Age determination of pinnipeds with special reference to growth layers in the teeth

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Introduction

Age determination is an important technique in mammalian ecological studies, and in general more precise methods are now in use for marine than for terrestrial mammals. It will be apparent that before one can investigate growth rates, longevity and population structure some reliable method of determining the age of individual seals should be available. This can either depend on a reservoir of known-age animals (branded or otherwise marked as pups), or upon a reasonably precise and accurate method of estimating age, the latter preferably checked against known-age individuals. Marking or branding must be long-term for, as we shall learn below, seals are long-lived animals, some species reaching ages in excess of thirty years. Although permanent marking schemes have been initiated for a number of species the only one which has yet been marked in adequate numbers and over a long enough period of years is the northern fur seal *Callorhinus ursinus*, nearly half a million individuals having been branded or tagged up to 1960. Complete data on other species will take many years to accumulate, though already branding of southern elephant seals is yielding some very interesting results. Reliable material of this kind for other species will take many years to accumulate, and indeed it is difficult to see how some of the more inaccessible species such as those that breed in the Antarctic pack-ice could be marked in this way, with present facilities. For the study of such species a reliable method of age determination is desirable, if not essential, as it is indeed for any studies which require results within a relatively short period of time.

In view of these considerations one of the most important developments from the point of view of investigations in the field of general biology, growth, life histories, and population dynamics was the discovery and practical application of a method of ageing most species of seals by examination of their teeth, which was made independently and contemporaneously by Scheffer (1950) and Laws (1952), 1953a). I shall describe this in some detail but first it seems appropriate to deal briefly with attempts to determine the age of seals from their other physical characteristics.

Colour and appearance

The coat can help to fix the age of very young seals of most species fairly precisely. In the grey seal, *Halichoerus grypus*, for example, pups less than about three days old can be identified by the persistent yellowgreen stain of the white coat (from amniotic fluid) and older pups can be aged approximately from the onset and progress of the moult (Hewer, 1957). The black coat of the cape fur seal, *Arctocephalus pusillus*, identifies them up to four months after birth (Rand, 1956).

In some species, particularly the harp seal, *Pagophilus groenlandicus,* the pelage helps to distinguish the younger age groups, or immature and mature seals (Sivertsen, 1941; Fisher, 1954), but for the most part this is not a helpful character since the changes are usually gradual and progressive. Ages of ringed seals, *Phoca hispida,* assessed by eskimos are not particularly accurate after the first year or two (McLaren, 1958). Relative ages may be assessed by considering other aspects of external appearance such as the degree of scarring (which is particularly useful in some polygynous species), tooth size (notably in walruses) colour, growth or wear of vibrissae, or general bodily proportions. In the southern elephant seal, *Mirounga leonina,* I found that with experience the general appearance was quite a useful criterion (Laws, 1953b) though by no means as precise as other means.

In the northern fur seal the kill is selected on the basis of size and general appearance and is virtually confined to two year groups the 3 and 4 year old males.

Body length

Body size is one of the more obvious indications of relative age, and has been used for want of a more precise method in many biological studies. For a short-lived animal or for one that grows steadily over a number of years (such as some fish) it can be very useful, but for most seals it can give only an approximate indication of age and in most cases where it has been possible to check conclusions based on a study of length frequencies, by a more reliable ageing technique, rather large discrepancies have been found. See for example Laws, 1953b p. 22 and 1958. The seal is rather a flexible and elastic animal and the body length probably cannot be measured with greater accuracy than about 2 % — 3 %. In a long-lived animal that grows at a progressively decelerating rate, the length frequencies of most age groups except the first one or two show an extensive overlap and cannot be used to determine age after the first year or so. Body length is often useful for studying puberty and the attainment of sexual maturity which appears to depend both on growth rate (i. e. physiological age) and chronological age (Laws, 1956, 1959).

Skull development

Skulls are easy to preserve and are widely used in systematic work; they are used for distinguishing genera and species of seals, but much of the earlier confusion in the systematics has been brought about by age and sex differences in the skulls compared. Comparisons should always be made between skulls of like sex and developmental stage. In current systematic work these sources of variation are taken into account and methods have been developed which make it possible to arrange a series of skulls in order of their relative age, though not usually to assign absolute ages (except in the case of very young animals).

Hamilton (1934, 1939) distinguished six stages of male skulls and ten groups of female skulls of the southern sea-lion, *Otaria byronia.* In arranging the skulls he considered their lengths, the proportions of skull length to body length, the proportions of various skull measurements to skull length, the osteological development (including closure of sutures) and the dental development. He called these groups year classes, but recent examination of teeth rings in this species indicates that this is incorrect and that later groups include several year classes (Laws, unpublished). Sivertsen (1954) examined the same skulls and compared the suture ages he obtained with Hamilton's year classes; the relative age distribution was in close agreement.

HAMILTON (1939) similarly created four skull groups of each sex of the leopard seal, *Hydrurga leptonyx*, the first three assumed to be year groups. PAULIAN (1955) and LAWS (1957) showed that tooth ring ageing did not agree with this assumption. LINDSEY (1937, 1938) and BERTRAM (1940) studied skulls of Weddell, *Leptonychotes weddelli*, and crabeater seals, *Lobodon carcinophagus*, by similar methods, but the latter concluded that the osteology was of less value than a broad correlation of body and skull characters and that age could not be estimated beyond 25 months. LAWS (1958) showed that there was a discrepancy between the growth curve of the crabeater seal estimated from tooth rings and those given by BERTRAM. This serves to emphasize the point that in general skull characters and body size cannot be used to define year groups with precision.

DOUTT (1942) in his review of the genus *Phoca* attempted to eliminate variation in skull characters due to age. He found suture closure was the most reliable criterion and most later workers have employed his method or a modification of it. DOUTT selected eight skull sutures and as closure is a gradual process he assigned values (1—4) according to the degree of closure; 1-open, 2-less than half closed, 3-more than half closed, 4-completely closed. The'suture age'is the sum of these values for the eight selected sutures. It is low for young animals and high for old animals. DOUTT also mentions possible sources of subjective error. The sutures selected by him were 1. occipito-parietal, 2. squamoso — parietal, 3. interparietal, 4. interfrontal, 5. coronal, 6. basioccipital — basishpenoid, 7. intermaxillary, 8. basisphenoid — presphenoid. This is the order of closure in *Phoca vitulina;* it varies from species to species but within a given species the order of closure is fairly constant.

SIVERTSEN (1954) found that these eight sutures were suitable for studies on *Arctocephalus* though he had a little difficulty with other Otariid genera. He added another suture, the premaxillary-maxillary, but otherwise followed DOUTT's procedure. For systematic comparison of skulls he used three 'age' groups, namely adult (suture age 19—36), young (suture age 10—18) and cubs (suture age 9—10).

KING (1956) in her work on the genus *Monachus* also used this method. Although there was no size discontinuity in her series of skulls, she found a marked discontinuity of suture ages, groups 19—25 being absent in her small series. She concluded that in *Monachus* suture age is not a recti-linear age index, but that at a certain stage in skull development there is a rapid closure of certain sutures and growth of the braincase ceases. After this stage other skull components, particularly the snout, continue to grow. She allowed for this discontinuity and derived a relative age scale which permitted her to compare the growth rates and growth patterns of different elements of the skull. In this paper the order of epiphyseal fusion in other parts of the skeleton (which is relatively late compared with the skull) is also given.

RAND (1956) used ten sutures of *Arctocephalus pusillus* to separate groups of progressively greater age, but instead of calculating 'suture ages' he was able to use the closure of particular sutures to delimit the groups. There are some differences between the sexes owing to the continued growth of the male. The validity of this method was checked for younger age groups by means of branded animals, but this has not yet been possible for older animals. In the northern fur seal (SCHEFFER & WILKE, 1953) the time of closure of three selected sutures has been checked with known age (branded) animals. The rate of suture closure is very variable; the basi-occipitai closes in the male between ages 2—6 and in the female from 2—3 years; the parietal — supraoccipital closes in both sexes between 2—6 years. In this species suture closure is an indication of age within wide limits only, and this probably applies to most, if not all, other species.

Although methods employing suture closure and suture age are valuable in systematic studies, it is clear that we must look elsewhere for a technique giving the precision necessary for studies of growth, population dynamics and management problems.

Ovaries

In mammals, the graafian follicle is transformed after ovulation into a remarkable transient endocrine organ, the corpus luteum or yellow body. This persists for a variable length of time depending on whether or not pregnancy follows ovulation. Then either one or two weeks later, or at the end of the pregnancy it regresses to form a hard fibrous body, the corpus albicans, sometimes as in the cow brightly pigmented, but usually whitish or brownish in colour. It usually continues to shrink in size and eventually becomes indistinguishable from the other tissues of the ovary except perhaps on microscopic examination. Mackintosh and Wheeler (1929) studying the large ovaries of baleen whales found considerable numbers of these scars (up to 50 or so) and found that the number present bore a relation to the length of a whale and hence to its age. If this were so and the rate of accumulation could be calculated, then here was a useful method of age determination. An obvious disadvantage is that it can only be used for ageing mature females. Various estimates of the rate of accumulation of these scars were made and it was assumed that they persisted throughout the life of the whale, although it was not until recently that this was definitely established (Laws, 1958, 1961; a historical review will be found in the second of these papers). It now appears that their macroscopic persistence is a function of the initial large size of the whale corpus luteum.

The method was used by Bertram (1940) in his study of Weddell and crabeater seals. He made an analysis of the frequency distribution of ovarian corpora and concluded that they persist throughout the life of the individual and permanently record all ovulations in the life of each female. Bertram remarked that as it is probable that each seal ovulates only once a year, "the number of *corpora lutea* persisting in each pair of ovaries is a direct measure of the number of pregnancies undergone. The individual age is therefore this number plus the two pre-adult years". Attempts to use ovarian scars for some other seal species have not met with success. Hamilton (1939) and Laws (1953b) found that the corpora albicantia are only visible in the ovaries for a short time after their formation. Fisher (1954) found that although they persist for a longer period in the harp seal a balance is reached between production of corpora albicantia and their resorption in females older than ten years of age. McLaren (1958) and Mansfield (1958) reached similar conclusions for the ringed seal and walrus, *Odobenus r. rosmarus*, respectively.

Claw markings

Plehanov (1933) drew attention to the presence of growth ridges on the claws of the harp seal and claimed to be able to estimate ages up to thirteen years by this method. Doutt (1942) described and figured "annulations or growth rings" on the claws of the foreflipper of the ringed seal, ribbon seal *(Histriophoca fasciata)* and harp seal and their absence on harbour seal *(Phoca vitulina)* claws. Chapskiy (1952) discussed in some detail the use of the claws of the harp seal and Laws (1953b) drew attention to the presence of light and dark bands on the claws of the elephant seal, though the number present is limited by attrition to 4 or 5. In the walrus no more than three bands are present on the claws owing to wear at the tip (Mansfield, 1958).

Recently McLaren (1958a) re-examined the claws of the ringed seal and was able to correlate bands on the claws with ages determined from the teeth. The claws show alternating dark and light bands, the latter usually marked in the middle by a narrow ridge. Claws with few bands have a tip section of more or less translucent material which is formed in the foetus; it is separated from the rest by a constriction representing the neonatal period. One light band is formed in spring and summer and one dark band represents autumn and winter; the slight ridges appear to be laid down in spring. Comparison with tooth rings suggests that the claws are invalid for estimating age of ringed seals beyond about 8–10 years. In the bearded seal, *Erignathus barbatus,* (McLaren, 1958b) wear at the tip eliminates the first formed band at about 9–16 years. The pattern is generally very regular and clear and is very useful for preliminary ageing in the field. It is invaluable for the study of bearded seal growth because the teeth are degenerate in this species and cannot be used for age determination. This method may be compared with the ageing of baleen whales from growth ridges on the baleen plates (Ruud, 1945).

Laminated bones

In 1953 I described and figured the appearance of cross sections of the dense bone of the tympanic bullae of some elephant seals (Laws, 1953b). The bulla undergoes a great increase in size during life and examination of sections of the bone shows it to have a layered appearance. The number of layers appeared to be correlated with the number of growth layers in the teeth. This is a rather unusual method of bone growth and appeared to have potentialities for age determination, but was not further pursued because a better method was available.

I was then unaware of an interesting paper by Chapskiy (1952) in which he described and figures such layers in the mandibles of *Pagophilus groenlandicus* and *Odobenus.* He was able to show that the number of layers is correlated in a general way with estimates of ages based on other characters, and suggested that the layers are annual formations. The greatest number present in his relatively small sample of harp seals was 25. Later I drew attention to the occurrence of similar layers in sperm whale *(Physeter catodon)* jaws and in the seal *Phoca vitulina* and two delphinids *Phocaena* and *Delphinus* (Laws, 1960).

This is a method which might be exploited as an alternative to tooth layers, when the latter cannot be used, as for example in the bearded seal. As with other methods of age determination its validity and application must be established for each species before it can be used.

Teeth

There can be no doubt that the best methods of determining the age of seals and some other mammals are those based on the structure of the teeth. These were discovered independently and contemporaneously by Scheffer (1950) and myself (Laws, 1952, 1953a). They are based on variations in the rate of deposition of tooth material which are visible as external annuli on the root (Scheffer) and/or as distinct growth layers seen in sections of the dentine and cementum (Laws). A statement by Tomes (1904, p.191) about walrus teeth shows that nearly sixty years ago he was aware that the external ridges on the tusk root might be annual formations. Mohr (1943) described the hypercementosis of hooded seal teeth and mentioned the presence of internal growth rings. Neither Scheffer nor myself were aware of these suggestions, before we found that the teeth could be used for ageing.

Doutt (1942) investigated by means of radiography the gross deposition of dentine as a measure of age, but he was working on a species *(Phoca vitulina)* which has indistinct growth rings in the dentine and he does not mention them. The gross deposition of dentine does not appear to give a sufficiently precise measure of age, and he relied on the calculation of suture age.

Many thousands of branded or tagged known-age northern fur seals are at large. SCHEFFER (1950) while examining the skull of one of these animals noticed faint ridges around the roots of the teeth which corresponded in number to the age of the seal in years. He found that these ridges were accurate up to four years, occasionally to seven or eight, but tended to give a false age above four years. The clarity of the ridges varies and they are less pronounced in females than in males. SCHEFFER tried various methods to facilitate the reading of age and concluded that thin sections were of little value. The growth layers in fur seal teeth appear to be much less distinct and therefore more difficult to read than those present in other species. SCHEFFER observed similar external rings on teeth of *Eumetopias* and *Arctocephalus,* and dubious

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Fig. 1. Canine tooth of female southern elephant seal, aged 14 years (bar = 1 cm)

Fig. 2. Cross section of canine tooth of male southern elephant seal aged 98 months; reflected light (bar = 1 cm.)

ones on *Zalophus.* They were present on *Phoca vitulina* but not on other species of *Phoca,* nor on *Cystophora* or *Monachus.* He noted that they were present on walrus tusks *(Odobenus)* and were especially prominent on elephant seal teeth *(Mirounga).* SCHEFFER developed this method of reading the external ridges for the northern fur seal, in which the internal layers are not very obvious, and later managed to estimate age in this way up to ten years (CHAPMAN et al., 1954). Recently WILKE, NIGGOL and FISCUS (1958) have been able to age this species up to 22 years by means of longitudinal sections.

I was fortunate enough to be working on the southern elephant seal in which external ridges (fig. 1) and also internal layers in both dentine (fig. 2) and cementum are exceptionally clear, although there were no known-age animals to indicate their correlation with age. The yearly cycle of the elephant seal is remarkable compared with most other pinnipeds in that there are two periods of complete or partial fasting, at the breeding season in spring and during the moult in summer. It is likely that these fasts are accompanied by changes in the general metabolism, and the teeth were examined to see whether they retain traces of cyclical variation in the rate and manner of calcification. They were found to show in section a regular paired pattern of rings in the dentine. The validity of these layers had therefore to be demonstrated indirectly by analysing the seasons at which they were laid down and showing that they correspond to the two fasting periods. In fact, it was not until 1960 that I was able through the kindness of Dr. R. G. CARRICK, to examine photomicrographs of sections of the teeth of known-age branded elephant seals and to confirm the age determinations directly (LAWS, 1960). In these first papers (LAWS, 1952, 1953a) I showed that internal growth rings occur in the dentine or cementum of the following species of pinnipeds: *Phoca vitulina, Pagophilus groenlandicus, Halichoerus grypus, Lobodon carcinophagus, Leptonychotes weddelli, Hydrurga leptonyx, Ommatophoca rossi,* and *Cystophora cristata,* as well as *Mirounga leonina.* It was suggested that such growth layers would be found in the teeth of all pinnipeds, and in other mammals, some of which were listed.

It is clear now that the internal layers are of more value than the external ridges because the latter are masked sooner or later by increasing cementum deposition. Dentine layers may cease to be deposited after a number of years, but give a valid indication of age for a longer period than the external ridges; in the older individuals cementum layers can be used. By means of these layers McLAREN (1958a) was able to determine the age of an old ringed seal as 43 years.

Dentine layers

It will be as well briefly to describe the process of tooth growth in seals. The milk dentition is poorly developed in pinnipeds. In the walrus and eared seals the deciduous teeth persist for several months after birth, but in most of the phocids the deciduous teeth are reduced and are re-absorbed in the foetus (BERTRAM, 1940; LAWS, 1953b; RAND, 1956; BROWN, 1957). In all species studied the permanent incisors, canines and post-canines are present at birth though they may not erupt until some time later.

The crowns of the teeth are covered with enamel caps, laid down in the gum by the enamel organ. Once a tooth erupts the enamel ceases to grow and begins to wear, so that it becomes smaller. In the walrus tusk for instance the enamel cap is completely lost.

Dentine is laid down inside the tooth by the odontoblasts lining the pulp cavity; first the tissue matrix, in which calcium deposition then occurs as calcospherites which enlarge and form the so-called "marbled" dentine. If calcification proceeds further they fuse to form a dense, more or less homogeneous layer. In the growth of seal dentine the type of dentine laid down varies seasonally; reticulated or vacuolated dentine is very poorly calcified; in "marbled" dentine calcification has proceeded further and dense dentine is fully calcified.

The alternation of these different types of dentine produces a macroscopic pattern, superimposed on a microscopic pattern (LAWS, 1935a) which may represent a daily pattern as in the rat, or a two, three or more day pattern. The microscopic stratification need not concern us here for age determination is based on the macroscopic layering, but it has a bearing on age determination in *Otaria* (see below).

The layers can be distinguished by variations in colour on examination of a cut and polished surface by reflected light, or by transmitted light in thin sections or in cut and stained sections of decalcified teeth. Dentine once laid down provides a permanent record, though in disease there may be some resorption of dentine. Canine teeth are usually most suitable for age determination, because they are larger than the other teeth and the root remains open for a longer period.

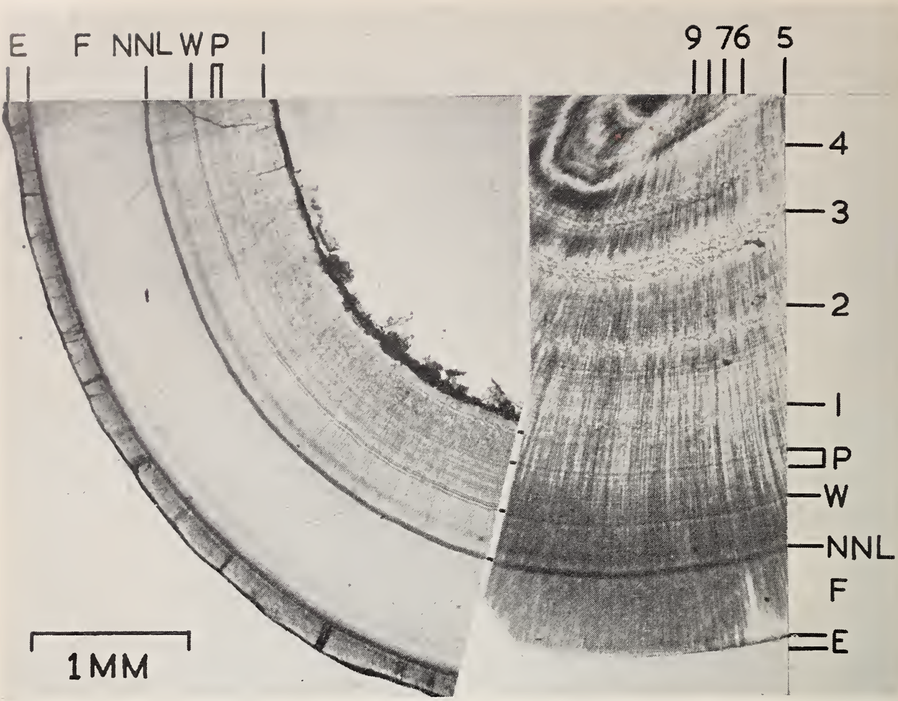

Fig. 3. Left, thin ground section of canine tooth of a 1-year-old male crabeater seal. Right, section of canine of 9-year-old female; transmitted light. (E — enamel, F — foetal dentine, NNL — neonatal line, W — weaning, P — position of inner border of dentine in 6-month-old pups, 1–9 = annual rings)

At birth foetal dentine is present and a discontinuity in growth makes it possible to detect a neonatal line (fig. 3). This is the reference point from which age determinations begin. The tooth grows in length as well as thickness, at least in the early years, and in some species growth in length continues throughout life. Each annual increment of dentine approximates in shape to a hollow cone successively decreasing in size until death or until the pulp cavity is filled. In species such as the walrus and elephant seal the pulp cavity of the continuously growing canine remains open for many years if not throughout life. A number of such cones superimposed result in the formation of ridges corresponding to the number of annual increments. The ridges are formed only because there is a discontinuity in the rate of growth in length but deposition of cementum, discussed below, tends to mask these ridges so that they disappear at an early age in most seal species.

The validity of the layers as indicators of age can be checked easily enough if known-age animals are available for study, but in most species known-age animals are not yet available. It is then necessary to resort to less direct checks such as a demonstration that particular layers are laid down at a particular time of year or attempts to correlate the number of layers with other measures of age, such as modes in length frequencies, claw bands, skull characters, etc.

A recent study of the teeth of the crabeater seal, *Lobodon carcinophagus* may serve as an example (Laws, 1958). The structure of the dentine in the canine teeth of this species is perhaps more typical of other seals than elephant seal and sea lion *(Otaria)* dentine, which will be described below.

In the crabeater seal the permanent dentition makes its appearance in the fourth month of pregnancy and the teeth are functional at birth, the milk teeth being shed in utero. The prenatal dentine and neonatal line are easily identified in examination both by reflected light and, in thin sections, by transmitted light (fig. 3).

The pupping season in this species is known to be short. This means that, by examination of dated specimens, the sequence of dentine deposition in the first and subsequent years can be elucidated. Interpretation is made easier by the presence of annual layers of vacuolated dentine; on examination of the polished cut face by reflected light these vacuolated layers, owing to the spaces, show up as shining foamy-white rings. The teeth which lack vacuolated layers show well-marked greyish layers (by reflected light) of poorly calcified dentine, alternating with light-coloured layers of well-calcified dense dentine. The basic annual pattern is remarkably constant. The typical sequence of dentine deposition in the tooth of an animal which died when about twelve months old is illustrated by a thin section viewed by transmitted light in figure 3. On the outside of the tooth at the level of the section is a layer of enamel (175 μ), then a thick zone (765 μ) of homogeneous dense dentine laid down in the foetus. Then comes a conspicuous neonatal line representing the discontinuity at birth. This was confirmed by examination of teeth from near-term foetuses and young animals.

After the neonatal line there is a second zone (315 μ) of fairly homogeneous, well calcified dentine, bounded centrally by a second conspicuous darker line. This probably represents the dentine laid down during the suckling period and the line terminating it represents a discontinuity at weaning. This was established by reference to the teeth of young, recently weaned pups (fig. 3). A dark line within this suckling dentine may represent the beginning of the pup moult and the attainment of full homoiothermy. After weaning the remainder of the dentine (575 μ thick) shows a series of fine lines (micro-laminations) representing small variations in the rate and manner of dentine formation. A layer of vacuolated dentine marks the end of the first year and the full thickness of the annual layer is 885 μ. In figure 3, a section of the canine tooth of an adult female is shown for comparison. The dentine pattern of the first annual layer in the two teeth is almost identical, but perhaps because the adult tooth has been sectioned at a lower level the foetal dentine is thinner.

This interpretation of the dentine formation in the first year is supported by examination of the teeth of young animals killed at different times and fuller details are given in the original paper.

It was possible to establish the time of formation of the poorly calcified or vacuolated layers as September to October, probably at the pupping season in September. Thus, animals which died or were killed in September or October were currently laying down a layer of poorly calcified dentine (86 %) or had recently laid down such a layer (14 %). On the other hand animals killed between November and April were laying down dense well-calcified dentine at the time of death and had earlier deposited a layer of poorly-calcified dentine. No material was available from the remaining months of the year (May to August) but the dentine layers become progressively thinner (Laws 1958, fig. 1) and consideration of the thickness of the last-formed layer indicates that only one vacuolated or poorly-calcified layer is deposited annually. In the crabeater seal the first few annual vacuolated layers are thin and irregular, but later-formed layers in the female are thick and conspicuous. It is suggested that the thicker rings in the female are related to the effect of parturition and lactation on dentine deposition.

The teeth of ringed seals and harp seals show a closely similar pattern of alternating dense dentine and thin or vacuolated dentine (Fisher, 1954; McLaren, 1958). McLaren showed that in the ringed seal dense dentine is mainly deposited from mid-July to the end of March and thin dentine in other months, mainly in spring (mid-April to the end of June) as in the crabeater seal. Fisher (1954) showed that a layer of well-calcified dentine was being laid down in the teeth of migrating harp seals in January and also during the pupping season (April). In this period the animals are feeding actively. The vacuolated layer is formed towards the end of the pupping season and appears to be correlated with the moult, when the animals fast. Similar, but not identical patterns are found in the dentine structure of other seals. The leopard seal, Ross seal, *Ommatophoca rossi*, and Weddell seal appear to be similar but they and some other species examined lack the vacuolated layer found in the species described above, and the elephant seal and sea lion *(Otaria)* have patterns of dentine formation which appear to be unique, at least among the species so far studied. For this reason although the value of elephant seal teeth was established earlier (Laws, 1953a) I have thought it desirable here to describe the more typical structure of the crabeater seal teeth first.

The sequence of dentine deposition in the elephant seal was worked out in a similar way and the pattern in the first year is very similar to that described for the crabeater seal. The neonatal line is clear in both polished, bisected teeth and in thin sections, and the suckling dentine is delimited by a line indicating weaning. Thereafter two types of dentine are laid down, dense well-calcified columnar dentine, and "marbled", poorly calcified dentine containing more organic matter. Optically the former is more translucent because there is less refracted light; these differ in their transmission of light in a manner analagous to clear and frosted glass (fig. 4). At first the alternating pattern is variable (in immature animals) but thereafter a fairly regular annual pattern of two dense layers (broad and narrow) alternating with two marbled layers (also broad and narrow) is laid down. These are correlated with the haul-outs and presumably reflect the physiological changes associated with the two

Fig. 4. Thin ground transverse section of canine tooth of 8-year-old male southern elephant seal; transmitted light (bar = 1 mm.)

Fig. 5. Thin cut longitudinal section of canine tooth of 17-year-old male southern sea lion; transmitted light (bar = 1 mm.)

annual periods of complete or partial fasting at the breeding season in spring and during the moult in summer. The great majority of breeding and moulting animals examined were laying down dense dentine.

Mansfield (1958) has described tusk growth in the walrus in some detail. These teeth are unerupted at birth but appear 2–3 months later. Enamel, dentine, and a layer of cement 2 mm thick are present at birth. A neonatal line is visible after birth, and initial growth is rapid to a length of 9—10 cm at the end of the first year. Regular incremental layers of dentine corresponding to external ridges of the root are laid down in older tusks in the form of truncated cones, and as the tusk elongates the more distal part of the pulp cavity is filled with secondary dentine, so that in old animals the pulp cavity may be obliterated. This layering gives rise to a macroscopic pattern of light and dark dentine in adults, but in immatures this macroscopic dentine pattern and also the external ridges are absent because growth is rapid and fairly continuous. Mansfield (1958) concluded that the ridges correspond to a discontinuity of growth in spring and are annual formations. Because the root ridges and dentinal layers are formed only during part of the life history they cannot in fact be used for accurate age determination and layers in the cementum must be utilized instead (see below). Several canine teeth of *Otaria byronia* collected by me in the Falkland Islands were available for study. They show external ridges on the root which become obscured with increasing age. In thin longitudinal sections (c. 100 μ) of undecalcified teeth conspicuous growth layers are seen, which correspond to the external ridges and to growth layers in the cementum. By comparison with other species I am confident that these layers represent annual increments, although it has not yet been possible to confirm this hypothesis directly. Fiscus (1961) concludes that similar layers in the related species *Eumetopias jubata* are annual. He does not however describe the microscopic appearance of the layers and the *Otaria* teeth are mentioned here because the structural pattern of the dentine appears to be quite different from that of the other pinnipeds described above.

In adults the dentine layers are very regular in appearance and the microscopic pattern within successive layers is remarkably constant. Within each layer there are a number of regularly arranged micro-laminations presenting, in thin sections viewed by transmitted light, an alternating pattern of dark and light striations (fig. 5). In each macroscopic layer there are 21–23 narrow light micro-laminations separated by dark laminations and one broad light micro-lamination which corresponds in thickness to 3–4 of the narrow layers, making about 24–27 light micro-laminations to one assumed annual layer.

This suggests the possibility of a lunar periodicity in the feeding regime, although it must be admitted that there is no supporting evidence. Whatever the regulatory factor may be, we may reasonably conclude that probably about two microlaminations are equivalent to one month.

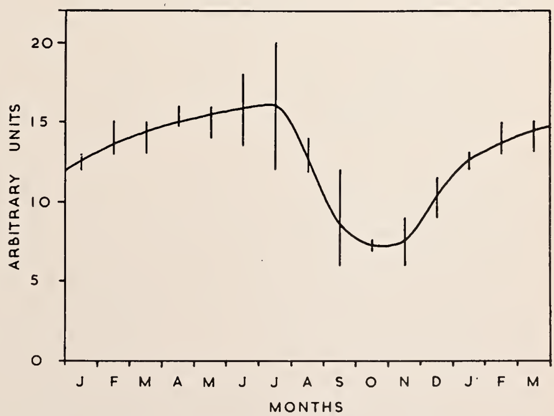

Fig. 6. Seasonal variation in deposition of dentine in the canine of an adult male southern sea lion. Vertical lines represent range in 4 successive annual layers, curve represents mean values (see text)

The teeth were collected in February and in each of them one of the broad micro-laminations was being laid down. The arrangement of micro-laminations within each annual layer (fig. 5) suggests a regular seasonal growth cycle of the teeth. Assuming that two dark and two light micro-laminations together represent a month's growth, a hypothetical seasonal cycle of tooth growth can be drawn up by plotting the thickness of the micro-laminations and assuming that the broad micro-laminations are laid down in February/March.

Measurements were made from enlarged photomicrographs of longitudinal canine tooth sections of a male sea lion (fig. 5) and the results are presented in figure 6. If the hypothesis is correct the narrowest layers are deposited in September-December and correspond to the breeding season (Hamilton 1934). It is at about this time that the layer of vacuolated dentine is deposited in crabeater seal teeth (see above). If these indications should be confirmed by further study, there may be possibilities for rather detailed studies of individual growth histories.

The dentine layers, when they can be used are preferable to other methods, and in some species can be read on the polished face of bisected teeth (e. g. elephant seal,

Table 1

Pinniped teeth in which growth layers have been found

Species	External ridges	Dentine layers	Cementum layers	Authorities
Otaria byronia	+	+	+	Laws (present paper)
Eumetopias jubata	+	+	+	Scheffer (1950), Fiscus (1961)
Zalophus californianus	+			Scheffer (1950)
Arctocephalus pusillus		+		Rand (1956)
Arctocephalus tropicalis	+	+		Laws (unpublished)
Arctocephalus australis	+	+		Laws (unpublished)
Callorhinus ursinus	+	+		Scheffer (1950), Wilke, Niggol & Fiscus (1958)
Odobenus rosmarus	+	+	+	Brooks (1954), Mansfield (1958)
Phoca vitulina	+	+	+	Scheffer (1950), Mansfield & Fisher (1960)
Phoca hispida		+	+	McLaren (1958)
Pagophilus groenlandicus		+		Fisher (1954)
Halichoerus grypus		+	+	Laws (1953a), Hewer (1960)
Lobodon carcinophagus		+	+	Laws (1953a, 1958)
Hydrurga leptonyx	+	+	+	Laws (1953a, 1957)
Leptonychotes weddelli		+		Mansfield (1957)
Ommatophoca rossi		+		Laws (1953a)
Cystophora cristata		+	+	Laws (1953a), Rasmussen (1957)
Mirounga leonina	+	+	+	Laws (1953a, 1960)

crabeater seal). Indeed in the elephant seal this is preferable to thin sections because the eye is not distracted by microscopic detail and can pick out the general pattern more easily. In species with small teeth, such as ringed and harp seals, thin sections are necessary.

Care must in any case be taken to make a cross section at the right level, so that no layers are missed, and in some cases longitudinal sections may be preferable. In somes species in which the teeth are difficult to read, longitudinal (saggital) sections are easier to read than cross sections, and this is the method now adopted for northern fur seals in preference to external ridges (WILKE et al. 1958).

Cementum layers

When the dentine layers are not readable, or when by closure of the pulp cavity they would give a false estimate of age, similar growth layers in cementum may be used. For example McLAREN (1958) counted 43 layers in the cement of a ringed seal tooth, whereas few could be aged from the dentine above 20 years. LAWS (1953a) figured the layers in the cementum of elephant seal and hooded seal teeth and they have subsequently been used by several workers. These layers are much thinner than the dentine layers and consequently must be studied in thin sections.

MANSFIELD (1958) describes and figures the layers in the cement of Atlantic walrus teeth. There is usually a darker inner layer of hypercalcified material merging gradually to a lighter translucent zone formed towards the end of spring, then there is an abrupt transition to the next dark layer, which marks the rapid summer growth after breeding. The distinction between the layers is most pronounced in old males, and the layers are more sharply defined on molariform teeth than on the tusk roots. There is an exponential decrease in thickness of the layers as more are formed, but no indication that deposition ceases during life. The layers in female teeth are similar but narrower, and their interpretation is more difficult. MANSFIELD suggests that the long pregnancy and very long lactation period of the walrus may complicate the pattern of cement deposition.

BROOKS (1954) found similar layers in Pacific walrus teeth and concludes that they "offer a useful, if approximate, key to the age of walrus". He analysed tusk and body length frequencies and interpreted certain groupings as age classes, but without giving good reasons for doing so. On the basis of these age groups he decided that dark cementum layers are laid down biannually in summer and winter and light layers in spring and autumn.

Similar cemental layers are present in a number of seals (table 1). They are very conspicuous and regular in hooded seal teeth, for the teeth of this species undergo hypercementosis and the cement layer in older animals may be much thicker than the dentine layer (fig. 7). Of relevance to the validity of this method is the fact that MANSFIELD and FISHER (1960) were able to count 18—20 growth layers in a tooth from a captive harbour seal 19½ years old. Similarly HEWER (1960) was able to count at least 25—26 cement layers in a tooth from a grey seal which died in captivity at the age of at least 26½ years; a tooth from another grey seal female exactly 6 years old showed 6 layers. These results confirm the annual nature of the layers and indicate the degree of error to be expected in counts. As HEWER observes, the primary cause of uncertainty in counting is that the earlier rings are broad without sharply defined edges, and difficulty may be experienced in assessing the last-formed ring. In the grey seal cementum is first deposited on the root about 3—4 months after birth.

A further point that should be made concerns the deposition of cement in relation to growth in length of the tooth. These layers usually vary in thickness and a particular layer may not be so easily distinguished in one part of the tooth as in another. For this reason they are usually best counted in longitudinal sections. Figure 8 shows their appearance in a large sperm whale *(Physter catodon)* tooth.

Fig. 7. Thin ground transverse section of canine tooth of a 20-year-old male hooded seal, showing incremental layers in cementum; transmitted light (bar = 1 mm.)

Fig. 8. Thin ground longitudinal section of mandibular tooth of a sperm whale. There are 36 incremental layers in dentine and cementum, not all of which are shown. Cementum to left of picture; transmitted light (bar = 1 mm.)

Methods of age determination based on the structure of the teeth have been described in some detail because of their fundamental importance. It is clear that the structure of the teeth provides a very useful research tool which is not restricted to seal studies. The teeth have also been used to age whales (Nishiwaki and Yagi, 1953; Nishiwaki et al., 1958; Sergeant, 1959), and certain terrestrial mammals (Christian, 1956; Sergeant and Pimlott, 1960). There can be little doubt that age determination from the teeth will come to have much wider application among terrestrial mammals, and it is hoped that this paper will stimulate further work.

Causative factors

The probable causative factors of discontinuous tooth growth have been discussed by Laws (1953a), Fisher (1954) and McLaren (1958). It seems likely that the rate and manner of dentine deposition is related to several factors, which may vary in importance according to the species and the type of annual cycle, and which probably include among others the feeding regime, moulting physiology and vitamin D levels. Vitamin D is necessary for full calcification of dentine and in the teeth of experimental animals receiving sub-optimal amounts calcification does not proceed beyond the 'marbled' condition. In dolphins, *Stenella caerulo-albus,* which feed on squid the normal dentine appears to be 'marbled' (Nishiwaki and Yagi, 1953) and this appears also to be the condition in the elephant seal. In this seal the dense well-calcified dentine appears to be laid down in the fasting periods. This led me to speculate that possibly vitamin D is in sub-optimal amounts in the diet, and that more vitamin D is produced by solar irradiation when the animals are on land.

In the ringed seal, harp seal and crabeater seal however, the periods of complete or partial fasting are correlated with the deposition of thin, reticulated or vacuolated dentine (fig. 3), and the denser material is deposited when feeding intensity is greater.

The very few teeth of *Otaria byronia* from the Falkland Islands that have been examined indicate that in this species the formation of dense and thin dentine may be associated with cyclical variation in feeding, possibly connected in some way with a lunar periodicity in the behaviour of the main food organisms.

It is clear that there is considerable variation in the pattern of dentine deposition in seals, although the species that I have been able to examine conform in general to these three basic types of pattern. More detailed studies of dentine formation and its correlation with the feeding regime and annual cycle of physiological processes and behaviour are required. Techniques of intra-vitam staining with Alizarin red or lead acetate might be employed.

The cyclical deposition of cementum results in relatively little variation in its appearance in different species. This may be due partly to the smaller scale of cement deposition compared with dentine, in most species, which may mask variations in pattern. In addition it has not been so closely studied.

A note on methods of preparing thin sections

Laws (1953a p. 2) prepared thin ground sections of undecalcified material by standard petrological methods for preparing rock sections. This involves bisecting a tooth, polishing the cut surface, and cutting a thick section. This section is then cemented with Canada balsam or dental wax to a glass slide, polished face down, and ground down to the required thickness. This is time consuming and Fisher and Mackenzie (1954) describe an improved method for the rapid preparation of tooth sections. A thick section is cut on a circular saw, and ground down to the required thickness on a specially made grinding machine.

I have used a circular saw mounted in a lathe with a milling attachment to cut thin longitudinal sections of large seal teeth. If the rate of feed of the tooth through the saw is carefully controlled large sections down to 100–150 μ in thickness can be prepared directly, without grinding or polishing. Reading of these sections is not complicated by saw marks and a photomicrograph from a section prepared in this way is shown in fig. 5. The teeth are held firmly in the machine by attaching them to a piece of angle iron. A flat is filed on one surface of the tooth and two holes, corresponding to holes in the angle iron, are drilled and tapped; the tooth is then screwed onto the angle iron which can then be clamped in position.

Summary

1. In studies of mammalian ecology there is a need for reliable and precise age determination, other than by permanent marking.
2. A variety of methods of ageing seals are discussed. These include, colour and appearance, body length, skull development, and ovarian scars, but none of them is sufficiently precise.
3. Claw markings and the laminations in certain bones are also discussed and may be valuable if teeth are not available.
4. The structure of the teeth affords the best means of ageing seals and some other mammals.
5. Dentine layers are described and their validity as an indication of age discussed. There appear to be three main cyclical patterns in the dentine of the seals in which the structure has been investigated. In a number of species dentine deposition ceases at a relatively early age owing to closure of the pulp cavity.
6. For some species, and/or for older individuals it is necessary to rely on the growth layers

in the cementum, which being deposited on the outside of the tooth are not affected by closure of the pulp cavity.
7. Possible causative factors for the cyclical patterns found in dentine and cementum are briefly discussed. There is need for further detailed study before these can be established, and they may vary according to the species.
8. Thin sections are necessary for reading dentine layers in small teeth and for reading cementum layers even in large teeth. A brief note on the preparation of thin sections is therefore included.

Zusammenfassung

1. Für Studien auf dem Gebiet der Säugetier-Ökologie besteht ein Bedürfnis nach verläßlicher und genauer Altersbestimmung auf anderem Wege als durch Dauer-Markierung.
2. Es werden verschiedene Methoden zur Altersbestimmung bei Robben besprochen. Diese umfassen Berücksichtigung von Färbung und Habitus, Körperlänge, Schädelentwicklung, Uterusnarben; aber keine dieser Methoden ist ausreichend genau.
3. Krallen-Marken und die Ringbildung an gewissen Knochen werden ebenfalls erörtert. Sie können wertvoll sein, wenn Zähne nicht verfügbar sind.
4. Die Zahnstrukturen liefern die besten Hilfsmittel für die Altersbestimmung bei Robben und einigen anderen Säugern.
5. Dentin-Ablagerungen werden beschrieben und ihre Verwendbarkeit als Altersringe besprochen. Es scheinen hauptsächlich drei verschiedene Muster cyclischer Ringbildung im Dentin der bisher untersuchten Robben vorzukommen. Bei einer Anzahl Robben-Arten hört die Dentin-Ablagerung in relativ geringem Alter auf, und zwar je nach Verschluß der Pulpahöhle.
6. Bei einigen Arten und oder älteren Individuen ist es nötig, auf die Zuwachszonen des Cements zurückzugreifen, die — an der Außenseite des Zahnes angelegt — nicht durch den Verschluß der Pulpa beeinträchtigt werden.
7. Mögliche Ursachen für die cyclischen Ablagerungsmuster in Dentin und Cement werden kurz erörtert. Weitere Untersuchungen sind nötig, bevor man die bisher erkannten als allgemeingültig hinstellt, zumal sie möglicherweise artweise verschieden sind.
8. Dünnschliffe sind nötig, um in kleinen Zähnen die Dentinringe, in großen auch die Cementlagen abzulesen und zu zählen. Deshalb ist ein kurzer Hinweis auf die Herstellung dieser Dünnschliffe angefügt.

Résumé

1. Dans les études d'Ecologie relatives aux Mammifères, une méthode autre que le marquage permanent est nécessaire pour une détermination certaine et précise de l'âge des individus.
2. Un certain nombre de méthodes d'évaluation de l'âge des Phoques sont discutées. Elles se fondent sur: la couleur et l'aspect général, la longueur du corps, le développement du crâne, les cicatrices de la ponte ovulaire, mais aucune d'entre elles n'est suffisamment précise.
3. L'utilisation des marques des ongles et des lamelles de certains os est également discutée. Ces méthodes peuvent être valables si les dents ne sont pas utilisables.
4. La structure des dents fournit le meilleur critère de détermination de l'âge des Phoques et de quelques autres Mammifères.
5. Les couches de dentine sont décrites et leur valeur comme indication de l'âge discutée. Il semble qu'il existe trois schémas cycliques principaux dans la dentine des Phoques chez lesquels la structure a été étudiée. Chez un certain nombre d'espèces, le dépôt de dentine cesse à un âge relativement précoce grâce à la fermeture de la cavité de la pulpe.
6. Chez quelques espèces et ou chez des individus âgés, il est nécessaire d'utiliser les couches de croissance dans le cément; celles-ci étant déposées à l'extérieur de la dent ne sont pas affectées par la fermeture de la cavité de la pulpe.
7. Des facteurs éventuels déterminant les schémas cycliques observés dans la dentine et le cément sont brièvement discutés. Des études détaillées seront nécessaires avant que ces facteurs soient établis, et ils peuvent varier suivant les espèces.
8. Des coupes minces sont nécessaires à l'étude des couches de dentine dans les petites dents et des couches de cément même dans les grandes dents; pour cette raison une brève note relative à' la confection des coupes minces est jointe au texte.

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Beiträge zur Biologie eines Steppennagers, *Microtus (Phaeomys) brandti* (Radde, 1861)

Freigehege-Versuch

Von HANS REICHSTEIN

Eingang des Ms. 15. 11. 1961

I. Einleitung

1956 nahm Prof. Dr. K. ZIMMERMANN an einer vielmonatigen Forschungsreise nach China teil, die von der Academia Sinica in Peking und der Deutschen Akademie der Wissenschaften zu Berlin gemeinsam getragen wurde. Von hier gelangten außer einem umfangreichen Balgmaterial auch Kleinsäuger lebend nach Deutschland, unter ihnen ein in vieler Hinsicht bemerkenswerter Steppennager, *Microtus (Phaeomys) brandti*. Es stellten sich im Zoologischen Museum Berlin bald Zuchterfolge ein. Von der rasch anwachsenden Nachkommenschaft wurden mir einige Tiere für eigene Untersuchungen an der Biologischen Zentralanstalt Berlin in Kleinmachnow überlassen, wofür ich Prof. ZIMMERMANN großen Dank schulde. Wir züchteten *M. brandti* zunächst im Laboratorium weiter, brachten dann jedoch einige Tiere in einen Freilandzwinger, um sie unter verhältnismäßig natürlichen Bedingungen beobachten zu können. Über Ergebnisse dieser Untersuchungen wird im folgenden berichtet. Für Überlassung von Angaben aus seinen Laboratoriumszuchten habe ich Prof. ZIMMERMANN zu danken. Zu Dank verbunden bin ich auch Prof. HEY und Dr. NOLL, die mir die Durchführung solcher Versuche im oben genannten Institut gestatteten.

II. Verbreitung, Vorkommen, Aussehen

Microtus brandti ist Bewohner der hochkontinentalen, zentralasiatischen Steppengebiete. Er bevorzugt die zusammenhängende Grassteppe und ist vor allem auf den in den Senken der Steppenseen-Gebiete gelegenen Wiesen anzutreffen. Sein Verbreitungsgebiet wird begrenzt durch die Transbaikalische Bahnlinie im Norden, durch den etwa 45. nördl. Breitengrad im Süden. Im Osten geht er bis zum Großen Chingan, im Westen bis zum Changai-Gebirge (OGNEW 1950). Die Versuchstiere stammen aus der Umgegend von Manschuli (Innere Mongolei). *Microtus brandti* neigt zu zyklischen Übervermehrungen und spielt daher in der Weide- und Viehwirtschaft der Mongolei eine tragende Rolle. Der Massenwechselrhythmus hat hier allerdings ein ungewöhnlich langes Intervall: die Übervermehrungsgipfel liegen 11—12 Jahre auseinander (DAWAA 1961). Die Steppenwühlmaus (wie *Microtus brandti* im folgenden bezeichnet wird,