AGE DETERMINATION AND GROWTH OF THE BAIRD'S BEAKED WHALE WITH A COMMENT ON THE FETAL GROWTH RATE

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ABSTRACT

Two kinds of cycles exist in the alternation of the stainability of dentine and cementum of the species. The longer is of annual, and the stainable layer is deposited from August to January and the unstainable in the rest of the year. The shorter cycle ranges from 27 to 31 days with possible individual variations. The deposition of dentine ceases within several years after birth, and the short cycle is distinguishable in the first few annual layers. In cementum, on the other hand, the annual layer is possibly formed for all the life time, and the short cycle on the anterior tooth until 40 to 60 years of age. The length of life time is 70 years. The gestation will last for about 17 months, one of the longest among the cetaceans.

INTRODUCTION

The morphology and life history of the Baird's beaked whale, *Berardius bairdii* Stejneger, 1883 in the western North Pacific and adjacent seas were studied by Omura *et al.* (1955) based on the catch statistics of the Japanese commercial whaling in the period from 1948 to 1952 and on many specimens investigated by them. Later Nishimura (1970) discussed the distribution of the species in the Sea of Japan based on several stranded animals. Nishiwaki and Oguro (1971) analysed the statistics of Japanese catch of the species in the years from 1965 to 1969. In recent years, the catch of *B. bairdii* is mostly restricted, by the economical factors, to the coastal waters of the Boso Penninsula on the Pacific coast of central Japan, and the annual catch seems to be less than 30 whales (Dr. Y. Naito, person. comm.).

In spite of the effort of these authers, very little is known about the life history of the species. The main obstacle in the study exist in the difficulty in obtaining the adequate number of samples and in the absence of the age determination technique. Though, Omura *et al.* (1955), studying the anatomy of the tooth of *B. bairdii*, indicated the presence of the annual layers in cementum and suggested the possibility of the age determination, they did not show the reason for the conclusion nor try to estimate the age of the whales. The present study was made in order to reconsider their study and provide some clue of the age determination of the species.

MATERIALS AND METHOD

Nineteen samples, in the twenty used in this study, were collected from the catch of coastal whaling off the Boso Penninsula (35°N, 140°E), of which 18 animals by Omura in 1957 through the cooperation of the Tokai Gyogyo Co., Ltd, and another sample WD-9 by Dr. Y. Naito. Whale no. 20 was collected at an whaling station at Ayukawa (38° 20'N, 141° 30'E) on the Pacific coast of Japan through the field investigation of the Whales Research Institute.

TABLE 1. LIST OF MATERIALS

Whale no.	Date of catch	Body length	Sex	Gonad[10] (kg)	Tooth position[1]	Tooth thickness	Tooth height
4	—, —, '57	—	—	—, —	Post.	16 mm	48 mm
20	13, Oct., '59	9.8 m	♂	6.4, 5.8	Ant.	26 mm	73 mm
36[5]	5, Aug., '57	10.8 m	♀	0.44, 1.55	Ant.	35 mm	81 mm
36					Post.	15 mm	49 mm
37[7]	6, Aug., '57	10.6 m	♂	4.10, 4.10	Ant.	—	76 mm
37					Post.	13 mm	—
38	8, Aug., '57	11.1 m	♂	5.20, 5.30	Post.	21 mm	52 mm
40	15, Aug., '57	10.6 m	♂	4.80, 4.90	Ant.	28 mm	73 mm
40					Post.	16 mm	48 mm
41	16, Aug., '57	10.9 m	♂	4.70, 5.80	Ant.	34 mm	89 mm
41					Post.	18 mm	90 mm
44	18, Aug., '57	11.4 m	♀	0.205, 0.245	Ant.	32 mm	84 mm
49	27, Aug., '57	10.7 m	♂	4.10, 3.90	Ant.	34 mm	80 mm
49					Post.	14 mm	51 mm
50	28, Aug., '57	10.7 m	♂	8.20, 8.20	Ant.	34 mm	56 mm
50					Post.	15 mm	47 mm
51	30, Aug., '57	10.7 m	♂	5.60, 5.80	Ant.	43 mm	68 mm
52	30, Aug., '57	10.8 m	♂	7.00, 6.90	Ant.	36 mm	79 mm
52					Post.	18 mm	64 mm
53	1, Sept., '57	7.8 m	♂	0.40, 0.36	Ant.	33 mm	86 mm
53					Post.	16 mm	51 mm
54	1, Sept., '57	10.4 m	♀	0.320, 0.275	Post.	18 mm	62 mm
55	15, Sept., '57	6.4 m	♀	0.062, 0.060	Ant.	32 mm	66 mm
57	14, Oct., '57	10.1 m	♂	5.50, 5.50	Ant.	35 mm	74 mm
57					Post.	20 mm	50 mm
58	15, Oct., '57	10.8 m	♂	7.00, 9.80	Ant.	41 mm	84 mm
58					Post.	18 mm	57 mm
60	6, Nov., '57	11.0 m	♀	0.235, 0.245	Ant.	35 mm	85 mm
60					Post.	18 mm	59 mm
61	14, Nov., '57	10.7 m	♂	1.20, 1.15	Ant.	39 mm	90 mm
61					Post.	18 mm	60 mm
WD-9	4, Aug., '76	10.5 m	♂	3.62, 4.94	Ant.	32 mm	67 mm

[1] Ant.: Anterior tooth, Post.: Posterior tooth. [2] —: Not erupted, +: Erupted and osteodentine covered, [4] In parentheses: Pulp cavity filled with osteodentine, Italics: No. of annual layers (long Pregnant with 12 mm fetus (Omura, 1958), physically mature. [7] Physically immature. [8] 30 short All the testes, except for the whale no. 20, were weighed by the Tokai Gyogyo Co., Ltd., and the ovaries

The body length recorded by foot (0.305 m) or shyaku (0.303 m) was converted into metric system. The records of sex and weight of gonad were obtained directly by the biologist or by the whaling company as in the case of the body length.

Teeth of 19 whales, other than that of WD-9, were preserved in dry condition after cleaning by boiling. Each tooth was cut on a lingua-buccal medial plane, and one 2 to 3 mm section was taken with a saw. Then, usually, either lingua or buccal half of the section was polished with whet stones and glued on a clear plastic plate. The other side was polished with the same way to a thickness between

USED IN THIS STUDY

		No. of long cycles[4]		Age with complete short cycle	Last long cemental cycle[5]	
attrition[2]	root[3]	in dentine	in cementum			
—	closed	[5]	38, *44*, 46	—	Unstainable	(wide, -)
+	closed	[7]	40, *41*, 42	≧41	Stainable	(thin, 2)
++	closed	—	35, *36*, 38	≧36	Unstainable	(wide, 7)
+	closed	[4]	30, 33, 35	—		
+	closed	[5]	16, *17*, 17	≧17	Unstainable	(wide, 7)
—	closed	[6]	17, 17, 17	—		
++	closed	—	25, *26*, 27	—	Unstainable	(wide, -)
++	closed	—	56, *57*, 61	≒57	Stainable	(thin, 2)
+	closed	[4]	56, 58, 63	—		
+	closed	[7]	40, *47*, 51	≧47	Stainable	(thin, 1)
+	closed	[5]	37, 40, 40	—		
+	closed	[5]	22, *25*, 29	≧25	Stainable	(wide, 3)
+	closed	[4]	20, *21*, 22	≧21	Stainable	(thin, 2)
—	closed	[5]	23, 23, 24	—		
++	closed	—	66, *67*, 71	≦52	Unstainable	(wide, -)
+	closed	[5]	54, 67, 68	—		
++	closed	—	68, *71*, 72	≦42	Unstainable	(wide, -)
+	closed	[5]	29, *30*, 31	≧30	Stainable	(thin, 1)
+	closed	[6]	30, 30, 32	—		
—	open	3	3, *3*[8], 3	≧ 3	Stainable	(wide, 3)
—	open	3	3, 3, 3	—		
+	closed	[7]	35, *36*, 37	—	Stainable	(thin, -)
—	open	2	2, *2*[9], 2	≧ 2	Stainable	(thin, 2)
++	closed	—	51, *58*, 59	≦57		
+	closed	[6]	49, 51, 56	—		
++	closed	—	50, *50*, 52	≧50	Stainable	(wide, 3)
+	closed	[6]	46, 47, 48	—		
++	closed	—	37, *39*, 40	≧39	Stainable	(wide, 3)
+	closed	[5]	44, 46, 51	—		
+	closed	[5]	40, *40*, 41	≧40	Stainable	(wide, 4)
+	closed	[6]	37, 39, 41	—		
++	closed	—	64, *65*, 66	≦56	Stainable	(thin, -)

not exposed, ++: Osteodentine exposed, [3] Closed: Root covered with cementum, Open: Root not cycle) used in other part of this study. [5] In parentheses number of short cycles if observable. [6] cycles in cementum and 31 in postnatal dentine. [9] 22 short cycles in dentine and cementum. [10] by Dr. H. Omura after the fixation in 10% formalin.

40 μm to 70 μm. The thin ground section was decalcified in 5% formic acid for several hours, stained with Mayer's haematoxylin solution for 30 minutes and mounted with permanent mounting medium. In case of the tooth of WD-9, which was fixed in 10% formalin, the section was at first step embedded in polyester resin, and then processed with the same method to a thinner decalcified and stained preparation. Its thickness was about 25 μm. This method did not give different result except for the technical convenience to produce thinner section. Many other ancillary thin preparations (10 to 15 μm) were made from small pieces of cementum, and used for limited observations.

The observation of the growth layers was made with a microscope (×40 and ×100) under transmitted light, and counting was always made on the stainable layers.

Though, the same process was made, if available, on both anterior larger tooth and posterior smaller tooth, the latter was used for restricted purpose. If it is not specified, in the latter part of this study, the analysis are for anterior tooth.

RESULT

Growth of the tooth

About 80% of individuals of *B. bairdii* have two pairs of mandibular tooth, and the rest of animals more (Kirino 1956). The tooth is shaped of a bilaterally compressed cone, and the fundamental structure is same for both the anterior and posterior tooth (P1. I). In case of the unerupted tooth, the cusp is covered with thin enamel layer, as already indicated by Omura *et al.* (1955) on a fetal tooth. The enamel layer of the postnatal individuals is often covered with cementum (Fig. 1).

Beneath the enamel layer there are dentinal layers and large pulp cavity. This pulp cavity is later filled with osteodentine and only narrow root canal, which is connected to the outside of the tooth through the thick cemental layer, is often left

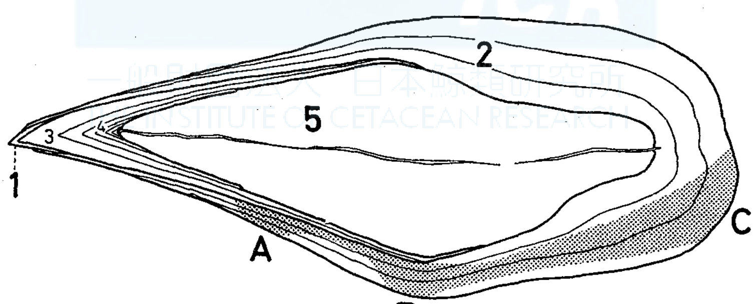

Fig. 1. Schematic figure of the lingua-buccal section of the tooth of *B. bairdii*. 1: Enamel. 2: Cementum, only three layers are indicated. 3: Fetal dentine. 4: Postnatal dentine. 5: Osteodentine. Alphabets indicate the positions for counting the layers used in Figs. 2 and 3.

in case of the older animals.

The cementum covers almost the entire length of the lateral surface of the tooth of postnatal animals. In young individuals such as nos. 53 and 55, of which ages are estimated in the later part of this study to be about 30 months, and 21 months respectively, the osteodentine is exposed on the base of the tooth, however, in the older animals, the root is covered with cemental layers. This stage is classified into the " closed " state in Table 1. This definition is different from that of Omura *et al.* (1955), where the root was considered to be closed if the osteodentine fills the pulp cavity. The closure of the root seems to occur at the age between 3 and 17 years.

The eruption of tooth was recorded at the whaling station and it was confirmed in the laboratory using, if necessary, a microscope. The eruption is considered to occur in relation to the attainment of sexual maturity (Omura *et al.* 1955). The present scanty materials suggest that the eruption of anterior tooth occurs at an age between 3 and 17 years, and the posterior smaller tooth between 21 and 30. The sexual difference of the eruption was not detected in this study. Matsuura (1942) considered that the posterior tooth of the female does not erupt, however, the present data, whale nos. 36 and 60, indicate that the posterior tooth of female also erupt at some age as already indicated by Kirino (1956).

Dentinal growth layers

As shown in Fig. 1 and Plate I, the outermost layer of the dentine is the fetal layer. This is the largest in the thickness, and the length of the contour is longest next to the first postnatal dentinal layer. There are observed obscured layered structures in the fetal dentine both in the thin ground section and in decalcified and stained section. Though most of the layers in the prenatal dentine are obscure, several contiguous layers are clear in most of the individuals (Pl. II). These clear layers are formed at the various stage of the deposition of the prenatal dentine, and the number of the clear layers is usually from 3 to 7 with 2 exceptional cases of 0 and 12 layers (13 individuals examined). The condition is same in the anterior and posterior tooth of the same individual. The total number of the layers in the prenatal dentine has a mode at 14 layers (Table 2).

The postnatal dentine is separated from the fetal dentine by a thin clear unstainable layer, and distinguished from the latter by the good stainability and clearer fine layers in it. Though the postnatal dentinal layers are irregular and

TABLE 2. FREQUENCY DISTRIBUTION OF FINE LAYERS IN PRENATAL DENTINE

No. of layers	Frequency	
	anterior tooth	posterior tooth
12	—	1
13	1	1
14	3	3
15	—	2

the counting is difficult, there are observed two kinds of accumulation cycles. The one is of long interval, which possibly corresponds to the annual growth layers of the dolphins and sperm whales studied by Ohsumi *et al.* (1963) and Kasuya (1976). These layers decrease in length and thickness in accordance with the progress of deposition, and the last layer is observed only near the apex of the pulp cavity. The number of these long cycle layers is between 4 and 7 layers on either anterior or posterior tooth where the pulp cavity is completely filled with osteodentine, clearly showing the end of the deposition at those ages (Table 1).

In the postnatal dentine, there are observed many alternation of stainability possibly reflecting the physiological changes of the shorter cycle. These layers are most conspicuous in the dentine deposited in the younger stages, and are almost indistinguishable in the 5th to 7th layers of long cycle described above. It is notable that in the anterior tooth of the whale no. 53 there are observed 31 small layers in the 3 long cycle layers, and 22 small layers in the 2 long cycle layers of the anterior tooth of whale no. 55 (Pl. II).

Cemental growth layers

There are observed two kinds of cycles in the alternation of the stainability of cemental groundsubstance, as in the case of dentinal layers. The one is of longer interval and the other the shorter. In other words, the stainable and unstainable layers of the long cycle are, usually, composed of several short cycles, and the cyclic change of the stainbility of these short cycle layers constitutes the long cycle (Pls. II and III). The cementocytes are diffusedly distributed at all the part of the cementum, and there is detected no relationship between its arrangement and the stainability of the cemental groundsubstance.

As the deposition of the cementum is restricted, after the eruption, to the proximal part of the tooth, the count of the cemental layers must be made for the correct age determination on the area connecting the lateral margin of the fetal den-

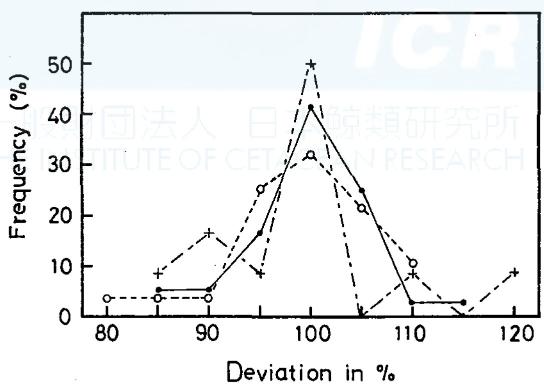

Fig. 2. The variation of the counts of long cycle cemental layers. Closed circle and solid line indicate the anterior tooth, open circle and dotted line the posterior tooth, and cross mark and chain the ratio of the number of layers in posterior tooth to that in anterior tooth of the same animal.

tine and the external margin where the layer of cementoblasts is present. In the present study, the cementoblasts were still observable on the section prepared from the tooth preserved for many years in dry condition.

The number of the long cycle cemental layers shown in Table 1 was counted on the area corresponding to " C " in Fig. 1, where the cemental deposition is most rapid and the two kinds of cycles are most clearly recorded. Usually three counts were made independently and a value at their middle was taken as the number of the cycles. The fluctuation of other two counts expressed by the percentage of the central value are shown in Fig. 2. It is usually within the range of 15% in either case of anterior or posterior tooth. The diversity between the anterior and posterior teeth of a same whale was expressed by the ratio of the two central values. Most of the difference is also found within the range of 15%. However, as the reading of the layers in the posterior tooth is difficult, its data is used only when the anterior tooth is not available.

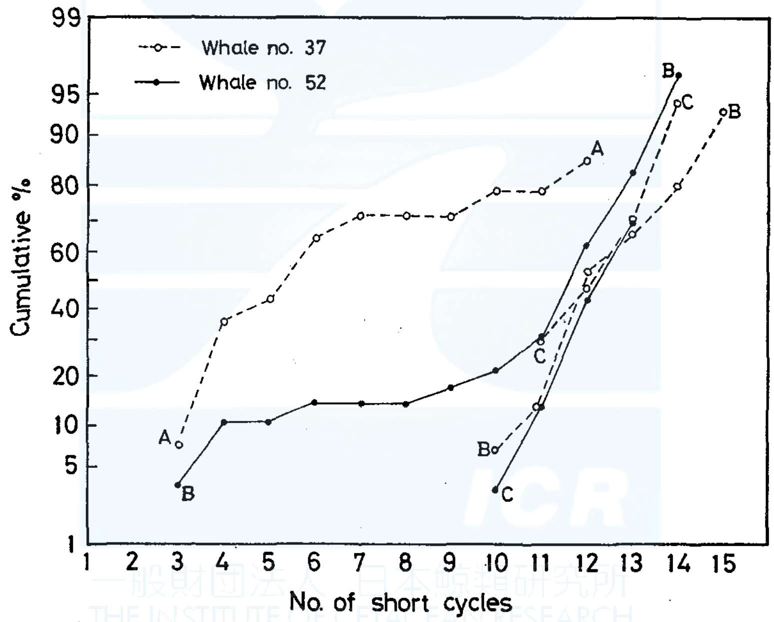

Fig. 3. Probability plot of the frequency distribution of the number of short cycles in a long cycle cemental layer. Alphabets indicate the position shown in Fig. 1.

The short cycle alternation of the stainability of cementum of the anterior tooth is analysed below. Fig. 3 shows the probability plot of the frequency of the number of fine layers in one long cemental cycle. If the number of the fine layers is normally distributed, the cumulative frequencies plotted in this way lie on a straight line. It seems that the points corresponding to 10 or more short cycles come on a straight line and considered to be normally distributed. However, the frequency of the long cycle layers which contain 9 or less fine layers is not normally distributed and the abundance of such long cycle layers decreases from the distal portion to the base of the tooth. This may suggest the next two possibilities, one is that the short cycle is not fully recorded nor distinguished on the distal part of the tooth where the deposition of the cementum becomes slower at earlier age, the second is that the distinction of long and short cycles is not correctly done at the distal part of the tooth.

Fig. 4 will solve the above question. In this figure, the numbers of short cycles in one long cycle are arranged in the order of their deposition. As the first and

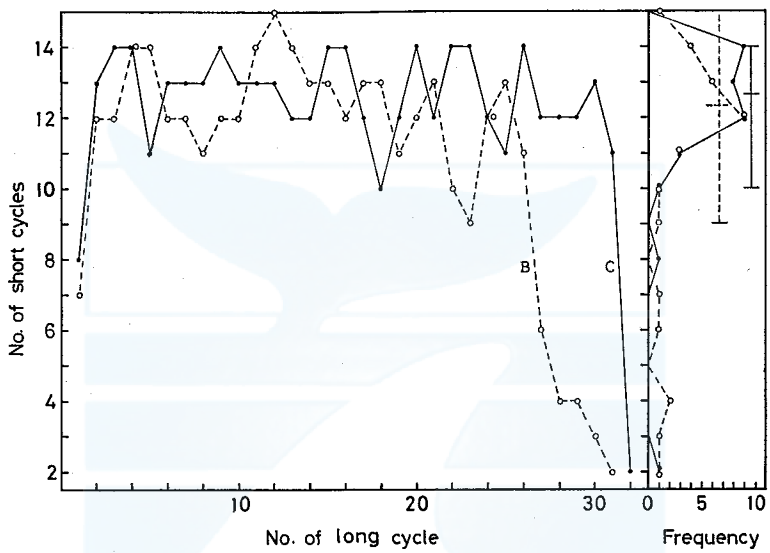

Fig. 4. Age and locality difference of the number of short cycles in a long cycle cemental layer, whale no. 52. Alphabets indicate the position shown in Fig. 1.

TABLE 3. FREQUENCY DISTRIBUTION OF NUMBER OF

Whale no.		55	53	37	49	52	60
Sex		♀	♂	♂	♂	♂	♀
No. long cycles present		1.8	2.4	17	21	30	37
No. long cycles checked		1	2	16	19	30	16
No. short cycles	9	—	—	—	—	—	—
	10	—	—	—	1	1	—
	11	—	1	4	—	3	3
	12	1	—	3	8	9	4
	13	—	1	4	5	8	7
	14	—	—	4	2	9	—
	15	—	—	1	2	—	2
	16	—	—	—	—	—	—
	17	—	—	—	1	—	—
	mean	12.0	12.0	12.7	13.0	12.7	12.6
Mean days in a short cycle[2]		30.4	30.4	28.8	28.2	28.7	28.9

[1] Mean of the 13 mean values. [2] 365 days are assumed for long cycle.

the last layers are incomplete, they are not adequate for the present discussion. The disagreement of one layer between the number of long cycles distinguished at distal area (B) and proximal area (C) is within the reasonable range of the error. Then Fig. 4 indicates that in the proximal portion of the tooth, about 10 to 14 short cycles are distinguished in every long cycle cemental layers, and that the same number of cycles are present in the distal portion only up to the age of 22 long cemental cycles. After this age the number of short cycles observed in the distal portion rapidly decreases. This was confirmed by the direct tracing of some long cycle layers, in which higher number of short cycles are observed in the proximal portion but only lower number in the distal portion. The thinner section, about 20 μm, of the latter part could not increase the number of observable short cycles. Accordingly, it will be safe to conclude that, after a certain age, the deposition of cementum becomes slower at the distal area of the tooth and the alternation of the stainability of short cycle is not fully recorded. This change will progress towards the proximal portion in accordance with the progress of the eruption of tooth. This is supported also by the fact that the number of long cycle layers where the complete number of short cycles are clearly recorded is very few on the posterior tooth. As the cemental layers are thin on the posterior tooth, the growth must be slower than the anterior tooth.

In order to estimate the relative length of the accumulation cycles of long and short cycle layers, the number of short cycles was counted on several contiguous long cycle layers at the selected position of 13 anterior teeth. As shown in Table 3, the fluctuation of the number of short cycles in one long cycle layer is wide. This is partially because the alternation of the stainability of long cycle is gradual and the distinction of each long cycle layer is not very definite. Accordingly, if one long cycle layer contains a relatively small number of short cycles the next long cycle layer often gives the higher count, and the reliability of the mean value in Table 3 might be higher than that expected from the fluctuation. The range of

SHORT CYCLES IN A LONG CEMENTAL CYCLE OF *B. BAIRDII*

20	41	58	40	57	50	51	Total	
♂	♂	♂	♂	♂	♂	♂	—	—
41	47	50	57	58	67	71	—	—
7	7	21	11	13	15	11	169	100%
—	—	—	—	—	—	—	—	—
1	1	4	—	—	—	—	8	4.7
1	1	3	5	3	4	—	28	16.6
1	2	4	3	3	7	2	47	27.8
—	3	6	2	5	3	4	43	25.4
4	—	4	1	2	1	4	31	18.7
—	—	—	—	—	—	1	6	3.5
—	—	—	—	—	—	—	—	0.0
—	—	—	—	—	—	—	1	0.6
12.7	12.0	12.1	11.9	12.5	12.1	13.4	12.1	12.4[1]
28.7	30.4	30.1	30.6	29.3	30.2	27.3	30.1	29.4[1]

the mean values is between 11.9 and 13.4 short cycles per one long cycle, and there is detected a significant difference of the mean values between some of the individuals as indicated in Fig. 5 and dealt with in the next section. The mean for the 13 whales is 12.4 short cycles per a long cemental cycle.

The number of short cycles constituting one stainable layer of long cycle was counted in 15 anterior teeth with from 5 to 10 long cycle layers each, and shown in Fig. 6. The mean counts per long cycle layer of each individual lie between 5.0 and 6.9 cycles, and the mean number of the short cycles calculated for all of the 86 data is 5.86 cycles. This result indicates that the stainable and unstainable layer of the long cycle represent approximately the same length of time, but only if each layer of short cycle represents equal time periods.

The age when the deposition of full number of short cycle layers (≧10 layers) ceases in the cementum of anterior teeth is estimated from the direct observation of

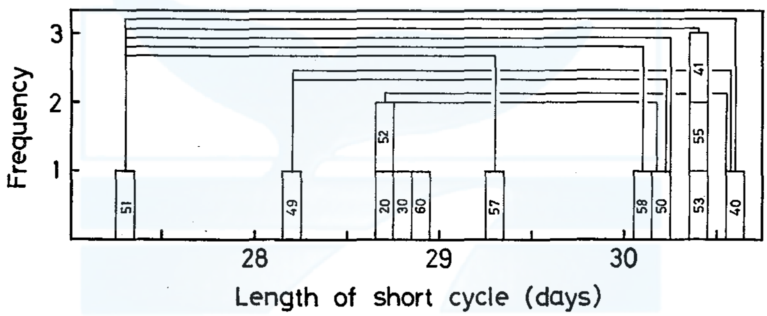

Fig. 5. Individual variation of the mean length of short cemental cycles. Numerals in the squares indicate the whale number, and the line the combination where the difference is statistically significant ($p<0.05$).

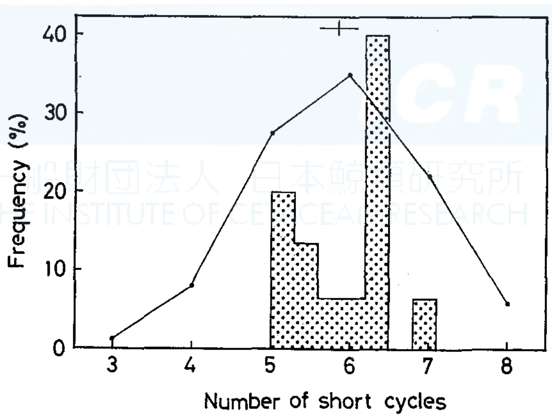

Fig. 6. Variation of the number of short cycles in a long cycle stainable layer in the cementum. Solid line and closed circle indicate the frequency, and dotted area the distribution of the mean values of each animal. Mean and the range of 2 standard errors are indicated at the top.

the teeth (Table 1). The youngest age when the short cycle layers deposition ceases is 39 long cycle layers, and the cumulative frequency of such animals increases with the age. The oldest animal found to be still forming the full number of the short cycle cemental layers is 57 long cycle layers and the cumulative frequency increases in the younger age. The two cumulative frequencies become equal at the age of 49.5 long cycle layers, which is the mean age at the cessation of the deposition of complete number of short cycle cemental layers.

Seasonal alternation of the layers

The condition of the last cemental layer, concerning the long cycle, was analysed in relation to the date of the catch. As shown in Tables 1 and 4, there are observed two kinds of layer states at equal abundance in August. One is in the process of forming the unstainable layer on the outer margin and the other stainable layer. The thickness of the former layer is large and the number of short cycles in it is 7 cycles in 2 countable cases. Whereas the thickness of the latter layer is thin and the number of short cycles in it is only 1 to 3 cycles in August. All the

TABLE 4. SEASONAL CHANGE OF THE CONDITION OF THE LAST CEMENTAL LAYER[1]

Month	Unstainable	Stainable		Total
	wide	thin	wide	
Aug.	5	5	1	11
Sep.	—	2	1	3
Oct.	—	1	1	2
Nov.	—	—	2	2

[1] concerning the long cycle

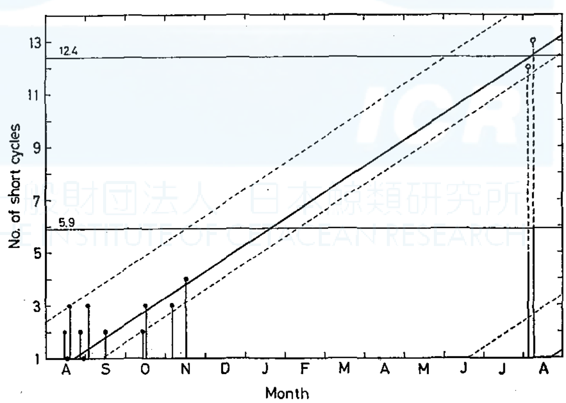

Fig. 7. Seasonal variation of the number of short cycles in the last incomplete long cycle cemental layer. Closed circle and solid line indicate the stainable long cycle layer, and open circle and dotted line the unstainable. Mean number of short cycles in one long cycle and that in one long cycle stainable layer are indicated. For further explanations see text.

seven whales killed after August were depositing the staniable layer of long cycle, and the thickness seems to increase with the progress of the season. It is safely concluded, from these informations, that the alternation of the layer from the unstainable to the stainable, occurrs, in the average, in August.

As the present sample is restricted to 4 months, it is impossible to detect the season when the deposition of the stainable layer of the long cycle ceases and that of unstainable layer starts. However, the analysis of the seasonal increment of the short cycle layer gives a suggestion for it. In Fig. 7, the number of short cycle layers in the last incomplete long cycle layer is plotted against the date of death. The two whales, nos. 36 and 37, which were accumulating the unstainable long cycle layer in August, are extended forward by 12 months and the number of short cycles in the preceding stainable long cycle layer was added. Then the linear regression was calculated by the least squares for the 8 whales, excluding the 5 whales killed in August, that had recently started the deposition of the stainable layer. The inclusion of these whales will cause a bias toward the higher number of short cycles, because half of the whales are still accumulating the unstainable long cycle layer in August. The regression is shown by

$$y = 0.03184x + 0.58$$

where x indicates the days from the first of August and y the number of short cycles accumulated since the start of the last stainable long cycle layer. It is, in a strict sense, incorrect to project the two whales for 12 months, because the accumulation rate of the long cycle is not proved to be 12 months. However the annual accumulation of the long cycle is considered to be correct based on the following reasons.

1. The gradient of the regression fits to the data of September and November, and other gradients assumed for the cycles shorter than one year do not.
2. If the length of the cycle longer than 1 year is assumed, there must be observed more varieties in the condition of cemental layers being accumulated in August and September.

Above regression indicates the accumulation of one short cycle in 31.4 days, and 12.4 short cycles, the mean number in one long cycle, in 389 days. This is sufficiently within the range of error for the conclusion of the annual formation of the long cycle cemental layers. The alternation from the stainable long cycle layer to the unstainable seems to occur in January. In other words, the long cycle stainable layer is formed in the season when the length of the daytime decreases, and the unstainable in the opposite season. This seasonal alternation is similar to that of the spotted dolphin studied by Kasuya (1976) except for the slightly earlier change in *B. bairdii*.

When the annual cycle is assumed for the long cemental cycle, the mean lengths of short cemental cycle of 13 whales come in the range of 27.3 to 30.6 days (Table 2). As shown in Fig. 5, the difference of the mean length of the cycle is significant between some animals ($p<0.05$), and there are expected the presence of 4 modes at 27, 28, 29, and 30 or 31 days. However it will be safe to retain the definite conclusion on this problem until the study is made on more animals, because the individual variation in the readability of the short cycle layer may influence the result.

In the natural environment, such a cycles which may cause the 29 or 30 days cycle of the cemental deposition seems to be the lunar cycle. For the check of this problem, the comparison between the state of the outermost cementum and the lunar cycle of the day of catch was made on selected 13 animals using the thinly prepared section (10 to 15 μm). However it gave a negative result. The stainable or unstainable layer of short cycle is considered to be formed at any period of a lunar cycle. Though more study is needed on this problem, it is probable that the short cycle is not a direct reflection of the environmental change, but a cycle hereditarily decided individual specific cycle just as the menstrual cycle of some of the female primates. This hypothesis can support the presence of the individual variation in the length of short cycle.

DISCUSSION AND CONCLUSION

In the present study no tooth of fetus or of newborn calf was studied. This obstructed the conclusion on the start of the deposition of cementum and on the relative rate of the formation of layers in dentine and cementum. However, Omura *et al.* (1955) studied the anatomy of the tooth of 9 feet, 2.7 m, fetus which had no cemental layer on it. The observation on the cementum of postnatal individuals showed that there is no clear layer such as neonatal line observed in dentine, and that the numbers of short and long cycles in cementum and postnatal dentine are almost same in the anterior tooth of young whales, nos. 53 and 55. In case of the dolphins, *Stenella attenuata* and *S. coeruleoalba*, the cementum is lacking on the tooth of fetal or newborn animals on which no postnatal dentine is deposited (Kasuya 1976, Kasuya unpublished), and it was considered that the cementum is laid down soon after the birth (Kasuya 1976). Accordingly I conclude that the deposition of cemental layer will start in *B. bairdii* soon after the birth as in the case of other odontoceti, and that the accumulation cycle of dentinal layers is fundamentally the same as that of cemental layers except for the earlier cessation of the accumulation in the former tissue. In order to estimate the age of the young animals of the species, it will be accurate to count both the long cycle layers (annual) and the short cycle layers (about 29.4 days) in dentine and cementum. However it is practical, in case of animals older than 3 years of age, to count the annual cemental layers. The age of the oldest animal thus estimated is 71 years, and seems to be reasonable compared with the same figure of the female sperm whale 64 years (Ohsumi *et al.* 1963).

The present study suggests that the short cycle layering in the postnatal dentine and cementum is probably caused by a genetic physiological cycle of about 29.4 days in the average. However, the effect of the lunar cycle is still left to be studied. The long cycle layer is formed by the enhancement of some of the short cycle layers, which seems to be caused by the annual cycle of the physiological condition possibly relating to some environmental changes. As the cause of the formation of the layers in the prenatal dentine, both the genetic physiological cycle (29.4 days in the average) of the fetus and of the mother can be expected. If the both factors work at the same intensity and the length of the cycle of the mother and of the fetus is equal, all the prenatal dentinal layers can be obscure by the complete masking of the opposite phases or can be clear by the complete or partial overlapping of the same phase. However, if the lengths of the cycle is not equal, the complete coincidence occurs once in the 27 to 31 cycles and the nearby several layers will be seen clear. Among the present materials, the prenatal dentinal layers of the whale no. 4 are almost completely obscure, in the whale no. 40 so many as 12 layers are clear, and other 11 individuals had 3 to 7 clear layers in the prenatal dentine. These facts can be explained by the above hypothesis, if the length of the gestation of the species is about 17 months as suspected from the fetal growth rate in later part of this section. However, it is also possible to explain the presence of the clear and obscure layers in the prenatal dentine solely by the strong effect of the mothers physiological changes of the short and long cycles, because the layers in the prenatal dentine formed in the season when the unstainable long cycle layer is deposited in the mother can be faint. Though the conclusion on the above problem must be left for the future study and the counting is not fully reliable at present, it will be possible to expect that the length of the cycle of the prenatal dentinal layering is nearly same with that of the short cycle layers in the postnatal dentine and cementum.

Omura *et al.* (1955) estimated the body length of the species at birth 15 feet (4.6 m) and the mean body length at the attainment of sexual maturity between 32 and 33 feet (7.8 and 10.1 m) for males and between 33 and 34 feet (10.1 and 10.4 m) for females. The length at the attainment of physical maturity was not estimated by them. However, there are, in the odontoceti, usually observed the coincidence of the body length and one of the modal length—if there are multiple modes that of the largest body length (for the bottlenose whale see Christensen 1973 and 1975, for the sperm whales see Clarke 1956 and Gambell 1972, and for the sppotted and striped dolphins see Kasuya 1972 and 1976 and Kasuya *et al.* 1974), and this is expected also for *B. bairdii*. The length frequencies of *B. bairdii* shown in Fig. 3 of Omura *et al.* (1955) indicates the mean length of the females at the attainment of physical maturity about 36 feet (11.0 m), and that of the males 35 feet (10.7 m). These values fit well to the age-length data in Fig. 8, and physical maturity of the species seems to be attained at an age over 20 years.

The growth curves in Fig. 8 are the von Bertalanffy growth equations calculated from the length at birth 4.6 m, asymptotic length 11.0 m (females) and 10.7 m (males), and 7.1 m the mean length of the two juvenile whales nos. 53 and 55 at the mean age of 2.1 years. The equations are shown by the following formulae

$$\text{male: } y = 10.7 \ (1-e^{-0.5620-0.2511x})$$
$$\text{female: } y = 11.0 \ (1-e^{-0.5416-0.2358x})$$

where y indicates the body length in m, and x the age in years. There is, at present, no reason to believe that the mean growth of *B. bairdii* can be exactly expressed by the von Bertallanffy equation and most of the known examples are opposite cases

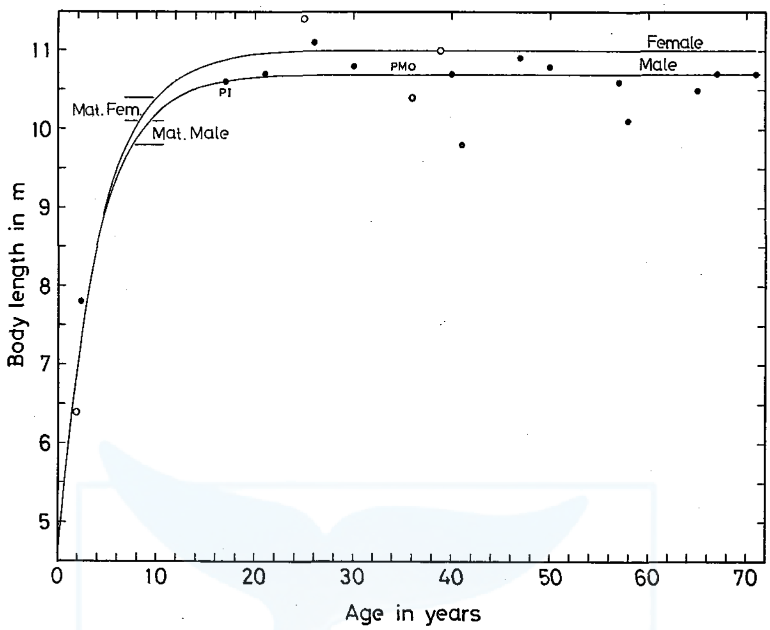

Fig. 8. Relationship between body length and the age of *B. bairdii*. Closed circle indicates male, open circle female, PM a physically mature female, and PI physically immature male. The ranges of the mean body length at the attainment of sexual maturity are cited from Omura *et al.* (1955). For the growth curves see text.

as seen in both sexes of the sperm whale (Nishiwaki *et al.* 1958), of the bottlenose whale (Christensen 1973), of the pilot whale (Sergeant 1962), of the white whale (Sergeant 1973), and of the striped and spotted dolphins (Kasuya 1976). One of the peculiar features of the growth curves of these species is the presence of a long prepubertal period when the growth is rather linear. Accordingly, if the above three points are given correctly, the von Bertalanffy growth equation gives slightly higher body length at pubertal stage. However, *B. bairdii* does not seem to have a post-pubertal growth spurt of the male often observed in polygynous marine mammals (Bryden 1972) because the asymptotic length of the male is smaller than that of the female and possible difference of social behavior is expected (Omura *et al.* 1955). Accordingly it is considered, at the present status of knowledge on this species, that the above growth equation will roughly indicate the mean growth of the species. These growth curves and the mean body length at sexual maturity presented by Omura *et al.* (1955) suggest that the species attains the sexual maturity at about 8 to 10 years of age (Fig. 8), which is close to that of the female bottlenose whale (Christensen 1973).

Omura *et al.* (1955) estimated 10 months for the length of gestation of *B. bairdii* based on the seasonal change of the fetal length. However, if the accumulation cycle of 29.4 days is assumed for the fine layers in the prenatal dentine as in the case of short cycles in postnatal dentine and cementum, the fetal period of the species after the start of deposition of fetal dentine is 29.4×14=412 days or 13.5 months.

Laws (1959) indicated that the fetal growth of odontoceti in body length is expressed by a earlier curvilinear growth and later linear growth, and that the period from the start of gestation to the x-intercept of the extended growth curve of the latter, t_0, varies between 7% and 15% of the total length of gestation (t_g) in accordance with the length of t_g. There are indicated large between species variation of the length of gestation and the fetal growth rate at the period of the linear growth (Laws 1959, Frazer and Huggett 1973), and there is observed a general tendency that the odontoceti species with large neonatal length has longer gestation period and faster fetal growth rate. In Fig. 9 the daily increment of the body length at

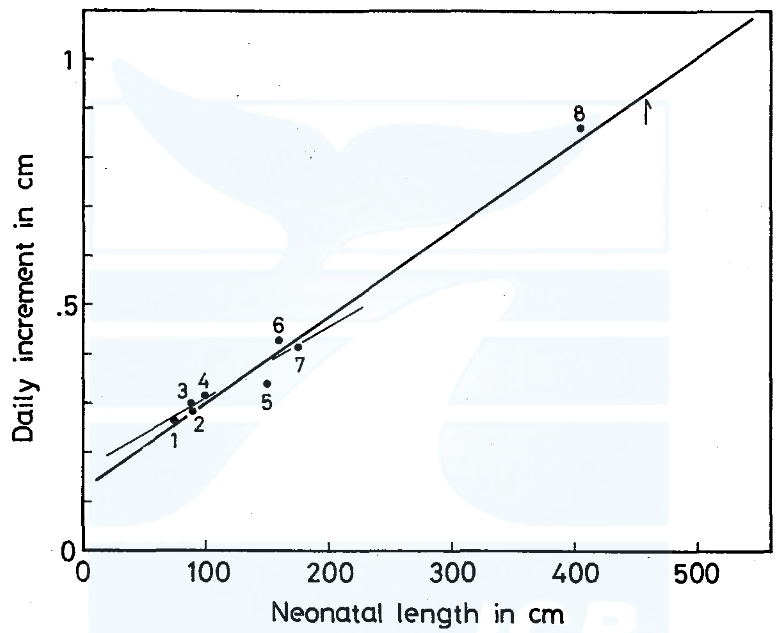

Fig. 9. Relationship between the neonatal length and the fetal growth rate in odontoceti. 1 : *Phocoena phocoena*, Laws 1959. 2 : *Tursiops truncatus*, Tabolga and Essapian 1957. 3 : *Stenella attenuata*, Kasuya *et al.* 1974. 4 : *S. coeruleoalba*, Kasuya *et al.* 1974. 5 : *Delphinapterus leucas*, Hudson Bay, Sergeant 1973. 6 : *D. leucas*, Kara and Barents Sea, Sergeant 1973. 7 : *Globicephala melaena*, Sergeant 1962. 8 : *Physeter catodon*, Ohsumi 1965. Arrow : neonatal length of *B. bairdii*, Omura *et al.* 1955. For further explanations see text.

the linear stage of the fetal growth is plotted against the mean length at birth cited from various authors. For *Tursiops truncatus* the neonatal length 90 cm and gestation length 12 months are cited from Tavolga and Essapian (1957), and t_0 was estimated as 0.135 × (gestation time)=49 days. This indicates the daily increment 90/(365−49)=0.285 cm/day. There is observed a linear relationship between the two parameters of the delphinoidea as shown below (thin solid line in Fig. 9).

$$y = 0.001462x + 0.1622$$

Where y indicates the daily increment in body length (cm) and x the mean neonatal length (cm). A set of parameters for the sperm whale seems to be slightly above the regression. If all the 8 data are dealt together, the least square regression is expressed by the following equation (thick solid line in Fig. 9).

$$y = 0.001802x + 0.1234$$

Though the former may fit better for smaller odontoceti, the latter seems to be suitable for the relationship in the general odontoceti. Using the latter equation, the length of the linear growth period, $t_g - t_0$, is expressed as follows, when x indicates the mean neonatal length in cm.

$$t_g - t_0 = x \,/\, (0.001802x + 0.1234)$$

As the neonatal length of *B. bairdii* is 15 feet or 458 cm (Omura *et al.* 1955), ($t_g - t_0$) and the growth rate of the period for the species is estimated from the above equations to be 483 days and 0.949 cm/day respectively. Accordingly, the days from the start of gestation to the x-intercept of the linear growth curve, t_0, is $(0.07 \times 483) / 0.93 = 36$ days, and the total gestation time is $36 + 483 = 519$ days or 17.0 months for *B. bairdii.*

The approximate age of the fetus of *B. bairdii* at the start of the deposition of the first dentinal layer is $519 - 412 = 107$ days of gestation. The body length at the time is $(483 - 412) \times 0.949 = 67$ cm. In case of *Globicephala macrorhynchus*, the fetal dentine starts to be laid down at about 40 cm in body length (Kasuya unpublished), the above figure is reasonable and the correctness of the estimation of the gestation length of *B. bairdii* is suggested. This fetal growth curve and the fetal length frequency reported by Omura *et al.* (1955) and Omura (1958) indicate that the mating peak of this species exists in October and November and the birth occurs from November to July with a peak in March and April. This feature is the reverse of that of the northern sperm whale (Ohsumi 1965).

The above equation indicates that the ($t_g - t_0$) of odontoceti has an asymptote of $1 / 0.001802 = 555$ days or 18.2 months. For the total asymptotic gestation time, t_0 or about 1 month shall be added to this value. Then it is considered that the gestation period of any recent odontoceti will not exceed 19 months, and that the fetal growth of the sperm whale or of the Baird's beaked whale is one of the most specialized. This specialization seems to have started from the fetal growth pattern of the small delphinids, which are less migratory staying usually in one water mass and have the mating and parturition in a same season in connection with the gestation of about one year, and attained the modification to have the mating and parturition in the opposite season of a year. This may have a relationship with the attainment of the augmentation of the body and that of the migration habit of longer distance, both of which are observed in the sperm whale and the Baird's beaked whale.

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EXPLANATION OF PLATES

PLATE I

Lingua-buccal medial ground sections of the teeth of *B. bairdii*. Photographed under transmitted light and the contrast is reversed. The outermost structure is the artefact of the resin, actual size. 1 : Fetal dentine, 2 : Postnatal dentine, 3 : Osteodentine, 4 : Cementum, 5 : Resin.

Fig. 1. Anterior tooth of the whale no. 55, 6.4 m, female, about 1.8 years old.

Fig. 2. Anterior tooth of the whale no. 53, 7.8 m, male about 2.4 years old.

Fig. 3. Anterior tooth of the whale no. 41, 10.9 m, male, 47 years old.

Fig. 4. Posterior tooth of the whale no. 53. For the explanations see Fig. 2.

PLATE II

Decalcified and stained sections of the teeth of *B. bairdii*. Scale indicates 0.1 mm.

Fig. 1. 1 : Cementum, 2 : Fetal dentine, 3 : Postnatal dentine. Bar indicates the long cycle stainable layer, and circle the short cycle stainable layer. Anterior tooth of the whale no. 55, 1.8 years old.

Fig. 2. Cementum of the same tooth. Circle indicates the short cycle stainable layer.

Fig. 3. Fetal dentine of the anterior tooth of the whale no. 53. Circle indicates short cycle stainable layer.

Fig. 4. Cemental layers of the whale no. 37, anterior tooth. Pulp side at the top. For the marks see Fig. 1.

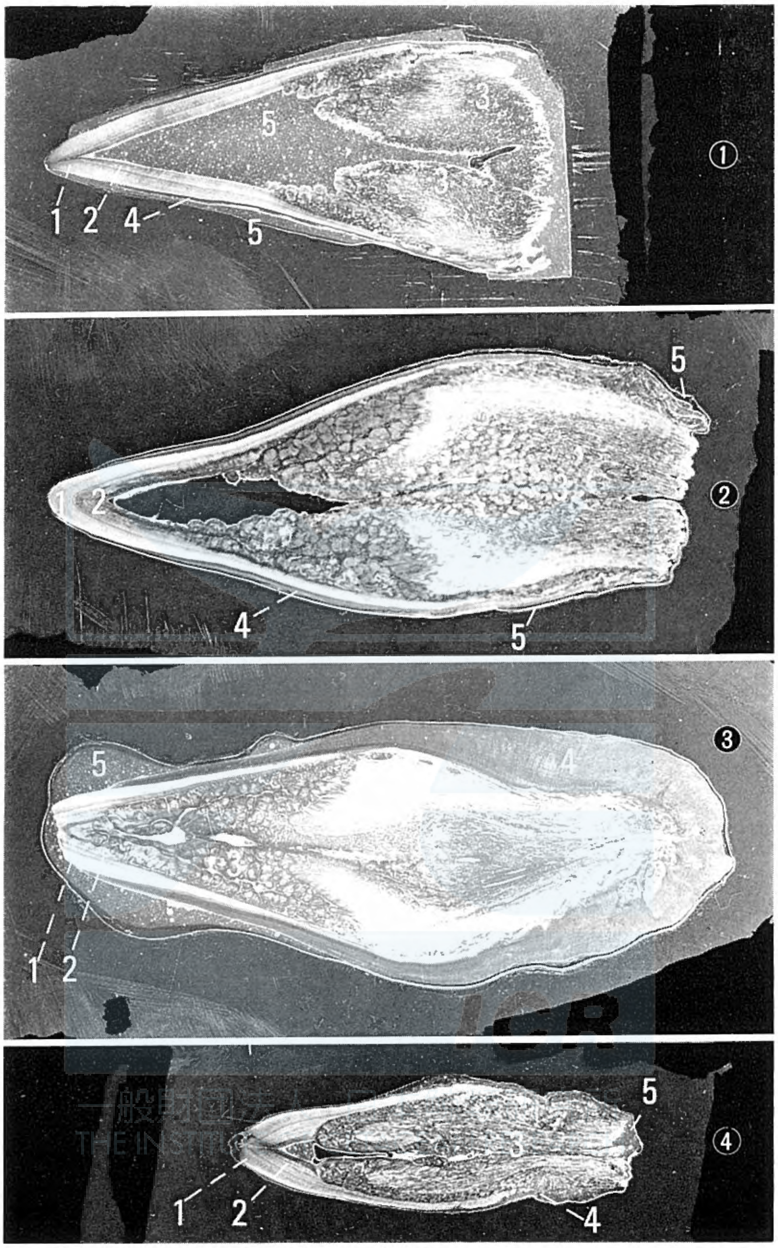
Fig. 5. Cemental layers of the whale no. 51, anterior tooth. Pulp side at the top. For the marks see Fig. 1.

PLATE III

Decalcified and stained section of the anterior tooth of *B. bairdii*, whale no. 49. Scale indicates 0.1 mm.

Fig. 1. Lower magnification, pulp side at the bottom, dentine is lost. Closed circle indicates the stainable layer of the long cycle.

Fig. 2. Higher magnification of the upper left part of Fig. 1.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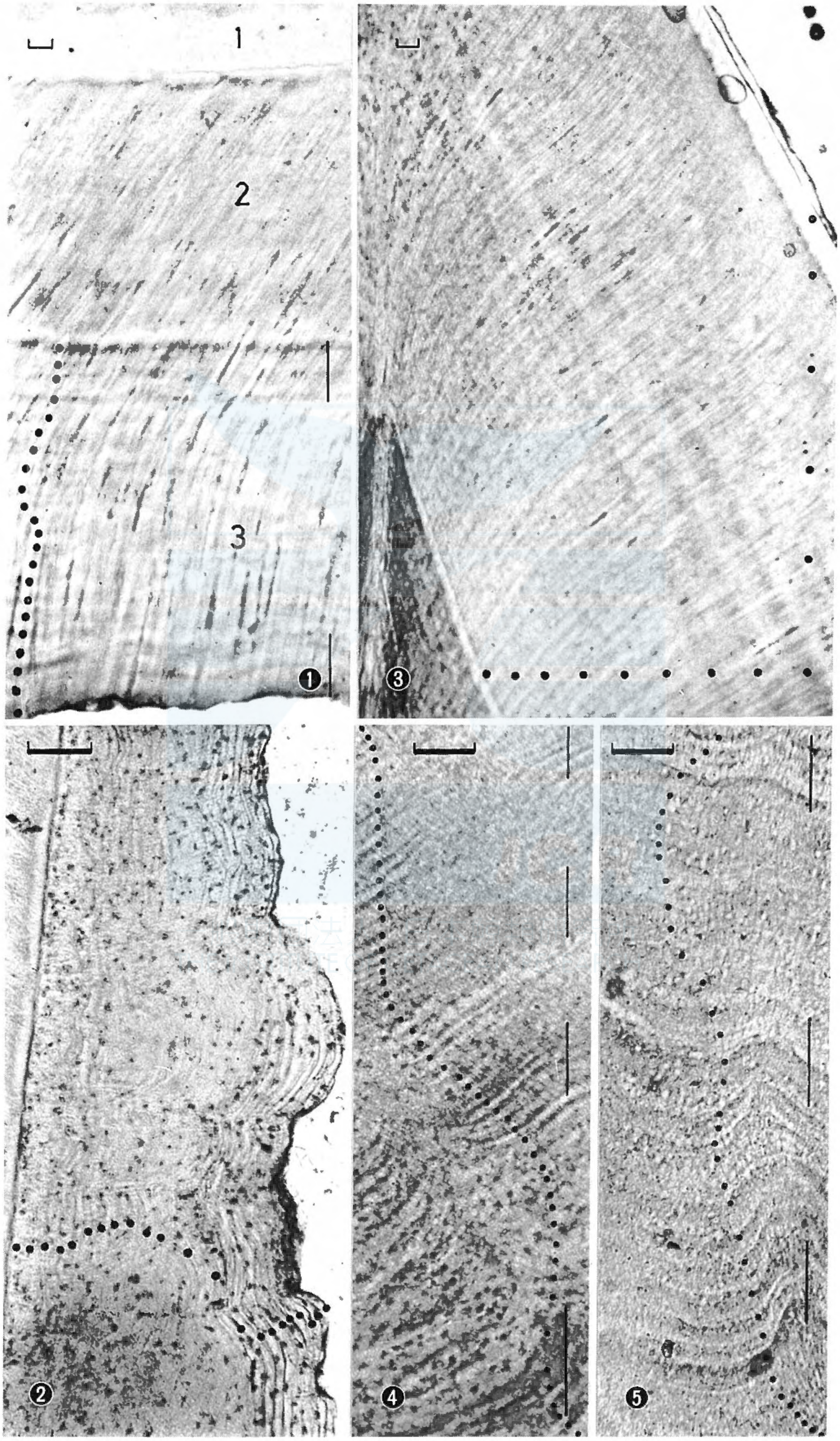
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