A Review of Studies to 1970 of Growth Layers in the Teeth of Marine Mammals

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ABSTRACT

This is a review of the discoveries of layers in teeth of marine mammals and subsequent researches that led to the widespread use of dental layers for age determination of marine mammals. Zoologists during the 19th century noted the existence of layers in marine mammal teeth, but it remained for Boschma, in 1938, to associate dental layers with age, and Chapskii, in 1941, to recognize the value of layers to wildlife research. Methods for aging and analyzing samples from marine mammal populations were developed in the early 1950s and have since been applied to most extant species of toothed marine mammals. A systematic account of the first 40 years of age determination research on 36 species of Cetacea, Pinnipedia, and Sirenia, is presented.

INTRODUCTION

> In the central blinds of bone, as they stand in their natural order, there are certain curious marks, curves, hollows, and ridges, whereby some whale-men calculate the creature's age, as the age of an oak by its circular rings. Though the certainty of this criterion is far from demonstrable, yet it has the savor of analogical probability.
>
> (Melville, 1851, p. 324)

Age composition is one of the life history parameters needed to assess the dynamics of mammalian populations. In the past, criteria such as body length, eye lens weight, degree of closure of cranial sutures, tooth wear, and the number of corpora albicantia have been used to estimate *physiological age* in many species. For marine mammals, growth layers deposited in the teeth are a more useful criterion because they indicate *chronological age*. Tooth-age determination has become standard procedure in stock assessment and management decisions for marine mammals. This paper is an account of the pioneering efforts and progress up to 1970 in estimating the age of marine mammals by counting dental layers.

HISTORICAL SUMMARY

Zoologists of the 19th century described or illustrated growth layers in teeth of marine mammals without seeming to understand their significance. Owen (1845) and Eschricht (1845, 1862) mentioned concentric layers in teeth of odontocetes. Witness also the sketches of a beaked whale tooth in Lankester's 1867 paper and the delicate lithographs of sperm whale and killer whale teeth in Van Beneden and Gervais' 1880 monograph (plates 20 and 49). The first person to correlate growth layers with age in years was Boschma, who in the late 1930s examined a longitudinal section of a sperm whale tooth.

Chapskii, in 1941, was among the first to foresee the value in wildlife research of counting layers. Through examination of cross sections of walrus premolars he estimated ages up to 27 years. The value of growth layers was recognized in 1948 by Scheffer (1950), who developed a technique for aging otariids. In the same year, Laws (1952), studying elephant seal teeth from South Georgia, developed a technique for aging phocids. In his 1952 paper, Laws stated that

> a superficial examination of material in museums indicates that the teeth of a number of other vertebrates, living and fossil, have internal rings or external ridges which, like those found in seals, may possibly be used for determining age (p. 974).

Nishiwaki and Yagi (1953) were first to use dental layers in determining age of cetaceans. After the early 1950s, research using this method of age determination increased rapidly, and by the late 1960s the method had been applied to most species of toothed sea mammals.

SYSTEMATIC ACCOUNT

(Terminology follows IWC recommendations)

Cetacea: Physeteridae

Physeter macrocephalus **(sperm whale)**

Boschma (1938) made a thorough study of the teeth of the sperm whale (our Fig. 1). He examined polished, longitudinal sections of a tooth from the Antarctic and was struck with the regular distribution of osteodentinal 'pearls' parallel to, and sandwiched between, the layers of orthodentin (p. 243). He likened the series to the 'winter-rings in the scales of fishes' and surmised that the animal must have been at least seven years old.

Nishiwaki *et al* (1958) made the first intensive study of growth zones in sperm whale teeth. In 40 whales, they found 21 to 28 teeth in each lower quadrant. In 27 of the whales, there were no visible upper teeth; in five there were from two to thirteen visible upper teeth, and in eight the presence of upper teeth was uncertain or unrecorded. The authors studied teeth numbers seven to ten in the lower series, the largest. They took teeth from 37 males and 51 females. With saw, rasp, and grindstone they made longitudinal sections and counted 'laminations' in the dentine. Laminations in the cementum were often worn or obscure, and were not

Fig. 1. "Longitudinal sections of a tooth of a sperm whale . . . showing successive masses of osteodentine" (Boschma, 1938, caption for pl. 13). Note the thick cementum, showing as a white border on the right and left sides of each section.

useful indicators of age. The authors concluded tentatively that two laminations are laid down in dentin each year. On this basis, males, with up to 48 laminations, should attain sexual maturity at age four or five years, with nine or ten laminations. Females, with up to 70 laminations, should attain sexual maturity at age four. A 'lamination' as used here is a seasonal zone, and two zones make an annual layer. Ohsumi *et al* (1963) were later to show that one layer, consisting of a dark and a light zone, is deposited annually.

In material from 24 sperm whales, Nishiwaki *et al* (1961) studied the relationship between the number of layers in mandibular bone and in teeth. Layering in bone does not present a permanent record.

As the bone tissue is resorbed from the mandibular

> canal, the laminations will disappear at different rates according to the positions on the mandible (p.502).

Layers are most persistent near the middle of the mandible, behind the symphysis. In females there is evidently a one-to-one relationship between the number of layers in bone and dentin until the period when about 13 layers have been formed. Thereafter the number in the bone remains constant at about 14, while that in the dentin continues to increase. Although the authors had jaws from only three adult males, with 14 or 15 bone layers, they stated that

> 18 laminations were observed in a mandible of an Antarctic male sperm whale, so it is probable that more laminations remain in the male than in the female (p. 503).

Berzin (1961a) reported that

> the age was determined from the teeth in 306 male and 61 female sperm whales. Assuming the annual deposition of two layers of dentin in the teeth (winter and summer), it can be calculated that the males reach sexual maturity at an age of four and a half to five years and a body length of 9.5 m to 10 m. The seventh and ninth pairs of teeth are the first to be cut, while the front and back are the last (at ten to eleven years). The pulp cavity of the first pair becomes filled in at the age of 30 to 35 years. The similarity in calcification of the two layers (winter and summer) indicates that the sperm whale does not have a prolonged winter fast . . . (p. 17279).

The oldest males and females were 28 to 32 years old, respectively.

Berzin (1961b) reported further details of his study of the 61 females. In sexually mature animals four to five years old or older he found one 'corpus luteum vestige' [corpus albicans] for each two layers of dentin. This relationship confirmed his opinion that two layers are deposited annually. In older females, however, the age estimated from tooth layers was greater than that estimated from corpora, from which he concluded that the cycle of ovulation is interrupted from time to time in older whales. The oldest specimen was 'barren', age 29 from the evidence of the ovaries and age 30-plus from the evidence of the teeth.

Omura *et al* (1962) described the skeleton of a male sperm whale 46 feet long. The animal was evidently not fully grown; the vertebral epiphyses were not completely ankylosed. The authors stated that 'the body length of male sperm whales at the attainment of physical maturity is thought to be between 52 and 53 feet' (p. 36). A longitudinal section of an upper tooth of this animal showed '32 laminae'.

Laws (1962, Fig. 8) reproduced a photograph of a thin longitudinal section of a lower tooth with '36 incremental layers' in dentin and cementum (representing about 18 years). The cementum layers show exceptionally well in this figure.

Ohsumi *et al* (1963) used maxillary teeth of the sperm whale in a study of growth layers. Most of the maxillary teeth, similar in the two sexes, remain hidden in the gum through life where they are protected from wear and damage. The authors saved one buried tooth from near the middle of an upper tooth row from each of 448 whales taken in the North Pacific in 1960–61. They also studied the teeth of eight whales which were marked in 1952–60 and recovered in 1962. In longitudinal sections the important layers were:

(1) the forming layer, next to the pulp, consisting of predentin and dentin, and

(2) the next-oldest layer, i.e. the one of the preceding season (our Fig. 2).

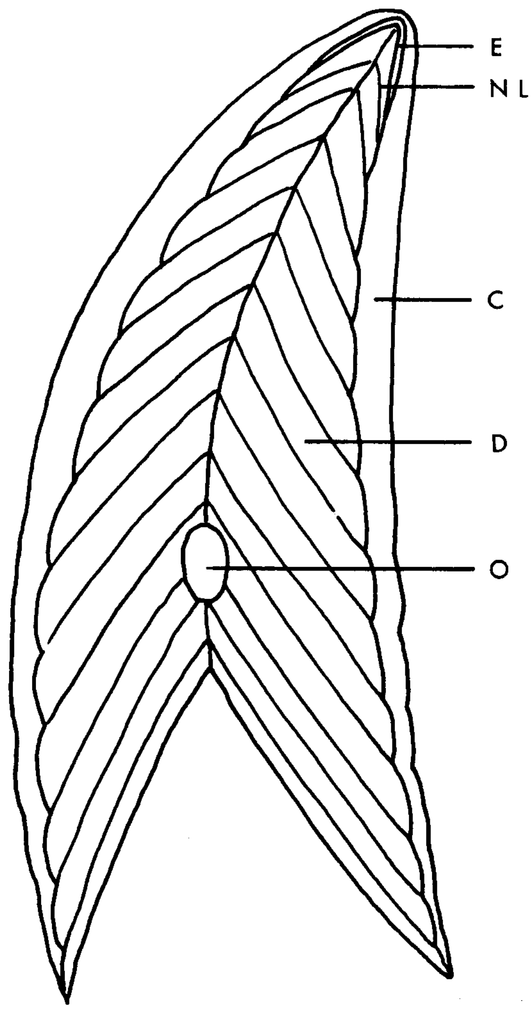

Fig. 2. Diagram of an unerupted maxillary tooth of an adult sperm whale; longitudinal section. E = enamel, representing a very small portion of the tooth, NL = neonatal line, C = cementum, D = dentine, O = osteodentin. (After Ohsumi *et al.*, 1963, Fig. 1).

A 'layer' was defined as the zone between narrow 'dark bands'.

The dark and light layers are seen by reflected light as translucent and opaque layers by transmitted light. Since the translucent layer is anisotropic in polarized light and is weakly stained by carbol-fuchsin, the authors concluded that it has a better developed crystalline structure than the thick opaque layer.

With increasing age, the thickness of the newest layer tends to decrease. Mean layer thickness in males is slightly greater than in females. In the authors' sample, the mean number of layers in males was 18.7 (5 to 35) and in females 14.4 (4 to 27).

By plotting the distance between the latest dark layer and the pulp against the date of capture, the authors deduced that the dark layer is laid down in midwinter, or January. In certain individuals, however, the layer may begin to form as early as mid-October and in others it may not be completed until April. 'The dark band [layer] . . . seems to be accumulated as the result of a good nutritious condition' (p.32).

Partly from these measurements of seasonal progression in thickness of dentin and partly from study of marked whales, the authors concluded that only one dark layer a year is deposited. A female about 37 feet long was marked at sea on 17 June 1953 and killed on 30 August 1961, when her length was verified as 35 feet. An upper tooth showed 14 layers and her ovaries two corpora albicantia. The evidence fits the assumption that she was nearly adult when marked (6 years, 6 layers) and fully adult when killed (14 years, 14 layers).

Gambell and Grzegorzewska (1967), using a sample of mandibular teeth from 659 sperm whales from South American and Antarctic waters, analyzed the rate of layer formation. They concluded that a layer containing a light and a dark band was laid down twice a year.

Cetacea: Monodontidae

***Delphinapterus leucas* (white whale)**
Yablokov (1958, pp. 41–3) figured the teeth of the white whale but did not discuss growth layers.

Sergeant (1959) examined teeth of several hundred white whales taken in the northeastern Canadian Arctic. He made longitudinal thin sections and counted up to 50 layers in the dentin. He tentatively concluded that two complete layers (four zones) are deposited yearly.

The relationship between layers and age is still unclear (Sergeant, 1962a, p. 4).

> Soviet workers, on the basis of length-frequencies, believe beluga to become white in colour and the females to mature sexually as early as the third year, males in the fourth. The discovery of growth-layers in the teeth has begun to allow accurate age determination; but the rate of deposition of the layers, and hence the absolute age which they represent, has not yet been determined.

Cetacea: Ziphiidae

***Berardius bairdii* (Baird's beaked whale)**
Omura *et al* (1955, p. 107) illustrated a longitudinal section of a tooth of a Baird's beaked whale and suggested the possibility of estimating age by growth layers (our Fig. 3).

The anterior teeth are peculiar in that the pulp cavity becomes filled with osteodentin and very little orthodentin.

> Outside the teeth a layer of cement is formed yearly, making a coating of cement from which, we think, it is possible to determine the age (p. 107).

There appear to be four layers of cementum on the tooth illustrated.

Yablokov (1958, Fig. 5) illustrated a longitudinal section of a *Berardius* tooth but did not show growth layers.

***Mesoplodon bidens* (Sowerby's beaked whale)**
Lankester (1867, pls. 5 and 6) illustrated one of the teeth of *Ziphius sowerbiensis*. He showed six or seven layers of dentin and cementum, but did not comment on the possibility of their being annual layers.

***Ziphius cavirostris* (Cuvier's beaked whale)**
Kenyon (1961) sectioned teeth of two *Ziphius cavirostris* – a 658 cm-long female having 24 to 28 growth layers and a 544 cm-long male having 13 growth layers. He thought that each layer represented a year's growth.

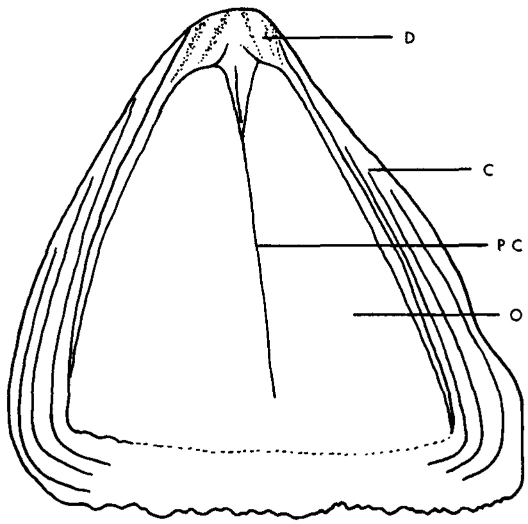

Fig. 3. Diagram of a tooth of a Baird's beaked whale about 4 years old; longitudinal section. D = dentin, C = cementum, PC = pulp canal, OD = "osteodentine". (After Omura *et al.*, 1955, Fig. 26).

***Hyperoodon planifrons* (southern bottlenose whale)**
One of the earliest illustrations of layers in odontocete teeth was presented by Eschricht (1845). There is no indication that he was aware of the significance of the layers.

Cetacea: Delphinidae

***Orcinus orca* (killer whale)**
Sergeant (1959) examined the teeth of a killer whale from eastern Canada. He stated briefly that the growth pattern was similar to that in *Globicephala* and *Tursiops.*

***Globicephala spp.* (pilot whales)**
Sergeant (1959, 1962b) made a detailed study of teeth from at least 694 long-finned pilot whales *(G. melaena)* collected in 1951–59 from Newfoundland. Both dentin and cementum are layered.

> The tooth of a pilot whale is relatively short, and a single cross-section cut in the upper part of the root will pass through all growth layers and enter the pulp cavity. A longitudinal section shows the varying thickness of each growth layer from its apex in the crown to its termination in the root, and the extent of the pulp cavity. [Ten to fifteen layers are deposited before the cavity fills.] However, transverse and longitudinal sections were found to give similar readings of numbers of dentine layers, and the more easily cut transverse sections were employed for routine ageing (1962b, p. 7).

The sequence of zone formation in the dentin is given below. Translucent dentin is said to be poorly calcified. 'This has recently been confirmed by radiography of thin tooth sections' (1962b, p.13).

1st layer. A zone of prenatal dentin followed by a narrow, translucent zone, the neonatal line, which is formed at birth, about mid-August.

2nd layer. An opaque zone passing into a translucent zone, the two representing the nursing period of nearly two years.

3rd and subsequent layers. An opaque zone passing into a translucent zone. Sergeant tentatively assumed that the opaque zone is laid down in August-January and the translucent zone in February-July. The translucent zone coincides with the six-month mating period which peaks in April-May. The largest whales had from 30 to 50 layers.

Although Sergeant had no known-age pilot whales to substantiate his conclusion, he assumed that one layer represents one year. On this basis, the mean age at sexual maturity of females is six years, or the same as the known age at maturity in captive *Tursiops* (interesting, in view of the great difference in size of the two animals; but, see Sacher, this volume).

He also examined the teeth of two short-finned pilot whales, *G. macrorhynchus,* from Florida. The teeth were

> considerably larger than those of *G. melaena* of the same body size. In section they show much thicker dentine, with early deposition of the secondary dentine. . . Growth layers appear to be more frequent than in *G. melaena* of the same length. . . The wide difference in tooth structure between these closely related species is noteworthy (1959, p.285).

Lagenorhynchus acutus **(Atlantic white-sided dolphin)**
Sergeant (1959) examined the teeth of one white-sided dolphin from the eastern coast of Canada. He found the growth pattern similar to that in *Globicephala* and *Tursiops.*

Delphinus delphis **(common dolphin)**
Sergeant (1959) examined the teeth of one common dolphin from eastern Canada and found the layered pattern similar to that in *Globicephala* and *Tursiops.*

Kleinenberg and Klevezal' (1962) estimated age in Black Sea common dolphins by comparing the number of dentinal layers in the teeth with the number of bone layers in the lower jaw and the number of corpora albicantia. They examined 33 dolphins taken in July and September 1961. They decalcified entire(?) teeth and cut longitudinal sections. Evidently one layer of bone is laid down each year and 'the number of layers in the dentine of the tooth exactly doubles the number of layers in the lower jaw plus or minus one' (translation, p. 6). Two light and two dark layers are laid down each year in the dentin. The oldest dolphin in the collection was an 11-year male with 11 layers in the jaw bone and 22 zones in the teeth. The authors concluded that most females attain sexual maturity at age two.

Tursiops truncatus **(bottlenose dolphin)**
Sergeant (1959) was fortunate in obtaining teeth of two bottlenose dolphins of known age, born in the aquarium at Marine Studios, Florida. One was six months old and the other 28½ months. He also obtained the teeth of two old males and one old female, both of unknown age, though held for known periods in the aquarium.

According to Sergeant *(op. cit.)* the growth of the root by increments of cone-shaped dentin resembles that of *Stenella.* The neonatal line, laid down shortly after birth, is clear and unstainable. Following the neonatal line are alternating zones of wide, dense, heavily staining dentin and narrow, clear, poorly staining dentin, repeated at regular and gradually decreasing intervals until the pulp cavity is reached. Two zones, or one layer, are deposited annually.

The daily rate of deposition of dentin as seen in a mid-longitudinal section was estimated to be:

in a known-age male, age 6 months	2.0 microns
in a known-age female, 28½ months	
during the first year only	1.8 microns
during the second year only	1.7 microns
in a male with 8 layers	1.0 microns
in a male with 10 layers	0.8 microns
in a female with 17 ± layers	0.2 microns

The rate of tissue deposition in the female seems to be considerably slower than in the male.

Stenella coeruleoalba **(striped dolphin)**
Nishiwaki and Yagi (1953) were pioneers in the search for age indices in the teeth of cetaceans. They sought first to learn the rate of deposition of dentin in the teeth of the striped dolphin, a species commonly taken in Japanese waters. In 1951 they injected lead acetate into four captives and released them in Mito Aquarium. The dolphins would not feed; the first one to die survived only five days and the last one fourteen days. From each dolphin they removed the 20th tooth from the posterior end of the jaw in each quadrant (our Fig. 4). They sectioned the teeth transversely

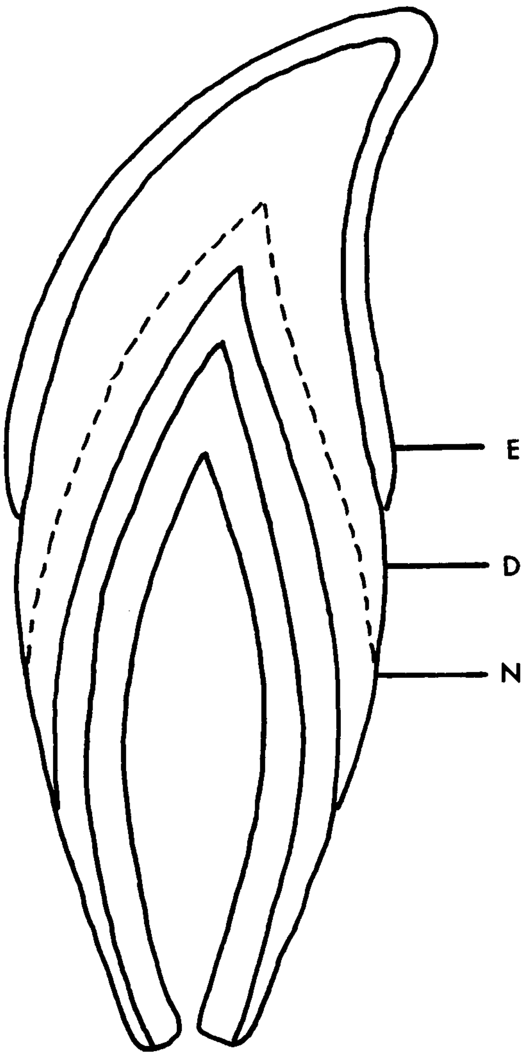

Fig. 4. Diagram of a tooth of a striped dolphin (*Stenella coeruleoalba*) 3 years old; longitudinal section. E = enamel, D = dentin, N = neonatal line (After Nishiwaki and Yagi, 1953, Fig. 3).

or longitudinally. A distinct lead line was visible in the teeth of two animals that lived seven and fourteen days.

Later, the authors examined teeth from 35 males, 55 females, and 16 fetuses collected in 1951. They concluded that the typical zones in a longitudinal section of the root of a large tooth are, in order of deposition: homogeneous fetal dentin; a neonatal line, poorly calcified and unstainable with hematoxylin; and 'striped' dentin with two to eight stripes, immediately external to the pulp cavity.

On the basis of their 1951 sample, plus 98 sets of teeth collected in December 1951 and in 1952, the authors explored further the relationship between dentinal layers and age (Nishiwaki and Yagi, 1954). The number of layers showed a close relationship to body length. The logarithm of the number of dentinal layers showed a positive linear relationship to body length; the shortest individuals had one layer and the longest individuals had eighteen layers. Well-stained zones are deposited in, or shortly before, December and again in May-June. 'Thus it seems by these facts that the deep stainable layer might be made twice a year, but we cannot say at present anything with certainty' (p. 403).

***Phocoena phocoena* (harbour porpoise)**

Sergeant (1959) examined the teeth of two harbour porpoises from eastern Canada. The growth pattern resembles that in *Globicephala* and *Tursiops.*

> In addition . . . the spade-shaped crown, typical of the group [subfamily Phocoeninae], is composed of thick, prenatal dentine and of enamel (p.285).

Pinnipedia: Otariidae

***Allodesmus kelloggi* (an extinct sea lion)**

Mitchell (1966, p. 21) counted 'more than thirteen pairs of light and dark zones' in sectioned teeth of adult male sea lions from the Temblor Formation, late middle Miocene, He saw ridges on the surface of one postcanine.

***Eumetopias jubatus* (Steller sea lion)**

Fiscus (1961) examined the right upper canines of 59 Steller sea lions taken in Alaska in 1958 and found up to 19 growth layers in males and 22 in females. He prepared longitudinal sections by the method of Wilke, Niggol and Fiscus (1958, MS).

Thorsteinson and Lensink (1962) studied another collection taken in Alaska in 1959 from 'harem bulls' only. The teeth were examined by Lensink and Fiscus; 'disagreements . . . occurred in 46% of the sample, but most involved differences of one year and were readily reconciled' (p. 356). The population had a mean age of 10.8 years (6 to > 17).

Spalding (1964) counted layers in the cementum in thin longitudinal sections of upper canines of 138 female sea lions. The first dark cemental zone is deposited in August and September in an animal about 15 months old. It is followed by a light zone, then a dark zone in late summer or fall of the second and succeeding years. He had only one known-age specimen, 16 months old.

***Zalophus californianus* (California sea lion)**

Scheffer (1950, p. 2) saw 'dubious' external growth ridges on the teeth of the California sea lion. Orr *et al* (1970) counted from one to fifteen annual zones on longitudinal sections of upper canines of 35 male sea lions from the Gulf of California.

***Otaria flavescens* (southern sea lion)**

Laws (1962) described growth layers in teeth of the southern sea lion on the basis of several canines collected in the Falkland Islands in late summer. He used longitudinal thin sections, some decalcified and stained. In his Figure 5, the zone pattern looks like a cross section of an old oak stump with numerous fine, regular layers. He suggested the possibility of lunar periodicity in feeding, with two dark and two light zones deposited each month. He measured the thickness of individual deposits and sketched a theoretical time schedule. The peak of deposition was in July (mid-winter) and the depression was in September-October, the breeding season.

***Callorhinus ursinus* (northern fur seal)**

In 1948, Scheffer (1950) examined teeth of known-age, tagged northern fur seals and found external ridges encircling the root, each ridge representing the accelerated growth of one winter-spring season. In 1950, biologists of the Pribilof seal industry standardized a technique for counting external ridges on the right upper canine tooth. They estimated age to ten years and pooled older ages as 'ten-plus'. The age composition of a fur seal population was first published by Wilke (1952, Table 2), for 451 seals taken in waters off Japan.

Wilke *et al* (1958, unpubl.) developed a better technique. They sliced each tooth longitudinally with a bandsaw, ground and polished the flat face, and counted zones in reflected light.

Kubota *et al* (1961, 1963) described development of growth zones on the upper canines (our Figs 5 and 6), as follows:

(1) At birth (e.g. in July) the root may not be visible beyond the enamel. The prenatal dentin, all or most of it within the crown, is light colored, the first postnatal dentin is darker; the light and dark zones meet at the 'neonatal line' (which is often not visible).
(2) (In summer and fall the root grows slowly.) 'Interglobular spaces' appear in the peripheral dentin, i.e. the region away from the pulp.
(3) (The growth rate accelerates in spring.) About the end of April in the life of the pelagic yearling a narrow 'transparent zone' begins to form in the dentin. It terminates on the surface of the root, at the crest of the ridge which marks the end of the seal's first year (in June or July).

Scheffer measured the apical growth on 25 known-age 3-year-old females taken at sea between 23 January and 3 October. He concluded that the ridge does not start to round off, and the summer-fall valley does not start to form, until June. The first indication of a thin shelf representing the beginning of the next ridge is formed in August.

Yagi *et al* (1963) administered lead acetate and tetracycline to a 4-year female fur seal in an aquarium. The seal lived 162 days after the first injection. Both drugs left traces in the dentin which were demonstrable by histochemical methods.

Scheffer and Kraus (1964) studied the morphology and development of seal teeth. Among their conclusions are the following:

(1) Dentin gradually fills the root canal until, at ages varying from 3 months (for small incisors) to more than 20 years (for the large upper canines of the male), the root is completely closed.

Fig. 5. Upper canine teeth of two female northern fur seals: (left) age 11, taken in mid-August; (right) age 12, taken in mid-July; longitudinal thin sections by reflected light. Numbers indicate the (translucent) dentin deposited in spring. (From Kubota *et al.*, 1963, pl. 1.)

(2) Growth layers in the upper canine of a seal held in captivity from age 3 months to 58 months were abnormal, though could be grouped into five annual series.
(3) 'Ridges on the surface of the growing root, finer than [yearly] annuli and spaced between them, are thought to originate in individual periods of intensive feeding' (p. 309).

Scheffer and Peterson (1967) continued the study of fine ridges. During the 16-week suckling period, about ten or eleven zones are laid down in the dentin of the pup, each representing one period of suckling followed by a fast. The zones are permanent.

Arctocephalus australis **(South American fur seal)**
Mansfield (1958a, p. 39) saw concentric rings in cross sections and surface ridges on canine teeth of ten South American fur seals.

> In the older specimens in which the pulp cavity was almost occluded, a . . . pattern of alternate light and dark rings of dentine was found. As in the Weddell seal a pair of these rings was assumed to represent one year of the life cycle, and the specimens were aged on this basis, the age . . . was found to agree within a year with the age determined by the number of external ridges on the teeth. These ridges are well marked, and the teeth resemble those of the Alaskan fur seal for which the method has been proven valid.

The source of the ten specimens was not given, though Mansfield wrote (in letter of 17 February 1967) that 'they most probably came from J.E. Hamilton's Falkland Islands fur seal collection in the British Museum.'

Arctocephalus pusillus **(Cape fur seal)**
Rand (1956, p. 12) found that in teeth of the Cape fur seal 'the numerous annuli showed no discontinuous pattern that

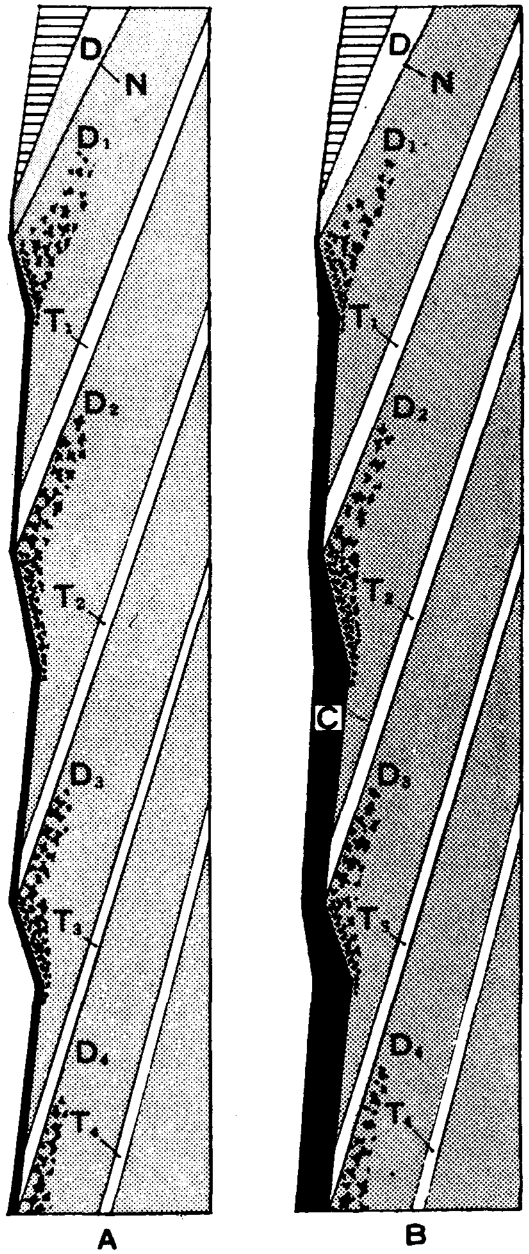

Fig. 6. Diagram of upper canine teeth of northern fur seals, (A) "young" and (B) "old"; longitudinal thin sections by transmitted light. C = cementum, D = prenatal dentin, N = neonatal line, D 1 to 4 = opaque dentin deposited in 1st to 4th years; T 1 to 4 = "transparent" [translucent] dentin deposited in 1st to 4th years. (From Kubota *et al.*, 1961, pl. 7.)

could be correlated with definite annual or other recognizable time units.'

Pinnipedia: Odobenidae

***Odobenus rosmarus* (walrus)**

It has long been known that ridges surround the root of the tusk in some old walruses, particularly old males (our Fig. 7). The ridges are partly obscured by cementum but are revealed when the cementum is chipped away or when the tusk is sectioned lengthwise. Cemental layers are also deposited on the premolars.

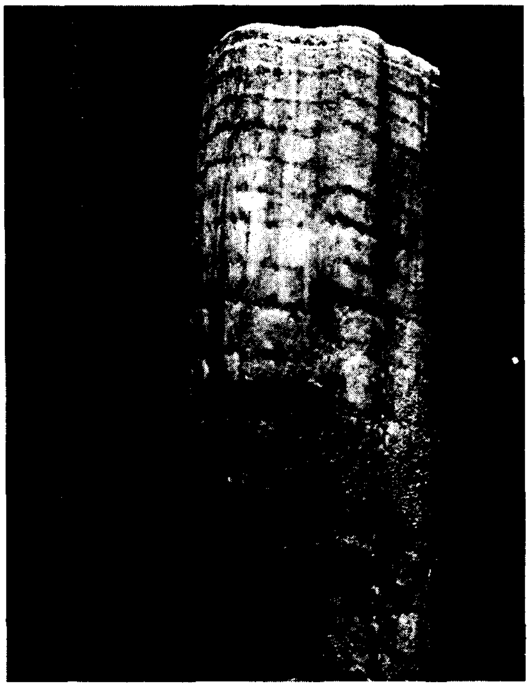

Fig. 7. Tusk of an old male Pacific walrus showing annual ridges. Date of death unknown, a subfossil from beach sands of St. Paul Island, Alaska. A very large tusk, total length along convex surface 917 mm (36.1 inches). (VBS photo 2509A.)

The pioneer work of Chapskii (1941) on walrus teeth has been mentioned. Mohr (1943, p. 259) stated that

> longitudinal and transverse sections through the teeth of walruses of known age reveal that the cemental hyperplasia takes place in the form of yearly rings, similar to the otoliths and bones of fish.

In 1952, Brooks and Fay independently undertook studies of the Pacific walrus *(O.r. divergens)* (Brooks, 1954, unpubl.; Fay, 1952, unpubl.). They focused on interpretation of the cemental layers of the premolars. Brooks concluded that one dark ring or none is deposited in the first year and two dark rings (summer and winter) in each year of life after the first. He correlated estimated age with number of cementum rings on the premolars and with tusk length. In his Figure 9, for example, he indicated that an 8-year-male with tusks one to fifteen inches long has fifteen rings.

Fay (1956, unpubl.) described criteria for each year class from newborn to age four, using length of tusk, wear of enamel on the tusk, degree of staining of the teeth, cranial and body size, observation of the adult female (presumptive mother) with the young animal, and reproductive history of the mother as revealed by autopsy. Available to him were teeth from seven Pacific walruses and nine Atlantic walruses of known age, raised in zoos. He counted the cemental layers on sections of the second upper premolar or the first lower premolar. In the Pacific walrus, two or three zones of cementum are deposited the first year, decreasing to one layer per year at time of sexual maturity. In the Atlantic walrus *(O.r. rosmarus)*, one or two layers are deposited before sexual maturity and one thereafter. In very old Pacific walruses, as many as four initial layers of cementum have disappeared through wear.

Longitudinal sections of the tusk of the Pacific walrus show up to 30 marginal ridges and indicate an age of 30-plus years. In specimens collected in May, the ridge is at the apex of the root. In specimens taken in the ensuing twelve months the zone between the ridge and the apex of the root widens progressively at a rate such that by the next May the ridge is again at the apex. Thus, the ridge is clearly an annual mark. Although the ridge count may be indicative of minimum age in years, the cemental layer count in the premolar roots is more consistent.

In the spring and summer of 1960, Samuel J. Harbo began a study of walrus in the Bering Strait and vicinity (Harbo, 1961). He collected the teeth, mainly lower canines, of 886 walruses. He standardized a method of sectioning the teeth longitudinally and of counting zones in cementum. He used the formula: two zones per year through the fifth year and one zone per year in the sixth and subsequent years; plus a factor varying from one to three years to correct for loss through attrition. He concluded that the oldest males and females were 28 and 26 years old, respectively, but according to Burns (1966, p. 5)

> . . . closure of the root apex most commonly occurs between the fifth and sixth years of life . . . it is probably not possible to determine the age of very old individuals.

Mansfield (1958b) studied 176 walruses from the northwestern Atlantic. He was able to classify calves, yearlings, and 2-year-olds, but not older animals, by body and tusk measurements. With regard to cemental layers on the premolars of the male, he stated:

> It is assumed that after the second year, one well defined layer of cementum is laid down annually, and this continues throughout the life of the animal (p.39).

He was confident that he could age males, but not all females, from counts of cementum layers on the premolars.

Pinnipedia: Phocidae

***Phoca vitulina* (harbour seal)**

Mansfield and Fisher (1960) examined an upper canine tooth of an old male harbour seal which had been held in captivity from its first summer. In thin cross sections they counted 18 to 20 cemental layers. They learned later that the seal was 19½ years old.

> There were no clearly marked dentinal layers . . . but examination of other canines from both male and female harbour seals has shown that, where dentinal layers are present, they agree in number with those in the cementum (p. 93).

Each cemental layer contains a wide opaque zone and a narrow translucent zone. The narrow zone is

> laid down in the spring and early summer and may represent a period of minimal feeding during the breeding period and the moult (p. 93).

In 1969, Michael Bigg completed a study of harbour seals from British Columbia. He wrote (1969, p. 8) that translucent layers are laid down in the cementum between late autumn and late spring, and opaque layers between late spring and late autumn.

***Phoca hispida* (ringed seal)**

McLaren (1958a) made cross sections of teeth from more than 750 ringed seals and estimated age from counts of dentin layers. The oldest seal, a male, had more than 43 layers. He validated his method by counting bands on the claws. Sections of the teeth show the following sequence:

> *Mid-July to mid-March of the following year* – translucent dentin is deposited.
>
> *Mid-March to mid-July* – opaque dentin is deposited. It becomes increasingly reflective and vacuolar in June and early July when the seals are fasting, basking on the ice, and molting.

Tikhomirov and Klevezal' (1964, Fig. 1) published a photograph of a cross section of a ringed seal tooth, as did Klevezal' (1964, Fig. 1).

***Phoca groenlandica* (harp seal)**

Fisher (1952) was first to estimate ages of harp seals by growth layers in the teeth. The oldest in a sample of 375 seals was about 28 years old. Fisher and Sergeant (1954, p.1) stated that

> because the reading of annual rings is not always exact, the totals for the ages of nine years and up are smoothed [on a graph] by fives.

And Sergeant and Fisher (1960, p. 36) noted that

> the relative strength of a year class can be detected [through tooth reading] up to five or six years; after this age, errors in age determination ... obscure the real fluctuations in year-class strength.

According to Fisher (1954) the zones of dentin are laid down as follows. The *translucent* zone is laid down in November-March during the period of active feeding on the southbound migration and during the breeding season. The *opaque* zone starts to form during the molt (April-May) and continues to form during the northward migration and summer wandering in the Arctic (June-September).

Rasmussen (1957) published a photograph of a thin cross section of a 7-year-old harp seal tooth. He described the formation of 'white' zones laid down in feeding periods, mainly during summer, and 'dark hyaline' zones laid down in fasting periods such as molting and breeding periods in early spring.

> As the animal becomes older, the pulp cavity becomes filled with dentine, and in old animals the cavity is completely closed. This sets a limit on how far we can trace the age of an animal. With reasonable accuracy, we can read ages of 15 to 17 years, but we have specimens showing clear readings up to 27 years (p.52).

***Phoca fasciata* (ribbon seal)**

Tikhomirov and Klevezal' (1964, Figs. 2 and 5) illustrated cross sections of ribbon seal teeth. They counted cemental layers but concluded (p. 19) that age determination from claws is easier and more practical, because these do not wear appreciably with age.

Klevezal' (1964) was interested in determining the age of sexual maturity in the ribbon seal. From counts of dentinal layers in cross sections of canines she showed that maturity in both sexes is reached by the end of the third or fourth year.

***Erignathus barbatus* (bearded seal)**

Allen (1880, pp. 654–655) described the dentition of the bearded seal as

> teeth small, molars spaced, slightly implanted, early becoming defective by attrition; partly deciduous in old age, . . . Quite early in life the teeth become much worn, and in old age the crowns of the three middle molars become often wholly worn away, leaving only the fangs [roots], and even these sometimes in part disappear.

McLaren (1958b) concluded that he could not determine age from the teeth but that growth increments in claws were useful as age indicators.

Tikhomirov and Klevezal' (1964, p. 19) concluded that bone strata in the lower jaw are the best indication of age.

***Cystophora cristata* (hooded seal)**

Rasmussen (1957) made the first systematic collection of hooded seal teeth in Denmark Strait in 1954. (Sealing crews had saved the lower jaws.) A male pup in the natal 'blueback' pelage was tagged in 1951 and recaptured at age five as a 'bladdernose' in 1956. Presumably its teeth were used to calibrate the age-reading method. In a sample of at least 25 males and 22 females, the oldest male was 25 years old and the oldest female 24 years.

In his report on a sample of some 6,000 hooded seals, Rasmussen (1960) provided the following description of the canines:

> In the tooth's dentine we find alternating dark and light bands. As the seal gets older, layer after layer of white dentine is laid down round the pulp canal divided by dark layers. The pulp canal is eventually filled with dentine and in very old animals the central part will be almost completely closed. In hoods [sic] a thick layer of cement is also laid down annually on the tooth's outer surface. This layer may become very thick, especially in older animals. In this outer layer we can find closely spaced rings which in numbers agree with those we find inside the tooth itself. By counting both the inner and outer rings one can get a good check on the accuracy of age determination, especially in older animals (1960, p. 14, in translation).

A study by Øritsland of the breeding of the female hooded seal was based principally on examination of ovaries from 371 animals, all aged by dentin layers in the canine teeth (Øritsland, 1964, p. 14). The seals were collected in waters of Jan Mayen and Denmark Strait. Thirteen (or 3.5%) were described as age '21+'.

'Hansi', an adult male hooded seal, died in Tiergarten Bremerhaven in 1954 after 14 months in captivity (Mohr, 1966). Mohr photographed a thin cross section of one of Hansi's lower canines and estimated his age at 14 to 15 years. The photograph shows a very wide series of cemental layers (our Fig. 8).

***Halichoerus grypus* (gray seal)**

Hewer (1960, 1964) examined teeth, mostly lower canines, of 295 gray seals. He had known-age specimens from classes 0 to 1 year, 6 years, 12 years, and 27 years. Since the pulp canal closes in the fifth or sixth year, he counted both dentinal and cemental layers up to about the fifth year, then cemental layers only (our Fig. 9).

Deposition of cementum in the gray seal is complex. Cementum first appears on the root of the lower canine

> about three to four months after birth, somewhat unevenly in two bands on the root. Afterwards, these bands coalesce (*op. cit.*, 1960, p. 960).

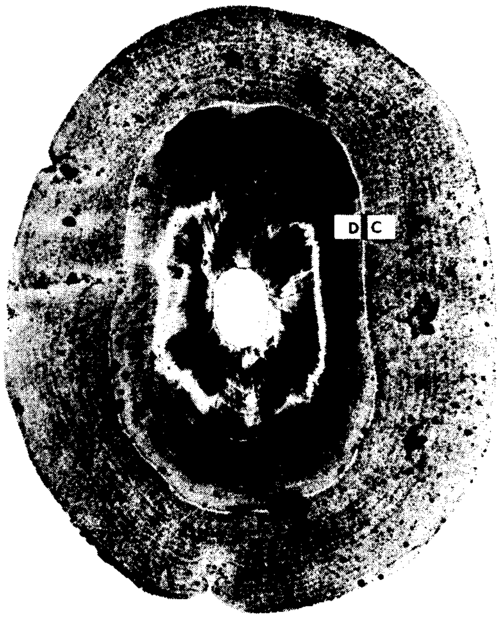

Fig. 8. Lower canine of a hooded seal, male 14–15 years old; thin cross section. DC = junction of dentin with the very thick cementum. (After Mohr, 1966, Fig. 2.)

For estimation purposes, October is assumed to be the mean month of birth; thus the first cementum appears in January or February.

The next layer of cementum is accumulated in September when the seal completes it's first year of growth. All annual layers can be identified by the more translucent appearance toward the outer (alveolar) edge. In the second year, cementum spreads rapidly over the apex of the root, stopping all further growth of the dentin toward the apex, but deposition of dentin continues as a series of decreasingly smaller cones for another four or five years.

***Monachus schauinslandi* (Hawaiian monk seal)**

Kenyon and Fiscus (1963) examined the right upper canines of two adult Hawaiian monk seals, a male estimated at 20 years old and a female at 11. There were no surface ridges; the pulp canals were closed; on longitudinal sections the dentin showed [annual] layers and layered cementum. The cementum on the male tooth was up to 7 mm thick and on the female tooth up to 3 mm. The layers of cementum did not decrease in thickness with advancing age.

The monk seal does not migrate.

> It may be concluded that . . . fasting, probably during molt, causes visible annular [i.e. annual] interruptions in the deposition of cementum and dentin which may be used as an indication of age . . . The pulp canal of the canines appeared to have filled completely at four or five years as indicated by visible layers in the dentin (p. 281).

***Mirounga leonina* (southern elephant seal)**

Laws proposed a new method of age determination for

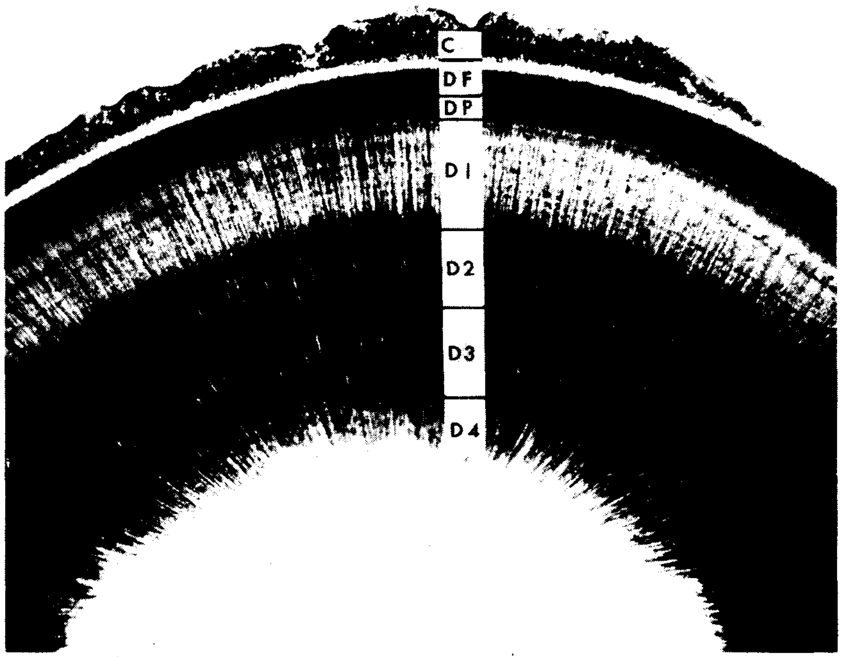

Fig. 9. Lower canine tooth of a gray seal, age 3 years, 8 months; thin cross section by transmitted light. C = cementum (separated from dentin by a clear artifact), DF = fetal dentin, DP = pup dentin, D 1 to 4 = dentin of 1st to 4th years. (After Hewer, 1964, pl. 1, Fig. 3.)

mammals largely from studies of elephant seals at the South Orkneys (1952, 1953a). He continued to study elephant seal teeth, with a special interest in microstructure and its metabolic implications (1953b, 1959, 1960, 1962).

> The canine teeth . . . grow continuously throughout life; the pulp cavity remains open and attrition is negligible (1953a, p. 3).

At the level of the alveolar aperture all annual layers are exposed.

The permanent canines erupt at an average age of eight days (lower) and ten days (upper). Inside the fetal dentin, a sharp neonatal line serves as a starting mark for counting annual layers. It is followed by a variable series of zones laid down through adolescence to sexual maturity. Maturity may occur at the end of the third year in males and the second year in females. In the fourth and later years, four zones a year are laid down rather consistently in both sexes. These include two zones of translucent dentin ('columnar') alternating with two zones of opaque ('marbled').

Although Laws did not have known-age seals older than pups, he proved indirectly that the four-zone group must represent one year's increment (1953a, p. 6). The first recaptures of known-age elephant seals, 18 branded individuals, were reported by Carrick and Ingham (1960, p. 329).

Laws (1953a, p.4; 1960, p.10) suggested the following development of hard and soft layers of dentin:

(1) a hard zone is deposited in the spring breeding period (mid-September to mid-November);
(2) a soft zone is deposited in the early summer feeding period (November and December);
(3) a hard zone is deposited in the late summer and autumn molting period (January to early May); and
(4) a soft zone is deposited in the winter feeding period (mid-May to mid-September).

Carrick and Ingham (1962) gave a detailed description, with 69 photographs and 2 diagrams, of canine tooth structure in the elephant seal. They used known-age animals, 20 males and 17 females branded as pups on Macquarie Island in 1951–59 and killed in 1956, 1957, 1959, and 1960. The oldest was 8 years, 3 months old. All four canines were saved and were treated by various methods designed to reveal dentinal layers to best advantage without the labor of cutting thin sections (our Fig. 10).

The findings of Carrick and Ingham differed from those of Laws for certain reasons:

(1) at South Georgia, where Laws worked, the male and female seals mature sexually at two and four years, respectively (Laws, 1960, p. 472; at Macquarie they mature at three to five and six years, respectively.
(2) Carrick and Ingham had the advantage of known-age specimens, many of them representing the younger ages. Furthermore, some of the marked animals had been seen and identified in the wild before death, and had been reported as 'ashore in May', 'pre-molt in February', or otherwise.
(3) Carrick and Ingham sectioned the teeth at the top of the pulp cavity where the zones are widest, and they stained the sections; both procedures contributed to a clearer picture of the zones. Carrick and Ingham concluded that 'the pattern of calcification is less simple than Laws suggests' (1962, p.111).

Lobodon carcinophagus **(crabeater seal)**

Laws, (1953a, Fig. 4) illustrated a cross section of a lower canine of a male crabeater seal estimated to be six years old. Later, he estimated the ages of 76 crabeaters, some found dead after an epizootic. The oldest were 19 years old (Laws and Taylor, 1957). Laws studied the same sample again (1958) in greater detail. The sequence of zone formation is approximately as follows:

(1) Thick fetal dentin laid down in the first six weeks of pregnancy.
(2) A sharp neonatal ring, about September.
(3) A (presumed) weaning ring five or six weeks later.
(4) A series of fine, irregular, post-weaning layers becoming vacuolated toward the end of the first year, in September or October (spring). The vacuolated zone is white or gray by reflected light and is the most useful zone for indicating age, for it appears each year in spring.

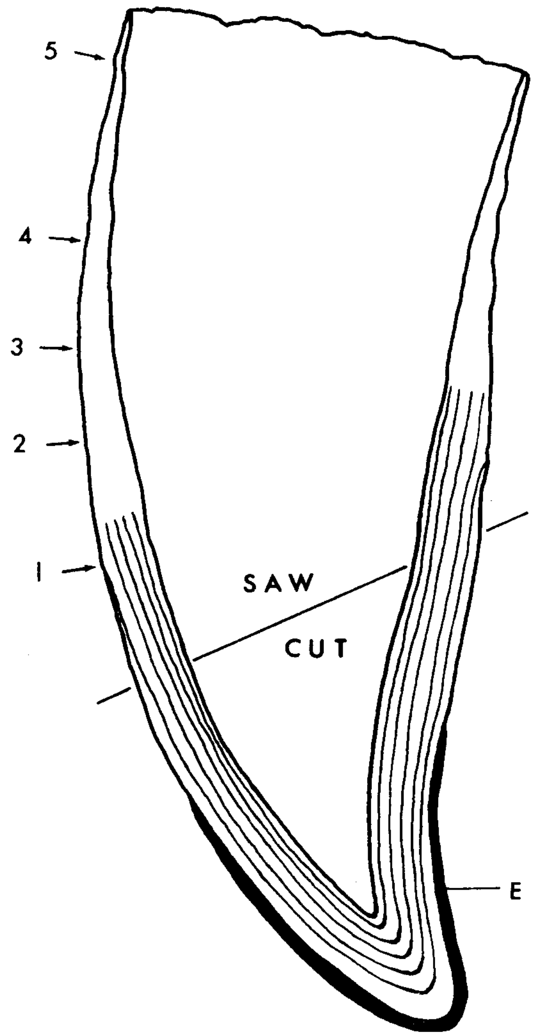

Fig. 10. Lower canine of an elephant seal showing where a typical saw cut is made at the level of the gum to obtain the crown and a portion of the root containing all annual layers. Longitudinal section, diagrammatic; 67-month ("6-year") male. E = enamel; arrows show approximate position of apex at birthdays 1 to 5. (After Carrick and Ingham, 1962, pl. 4.)

***Ommatophoca rossii* (Ross seal)**

Laws (1953a, p. 9) saw concentric rings on cross sections of a Ross seal tooth.

***Hydrurga leptonyx* (leopard seal)**

Laws (1952) saw concentric rings on cross sections of leopard seal teeth and subsequently (1953a, Fig. 4b) illustrated a section from a canine of a 6-year-old female.

Paulian (1955) counted 'stries d'accroissement' on teeth of six leopard seals from Kerguelen Islands. He felt certain of the ages of three males, one, two, and three years old, but less certain of the ages of three other seals about five to eight years old.

Laws (1957) estimated the ages of 39 leopard seals; the oldest was a male of 16-plus years.

***Leptonychotes weddelli* (Weddell seal)**

Laws (1952, 1953a) saw concentric rings on cross sections of teeth of the Weddell seal.

Mansfield (1958a) examined the teeth of six male and twelve female Weddell seals from the South Orkneys (our Fig. 11). He estimated the age of the oldest male at 16 years; of the oldest female at 14 years. From outside in, by reflected light, the sections show:

(1) wide, dark zone (translucent) dentin deposited in fetal and suckling life;
(2) a wide, light zone of opaque dentin assumed to represent the winter period of feeding at sea;
(3) another translucent zone, now called 'columnar' dentin, assumed to represent the summer period of breeding and molting, with irregular feeding;
(4) another opaque zone, and so on.

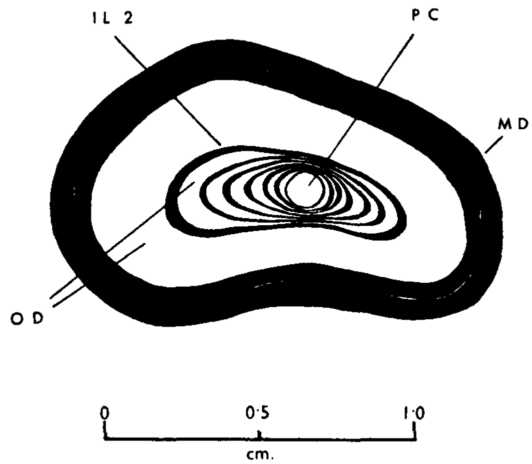

Fig. 11. Diagrammatic cross section of a canine tooth of a female Weddell seal about 8 years old, by reflected light. PC = pulp cavity, MD = "mantle" or translucent dentin presumably laid down up to the end of lactation, OD = opaque dentin, IL 2 = inner limit of 2nd year's growth. (After Mansfield, 1958a, Fig. 17.)

Sirenia: Dugongidae

***Dugong dugon* (dugong)**

Pocock (1940) used body length and cranial sutures as criteria of physiological age in dugongs. Scheffer (1970) studied dentinal layering in the tusk, using etched, half-tooth and longitudinal thin sections. Dentin seems to be deposited with annual, monthly, and perhaps even daily periodicity.

CONCLUSION

Research interest in the layering of marine mammal teeth began to quicken about thirty years ago. Now the tooth layers of thousands of individuals are routinely read each year as a procedure in life-history analysis. Despite their wide use as age indicators, tooth layers remain poorly understood with respect to their etiology, biochemistry, and physiology. The problems of preparing teeth for examination and examining and interpreting teeth layers will be dealt with in the papers which follow.

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