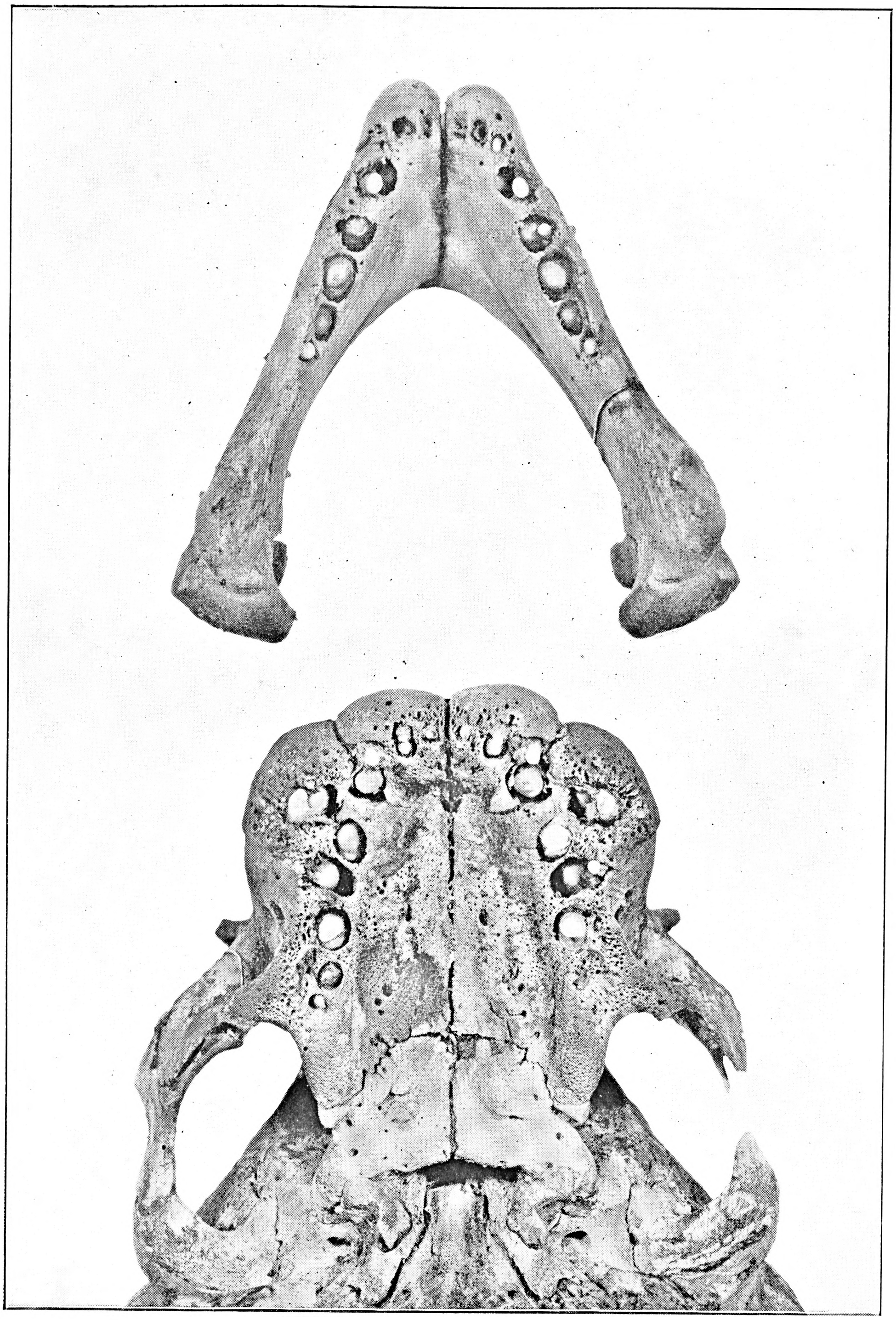
Dental battery: (*a*) Teeth not in occlusion, showing occlusal and abrasive surfaces and flanges of wear (*cf.* text). Buccal view of members of right side; lingual view of left. U.S. Nat. Mus. No. 35518. (*b*) Teeth in occlusion.

Plate V.

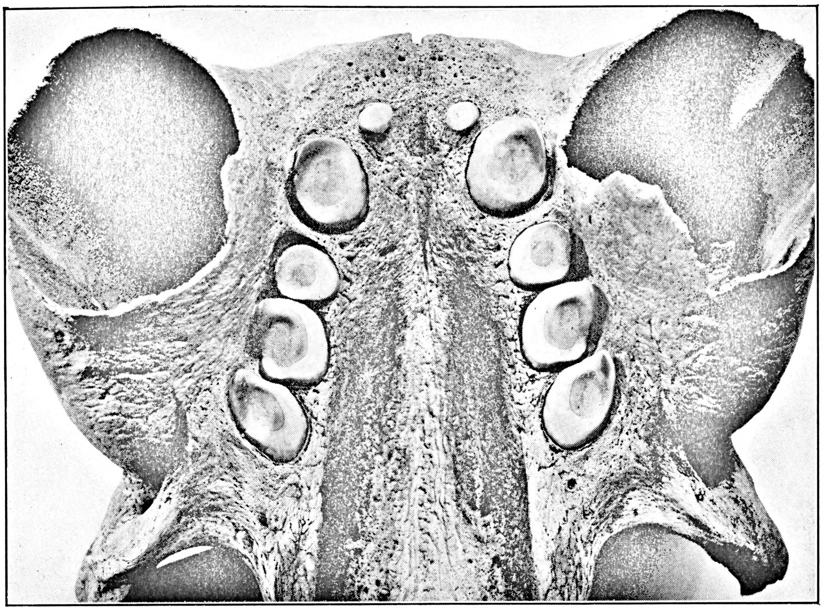
Dental battery: (*a*) Teeth are of right side, not in occlusion. Large "specialized" incisor. Occlusion alternate approaching "end-to-end" type. U.S. Nat. Mus. No. 16437. (*b*) Teeth in occlusion.

Plate VI.

Adult skull (*a*), with mandible (*b*): full functional dentition. Typical alternate occlusion in left premolars; "end-to-end" in right. Exchange of wear pattern between upper and lower teeth in first two members of right side. U.S. Nat. Mus. No. 22200.



Dentition of the Walrus, *Odobenus obesus.*



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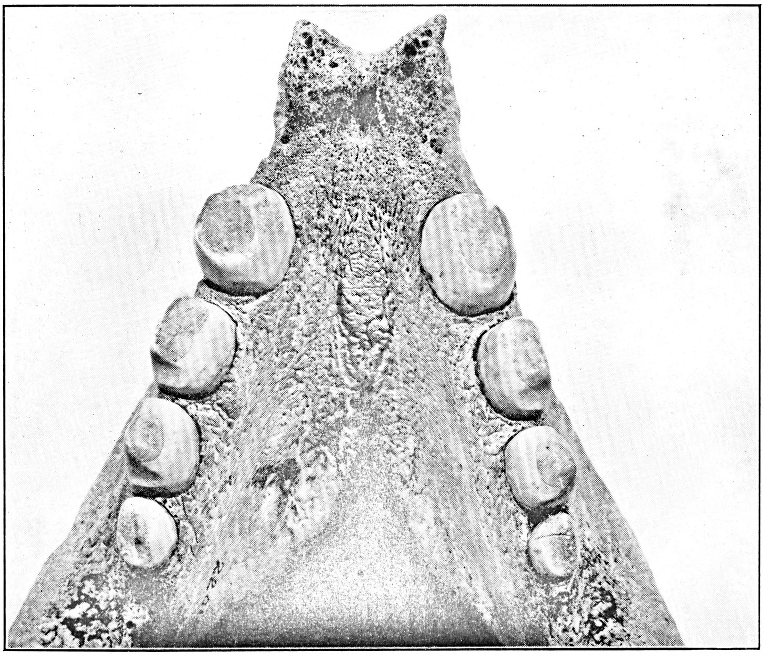
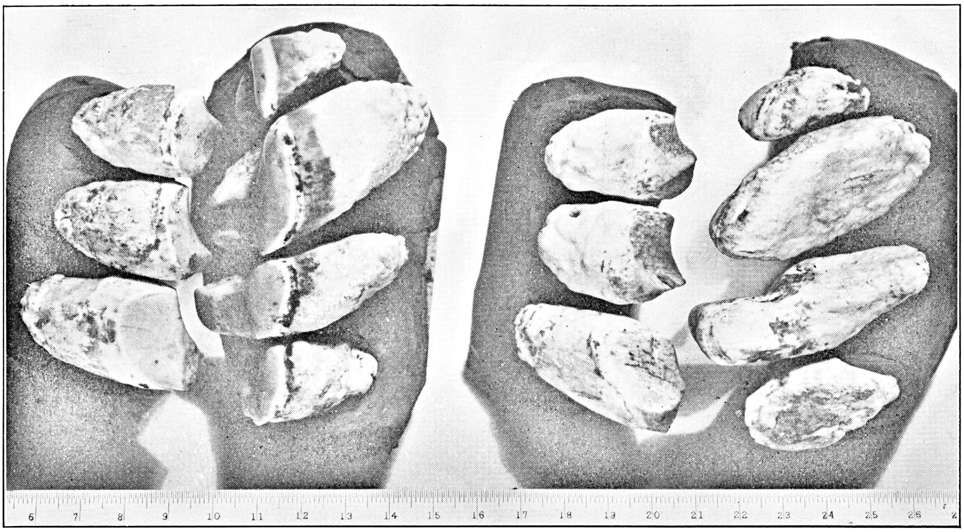


B.

Dentition of the Walrus, *Odobenus obesus*.

DENTITION OF THE WALRUS, *ODOBENUS OBESUS*.



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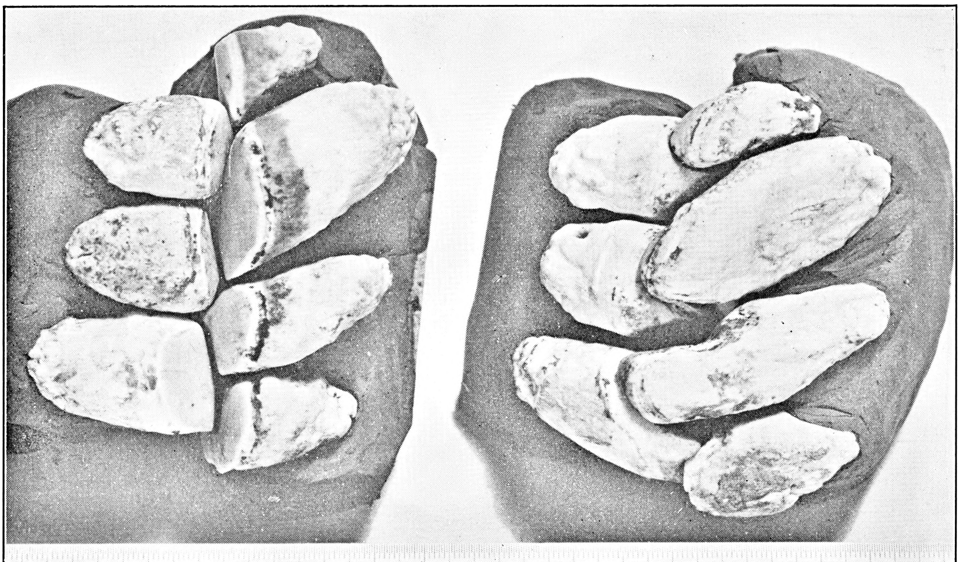

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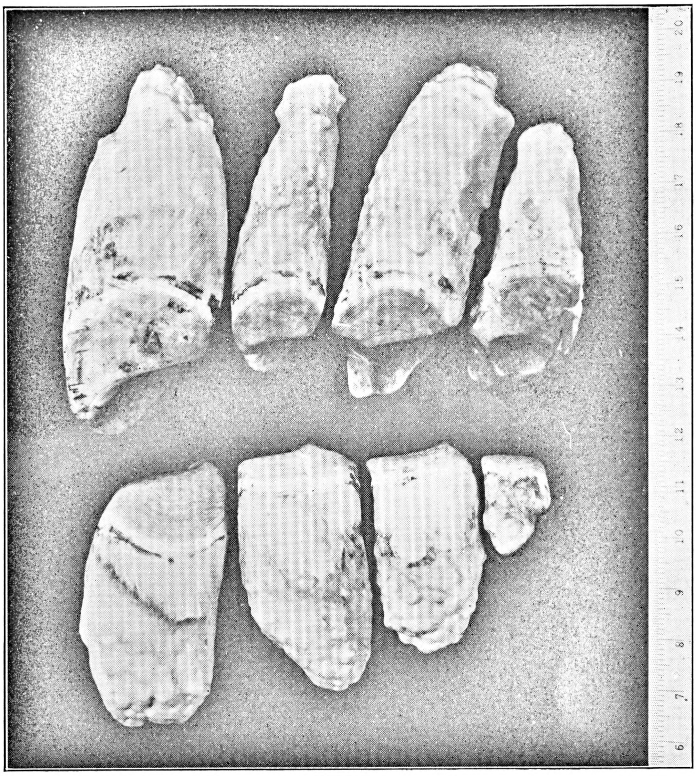
DENTITION OF THE WALRUS, *ODOBENUS OBESUS*.



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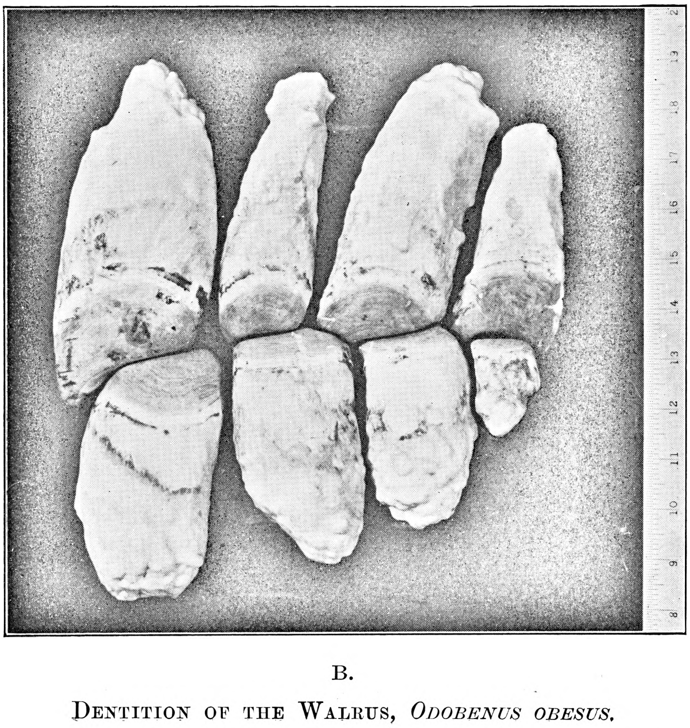

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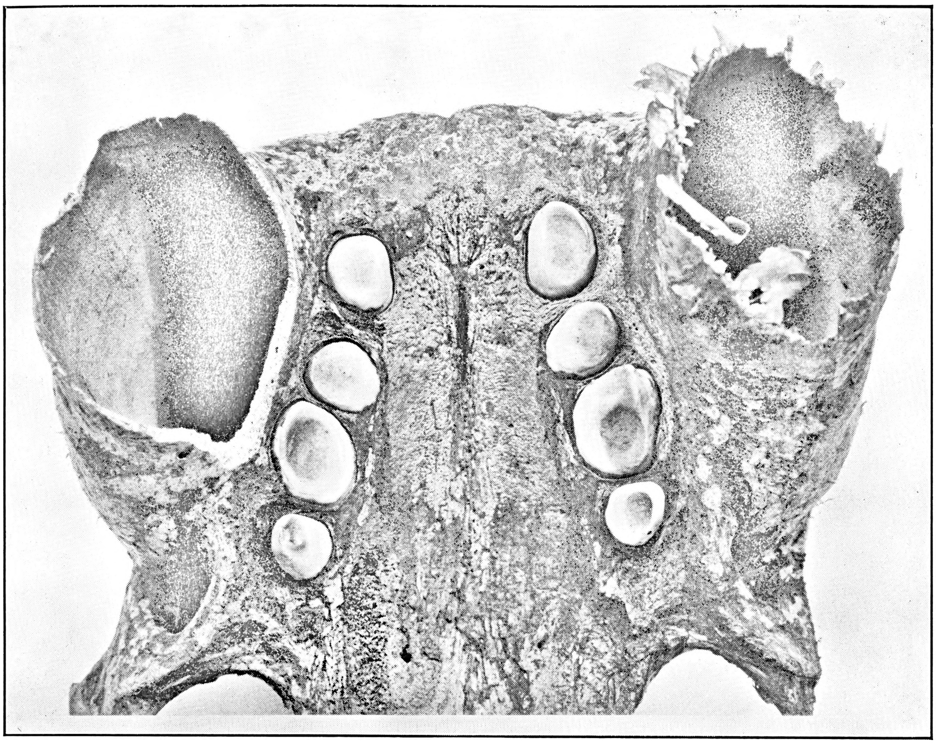
Dentition of the Walrus, *Odobenus obesus.*



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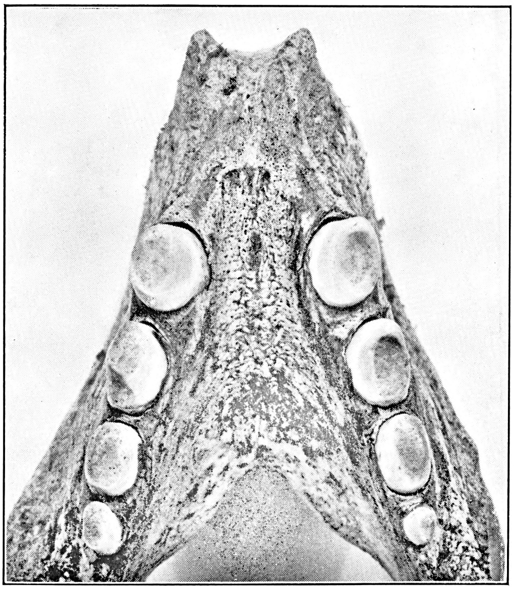

B.

DENTITION OF THE WALRUS, *ODOBENUS OBESUS*