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# COMPARISON OF ACCUMULATION PATTERNS IN LAYERED DENTINAL TISSUE OF SOME ODONTOCETI AND CORRESPONDING PATTERNS IN BALEEN PLATES AND EAR PLUGS OF BALAENOPTERIDAE

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ABSTRACT

The data of the present examination show that the teeth of delphinids reach their ultimate diameter before eruption from the gum. However, growth in length continues during the first three or four years after birth, thereafter the increase in length is neglegible. In the same period the width of the dentinal growth layers decreases rapidly to approach an asymptote when about 10 layers are deposited. In *Phocoena phocoena* and *Delphinus delphis* the greatest thickness of the first dentinal layer is about 350 μm and never exceeds this figure. The decrease in width of the layers can only be expressed by a straight line in a logarithmic plot. Due to this decrease the layers are not comparable to each other.

Secondary layers can only be seen in the first three or four layers. In *P. phocoena* the numbers of hollows in the densitometer records of the cementum, representing the dark lines, are in accordance with the numbers of dentinal layers that could be counted. However, the part in the records representing the dentine can not be divided into "growth periods", due to the decrease in width of the growth layers. Hence, the records of the teeth are incomparable to those of ear plugs and baleen plates of baleen whales, as these latter continue to grow at a nearly constant rate. The formation of growth layers in the teeth of *Sotalia fluviatilis* differs from that in the teeth of other delphinids examined so far. The formation of the first seven or eight layers is the same as in all other species. However, the process of dentine formation then changes as also the structure of the dentine, so that no real layers are formed.

## INTRODUCTION

In most species of odontocetes the teeth consist of three structurally different elements, the enamel cap, the dentine body and the cementum. The two parts last mentioned show a more or less clearly defined layered structure. In the cementum the layers are often parallel to each other and to the borderline between the cementum and the dentine. In the dentine the layers are parallel to each other and in most species of odontocetes more or less parallel to the longitudinal axis of the teeth, except in the Physeteridae where the dentinal layers form an acute angle with the long axis. The layers in the dentine can be used for age determination (Laws, 1952; Sergeant, 1959, 1962; Klevezal' & Kleinenberg, 1967, Kasuya, 1972, 1974, 1976, 1977 a and b; Perrin, 1975, 1976, 1977; Gaskin & Blair, 1977; Van Utrecht, 1978).

Kasuya (1976) demonstrated that at least in *Stenella attenuata* (Gray, 1846) and *Stenella coeruleoalba* (Meyen, 1833) the dentinal growth layers are only of value for age determination in young animals. In the older individuals a greater number of cemental layers was found. In *S. attenuata* this was after the deposition of nine dentinal layers and in *S. coeruleoalba* after 11 layers were formed. Perrin et al. (1976, 1977) are in

Table I. Measurements of the studied material.

ZMA = Zoölogisch Museum, Amsterdam; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden.

| Coll. no. | | length (mm) | weight (kg) | tooth length (mm) | tooth diam. (mm) | % testis weight | age | |
|---|---|---|---|---|---|---|---|---|
| *L. albirostris* ♂♂ | | | | | | | | |
| ZMA | 10.746 | 269 | 309 | 27.7 | 5.4 | 0.13 | 13 | |
| ZMA | 11.369 | 250.5 | 345.2 | 25.5 | 6.5 | 0.10 | 15 | |
| ZMA | (W.O.192) | 257 | 220 | 29.2 | 5.4 | juv. | 11 | |
| ZMA | 20.977 | 239 | 134 | 25.4 | 5.7 | juv. | 7 | |
| *L. albirostris* ♀♀ | | | | | | | | |
| | | | | | | ovaries | | |
| ZMA | 11.384 | 262.5 | 306.2 | 25.4 | 6.0 | mat. | 11 | |
| ZMA | 11.517 | 218 | 186.5 | 25.6 | 5.7 | juv. | 2½ | |
| ZMA | 12.982 | 255 | 240.5 | 30.1 | 6.1 | mat. | 11 | |
| ZMA | 15.208 | 264 | 242 | 23.6 | 5.4 | mat. | 17 | 1) |
| ZMA | 17.230 | 269 | 280 | 28.0 | 5.4 | mat. | 11 | |
| ZMA | 17.231 | 252 | 255 | 26.2 | 6.1 | mat. | 12 | |
| ZMA | 18.107 | 236 | 160 | 28.4 | 5.8 | juv. | 5 | |
| | 41077II | 242 | 100 | 29.2 | 5.4 | juv. | 4½ | |
| | 27/28977 | 246 | 132.5 | 29.0 | 5.9 | juv. | 5 | |
| ZMA | 19.652 | 251 | 254 | 28.9 | 5.8 | mat. | 10 | 2) |
| ZMA | 6.851 | 259 | 242 | 16.8 | 6.2 | mat. | 11 | |
| ZMA | 9.478 | 223 | 248.7 | 29.3 | 5.7 | juv. | 6 | |
| *D. delphis* ♂♂ | | | | | | | | |
| ZMA | 11.888 | 183 | 43 | 13.5 | 3.1 | 0.03 | 5 | |
| ZMA | 14.002 | 217 | 111 | 11.6 | 3.3 | 0.6 | 19 | |
| ZMA | 14.516 | 176 | 56.5 | 13.8 | 2.6 | 0.03 | 3 | |
| ZMA | 14.450 | 207.5 | 104 | 14.4 | 3.2 | 0.6 | 10 | |
| ZMA | 15.139 | 230 | 125 | 10.6 | 3.4 | 2.0 | 13 | |
| ZMA | 15.140 | 235 | 122 | 13.2 | 3.2 | 2.0 | 13 | |
| ZMA | 15.166 | 194 | 67 | 15.8 | 3.1 | 0.02 | 5 | |
| ZMA | 15.169 | 199 | 76.5 | 14.3 | 3.2 | 0.1 | 8 | |
| ZMA | 15.513 | 188 | 77 | 12.9 | 2.9 | 0.1 | 8 | |
| ZMA | 15.920 | 203 | 95 | 8.8 | 3.4 | 0.24 | 12 | |
| *D. delphis* ♀♀ | | | | | | | | |
| | | | | | | ovaries | | |
| ZMA | 14.119 | 206 | 108 | 12.3 | 3.1 | mat. | 14 | 3) |
| ZMA | 14.289 | 137 | 46.5 | 13.8 | 2.5 | juv. | 2 | |
| ZMA | 15.165 | 198 | 84 | 12.2 | 3.4 | mat. | 14 | |
| ZMA | 15.168 | 174 | 56 | 13.9 | 2.9 | juv. | 3 | |
| ZMA | 15.211 | 106.5 | 16 | 8.9 | 2.4 | juv. | -1 | |
| ZMA | 15.425 | 193 | 64.5 | 14.6 | 2.9 | juv. | 6 | |
| ZMA | 15.528 | 142.5 | 36.5 | 12.6 | 3.4 | juv. | 1½ | |
| *Sotalia fluviatilis* ♂♂ | | | | | | | | |
| RMNH | 22258 | 157 | 52 | 17.2 | 4.1 | 0.04 | 6 | |
| RMNH | 22256 | 146 | 35 | 16.7 | 4.2 | 0.03 | 3-4 | |
| RMNH | 22257 | 167 | 60 | 16.8 | 4.4 | 1.2 | 11 | |
| RMNH | 22259 | 187 | 83 | 17.3 | 4.4 | 1.4 | 12 | |
| RMNH | 22260 | 183.5 | 66 | 16.4 | 3.5 | 1.6 | 10 | |
| ZMA | 19.775 | 170 | 55 | 18.9 | 4.5 | 0.4 | 9 | |

| Coll. no. | | length (mm) | weight (kg) | tooth length (mm) | tooth diam. (mm) | % testis weight | age | |
|---|---|---|---|---|---|---|---|---|
| *Sotalia fluviatilis* ♀ ♀ | | | | | | | | |
| | | | | | | ovaries | | |
| RMNH | 21756 | 165 | 57 | 16.9 | 4.1 | juv. | 7 | |
| RMNH | 21755 | 182 | 78 | 18.5 | 4.6 | mat. | 11 | 4) |
| ZMA | 19.776 | 162 | | 17.2 | 4.5 | mat | 12 | |
| ZMA | 19.780 | 169.5 | 50.3 | 16.7 | 4.5 | juv. | 8 | |
| *Kogia breviceps* ♂ ♂ | | | | | | | | |
| ZMA | 16.031 | 200.6 | | 13.4 | 3.9 | juv. | 1½ | |
| ZMA | (a) | 289.6 | | 20.5 | 4.9 | | 6 | |
| ZMA | 16.996 | 266.7 | | 20.8 | 4.3 | | 6½ | |
| ZMA | 16.028 | 322.6 | | 31.5 | 4.6 | | 8 | |
| ZMA | 16.032 | 251.4 | | 25.5 | 3.8 | | 10 | |
| ZMA | 16.986 | 312.4 | | 31.9 | 5.3 | | 10½ | |
| ZMA | 14.539 | 350.5 | | 27.5 | 4.3 | | 12½ | |
| ZMA | 16.029 | 307.4 | | 28.8 | 5.0 | | 14 | |
| ZMA | 16.030 | 320.0 | | 35.4 | 5.1 | | 18 | |
| ZMA | 12.894 | 304.8 | | 30.2 | 4.3 | | 19 | |
| ZMA | 14.817 | 335.3 | | 42.8 | 6.4 | | 32 | |
| *Kogia breviceps* ♀ ♀ | | | | | | | | |
| ZMA | 14.824 | 236.2 | | 19.1 | 3.1 | juv. | 4 | |
| ZMA | 16.984 | — | | 34.2 | 5.0 | preg. | 8 | |
| ZMA | 16.034 | 274.3 | | 29.5 | 4.7 | preg. | 8 | |
| ZMA | 16.027 | 299.7 | | 23.6 | 5.3 | | 9½ | 5) |
| ZMA | 16.997 | 269.2 | | 31.4 | 4.9 | | 11 | |
| ZMA | 13.224 | 304.8 | | 34.9 | 5.9 | preg. | 11 | |
| ZMA | 15.241 | 302.2 | | 26.0 | 4.3 | | 19 | |
| ZMA | 14.559 | 294.6 | | 22.0 | 5.5 | preg | 23 | |
| ZMA | 14.821 | 304.8 | | 27.2 | 3.8 | | 12 | 6) |
| ZMA | 13.439 | 292.0 | | 26.3 | 4.8 | | 13 | 6) |
| ZMA | 12.890 | — | | 30.8 | 4.3 | | 17 | 6) |

1) tooth broken or worn down; 2) pregnant, foetus ♀, 56 cm; 3) pregnant, foetus ♀, 84 cm; 4) pregnant, foetus ♀, 59 cm; 5) tooth broken; 6) sex unknown. N.B. All male animals which have a testis weight of well over 0.1% of the body weight are considered to be sexual mature.

doubt whether in *Stenella* the formation of dentinal layers is annual throughout life or whether the formation rate changes.

In the enamel cap, when present, layers or the so called striae of Retzius, are present. However, after the formation of this part and the eruption of the tooth from the gum, no more material is added here and the enamel organ disappears, so these layers can not be used in age determination.

Both the cementum and the dentine are of mesenchymal origin (see Keil, 1966). This makes a parallelism in the growth features in both components of the teeth plausible. The enamel cap is of ectodermal origin. So are the baleen plates of the Balaenidae and Balaenopteridae, however, these plates continue to grow during life.

The analysis of changes and variations in the thickness in the baleen plates of Fin Whales revealed features which are evidently related to cyclic and incidental variations in the physiological balance of these animals, related to, e.g., changes in the environment. Moreover, in females changes in thickness of the baleen plate were found, which are evidently related to ovulations (Van Utrecht, 1966; Van Utrecht-Cock, 1966). The same is true for growth features visible in the ear plugs of these animals. These plugs are also of epidermal origin (Van Utrecht & Van Utrecht-Cock, 1969). Records made of the variations in thickness in the baleen plates revealed sexual dimorphism in the pattern of peaks and hollows. In sexually mature males the records have a far more regular pattern than those of sexually mature females. When the records of baleen plates of the various species of Balaenopteridae are compared, a difference in the repeated pattern of peaks and hollows becomes evident.

The aim of the present analysis of the growth of the dentinal layers in the teeth of some species of delphinids is to see whether features found here are comparable to those found in the baleen plates, and also to compare the results obtained from the teeth of various species of odontocetes.

## MATERIAL AND METHODS

For the present study the teeth, taken from the middle of the left mandibula, of 20 males and 34 females of *Phocoena phocoena* (Linnaeus, 1758) and four males and 12 females of *Lagenorhynchus albirostris* (Gray, 1846), both from the North Sea, six males and four females *Sotalia fluviatilis* (Gervais, 1853) from Surinam, 10 males and seven females of *Delphinus delphis* (Linnaeus, 1758) from New Zealand, and 11 males and 8 females of *Kogia breviceps* (De Blainville, 1838) also from New Zealand, are used. The results are compared with the features in the teeth of a few individuals of *P. phocoena* from the Baltic area and from the waters off Dakar. Moreover, the results are compared with those from the teeth of *Globicephala melaena* (Traill, 1809) and *Tursiops truncatus* (Montague, 1821).

Prior to sectioning the teeth for age analysis, their length and diameter were measured. The sections, about 120 $\mu$m thick, were made with a low speed diamond circular saw as previously described (Van Utrecht, 1978). The dentinal growth layers were counted repeatedly, in polarised light as well as in normal transmitted light, using 37.5 × magnification. The thickness and length of the successive layers were measured. All measurements of the thickness of the layers were taken across the sections at the level of the surface of the gum, to be sure that they were at a comparable level in all individuals. The total thickness of the dentinal layers, thus including in each measurement a translucent and an opaque zone, was measured. Moreover, the variations in density in the growth layers and cementum were measured and recorded by means of a set of apparatus described by Van Utrecht (1971) and Van Utrecht & Schenkkan (1972), in order to get detailed information.

## RESULTS OF MEASUREMENTS

In table I the data are mentioned, except for *P. phocoena*, which were given elsewhere (Van Utrecht, 1978). The teeth of males of *P. phocoena* in the present material have a mean length of 11.4 mm (*var.* = 1.4, S.D. = 1.2, $N$ = 19, min. = 9.0 mm, max. = 12.8 mm). In females the mean length of the teeth is 11.8 mm (*var.* = 1.7, S.D. = 1.3, $N$ = 32, min. = 8.6 mm, max. = 14.4 mm). In males the mean diameter is 2.4 mm (*var.* = 0.1, S.D. = 0.3) and in females 2.3 mm (*var.* = 0.1, S.D. = 0.4). So in this species there is a slight difference in length of the teeth between the sexes, however, there is no difference in their diameter.

In *L. albirostris* the teeth of males have a mean length of 26.9 mm (*var.* = 5.5, S.D. = 2.3, $N$ = 4, min. = 23.8 mm, max. = 29.9 mm). The teeth of females have a mean length of 27.5 mm (*var.* = 4.1, S.D. = 2.0, $N$ = 12, min. = 23.6 mm, max. = 30.1 mm). In *L. albirostris* there is the indication of a small difference in length of the teeth between males and females. In this species, as in the one first mentioned, the teeth are oval, with the long axis about parallel to the long axis of the mandible. As this is also the plane in which the sections are made, only the greatest diameter of the teeth is given. In males the mean for the greatest diameter is 5.7 mm (*var.* = 0.3, S.D. = 0.5, $N$ = 4). In females the mean is 5.9 mm (*var.* = 0.1, S.D. = 0.4, $N$ = 12). There is no difference in the diameter of the teeth between males and females of *L. albirostris*.

In *S. fluviatilis* the mean length of the teeth is 17.1 mm (*var.* 0.4, S.D. = 0.6, $N$ = 7, min. = 16.4 mm, max. = 18.5 mm), while the mean for the greatest diameter is 4.19 mm (*var.* = 0.1, S.D. = 0.3, $N$ = 7). The data for males and females are taken together, as the number of animals of this species examined so far is only seven.

In *D. delphis* the mean length of the teeth in males is 13.3 mm (*var.* = 2.1, S.D. = 1.5, $N$ = 9, min. = 10.6 mm, max. = 14.4 mm). In females the mean length of the teeth is 12.6 mm (*var.* = 3.0, S.D. = 1.7, min. = 8.8 mm, max. = 14.6 mm). When a very young animal, less than one year old, is excluded, the mean length becomes 13.2 mm (*var.* = 0.8, S.D. = 0.9, $N$ = 6). In this species there is no or only a small difference in tooth length in both sexes. The mean for the greatest diameter of the teeth of males of *D. delphis* is 3.1 mm (*var.* = 0.05, S.D. = 0.23, $N$ = 10), for females the mean is 2.9 mm (*var.* = 0.13, S.D. = 0.37, $N$ = 7).

When these data are related to the age readings given in table I, it is obvious that in the species examined so far the teeth reach their ultimate diameter very early, most probably before eruption from the gum. However, the teeth attain their maximum length later, as a mean when the third or fourth dentinal layer is completely formed.

The growth in length of the teeth was examined in *P. phocoena.* For this purpose, in the sections the distance was measured along the outer wall of the teeth, from the point where the lower end of the neonatal or primary line meets the outer surface, to the lower end of the first dentinal layer where this meets the outer surface, and from this point to the corresponding point for the second dentinal layer, and so on. These measurements give an indication of the increment in length of the teeth. The means and other data are given in table II.

From these data it is evident that there is a rapid decline in the increment in length of the teeth of *P. phocoena* in the period the first four layers are formed. After that the rate of deposition becomes fairly constant. In table II it is shown that there is a great individual variation in the length of the growth layers I and II. After the deposition of the third growth layer, the yearly increment in length of the teeth is in *P. phocoena* about 0.2 mm or 200 μm per annum. It is hard to get enough information about older animals, with eight or more dentinal layers. However, as far as data of older animals were available they indicate that there is only a small decrease in this figure. From the figures given it is clear that the main growth in length in the teeth of *P. phocoena* takes place in the first three or four years, provided that the growth layers are annual depositions.

Table II. Measurements of dentinal growth layers in the teeth of *Phocoena phocoena.*

| dentinal growth layer | mean | var. | S.D. | $N$ |
|---|---|---|---|---|
| I | 4.34 mm | 1.16 | 1.21 | 25 |
| II | 0.91 mm | 0.41 | 0.43 | 24 |
| III | 0.47 mm | 0.04 | 0.04 | 23 |
| IV | 0.26 mm | 0.01 | 0.01 | 16 |
| V | 0.23 mm | 0.01 | 0.01 | 13 |
| VI | 0.22 mm | 0.01 | 0.01 | 6 |
| VII | 0.20 mm | 0.01 | 0.01 | 4 |

From the above given data it is evident that there is not much variation in the diameter of the teeth in relation to the number of growth layers present. In order to see whether changes in thickness of the dentinal layers parallels the above given data, the thickness of the successive layers was measured across the root, somewhat below the level where the end of the neonatal line meets the outer surface of the tooth. The results of these measurements are given in the figures 1, 2, 3, 4 and 5, for *P. phocoena, L. albirostris* and *D. delphis.*

In figs. 1 and 2 the results are given for males and females of *P. phocoena* from the North Sea. There is a steep decline in thickness in the first three or four dentinal layers, in both sexes. After the deposition of the fourth layer the decrease gradually diminishes. In males the thickness of the first layer varies from about 120 μm to about 360 μm (mean = 197 μm), and in females from about 100 μm to about 320 μm (mean = 206.8 μm). The graphs show great individual variation. However, in both sexes the thickness of the first dentinal layer never exceeds 400 μm. In most animals this layer is well below 300 μm thick. The thickness of the following layers gradually diminishes to about 40 μm-60 μm, as measured in the

12th dentinal layer in the present sample. These results differ from those for *P. phocoena* from the western North Atlantic (Gaskin & Blair, 1977), in which considerably greater thickness for the dentinal layers was found. In the material studied by Gaskin & Blair (loc. cit.) the thickness is between 200 μm and 850 μm. Moreover, the decrease in thickness of the layers showed a linear relation with the increasing number of layers (see their figs. 8 and 9, p. 23). It means that in this case the teeth should have a far greater diameter than was found for *P. phocoena* from the North Sea. The data and graphs of North Sea animals show that the reduction in thickness of the dentinal layers is not linear. This is also the fact for the other species examined. This difference in the trend of the lines can certainly not be explained from the fact that for *P. phocoena* the data from two different populations are compared.

In *P. phocoena* there is a rapid decline of the thickness in the first three or four layers. Afterwards, the decline diminishes and approaches an asymptote. Therefore, the relation between the age of the animal to the thickness of the dentinal layers can not be expressed rectilinear, unless the data are plotted logarithmically. For *P. phocoena* from the North Sea the relation is in males: $\log Y = -0.47 \log X + 2.79$ (r. = 0.69, $N$ = 62, $P < 0.001$, X is the age in months, Y is the thickness of the dentinal layer at that age). In females this relation is: $\log Y = -0.44 \log X + 2.74$ (r = 0.64, $N$ = 125, $P < 0.001$). There is no difference in this aspect between both sexes, contrary to the results of Gaskin & Blair (1977), in which a considerable difference in the equations for the linear regression for the dentinal layers was found between males and females.

The teeth of three animals from the Baltic Sea

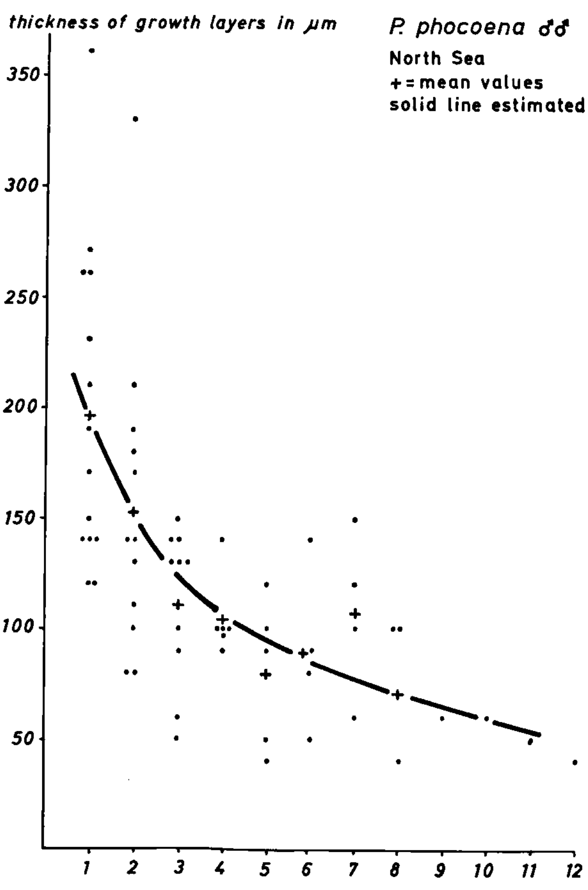


Fig. 1. *P. phocoena*, males. Decrease in thickness of the dentinal layers with the increasing numbers of layers.

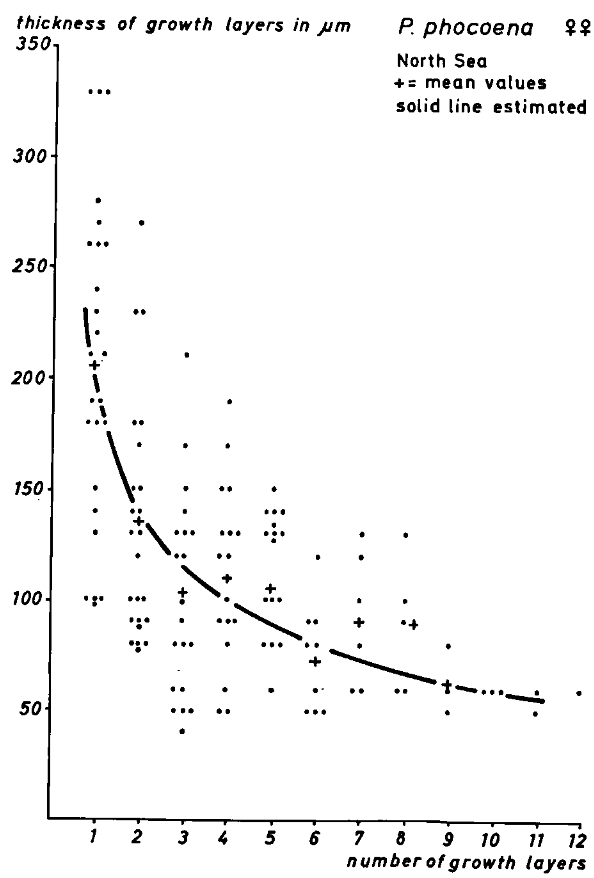


Fig. 2. *P. phocoena*, females. Decrease in thickness of the dentinal layers with the increasing numbers of layers.

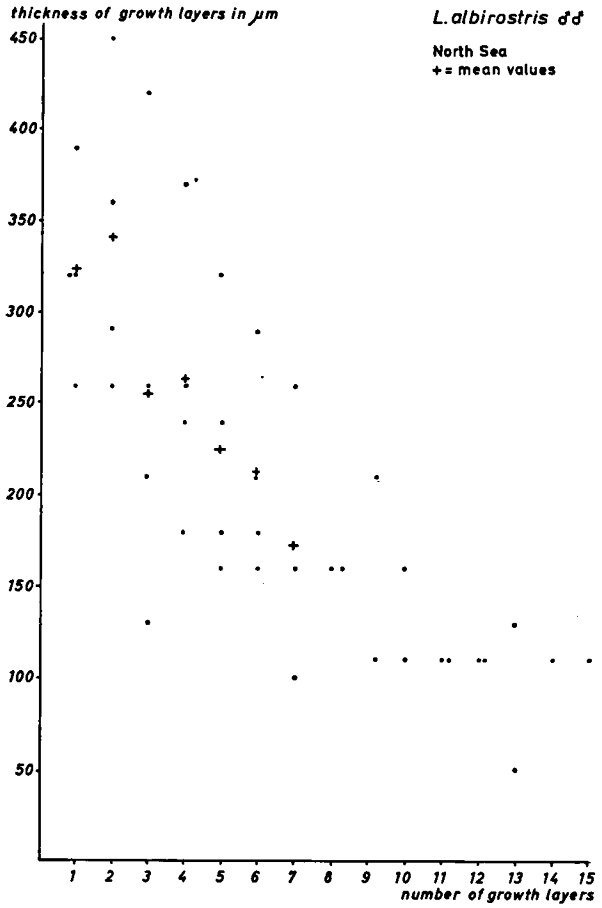


Fig. 3. *L. albirostris*, males. Decrease in thickness of the dentinal layers with the increasing numbers of layers.

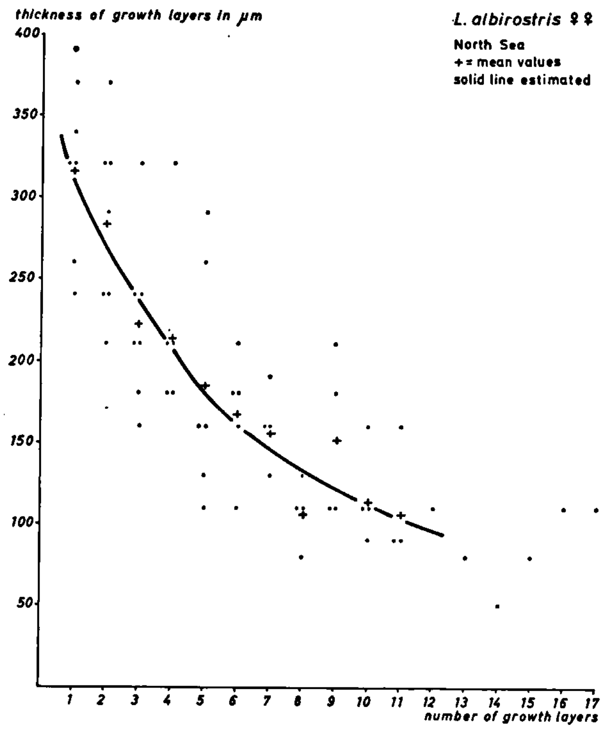


Fig. 4. *L. albirostris*, females. Decrease in thickness of the dentinal layers with the increasing numbers of layers.

were examined. They had six, nine and ten layers in their teeth respectively. The thickness of the dentinal layers and the decrease in thickness of subsequent layers is equal to what was found for animals from the North Sea. Only one *P. phocoena* caught off Dakar was available for examination. In the dentine of this animal nine layers were present. In this case the thickness of the layers was well below that found for the animals from the North Sea. In this animal, after a decrease in thickness in the first three layers from about 230 µm to about 30 µm, the following layers were all about 40 µm thick. Here the formation of the dentinal layers, with respect to their thickness, is different from what was found for the teeth of animals from the North Sea population. In none of the teeth of this species examined so

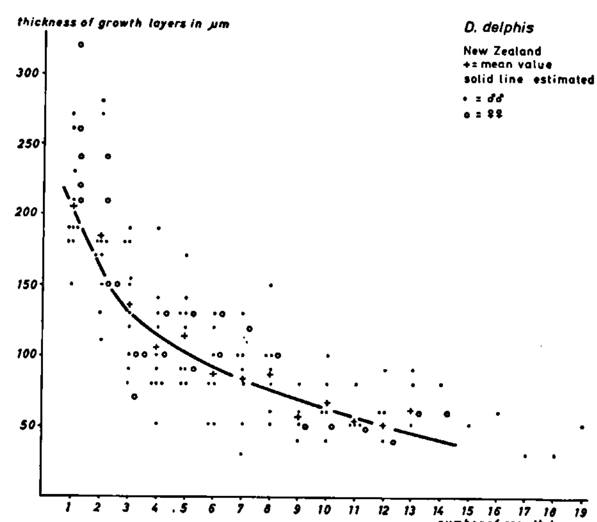


Fig. 5. *D. delphis*. Decrease in thickness of the dentinal layers with increasing numbers of layers.

far, osteodentine pearls or secondary dentine was found.

In the course of a number of years data and material of four males and twelve females of *L. albirostris* became available. All animals were found along the Dutch coasts, except a few animals which were accidentally caught in trawlnets in the North Sea. For males and females the mean length and diameter of the teeth is given above. Though the present sample is too small for definite conclusion, the available data show that, just as for *P. phocoena*, the teeth of *L. albirostris* attain their maximum length when the third or fourth dentinal layer is formed. The maximum diameter is reached at a much earlier moment. In this species the thickness of the layers in the dentine was measured in the same way as in the teeth of *P. phocoena*. However, in *L. albirostris* the regular development of the layers was disturbed by the formation of osteodentine pearls. This was also found in the teeth of *T. truncatus* and *D. delphis*.

In the figs. 3 and 4 the thickness of the successive layers and their decrease in thickness, together with the mean values are given for males and females. In the teeth of females the thickness of the first layer varies from about 250 $\mu$m to about 400 $\mu$m and does not exceed this last figure. The same is found for males. The mean value for the thickness of the first dentinal layer is 322.5 $\mu$m in males and 320 $\mu$m in females. The following layers gradually diminish to a thickness of about 100 $\mu$m when eight layers are deposited. In *L. albirostris* the decline in thickness of the layers follows the same course as in *P. phocoena*, although at a higher level. In *L. albirostris* the mean thickness of the layers is about twice as found for *P. phocoena*. In males the thickness of the layers is slightly greater than in females. The logarithmic plot for the regression of the thickness of the dentinal layers in *L. albirostris* shows the relation:

$\log Y = -0.52 \log X + 3.17$ ($r = 0.79$, $N = 104$, $P < 0.001$). For the calculations the data for males and females are taken together.

Teeth were available from seven females and 10 males of *D. delphis*, from New Zealand waters. As the results of the measurements do not differ much in both sexes, they are given together in fig. 5. In males the thickness of the first dentinal layer varies from about 150 $\mu$m to about 260 $\mu$m. and in females from about 210 $\mu$m to about 330 $\mu$m. The thickness of the following layers decreases gradually to about 50 $\mu$m-100 $\mu$m (mean 60 $\mu$m) when 10 layers are deposited. In the next 10 layers this decrease continues, although at a lower rate. At last the thickness is about 50 $\mu$m. In this species the logarithmic plot for the decrease in thickness has the relation:

$\log Y = -0.55 \log X + 2.98$ ($r = 0.81$, $N = 123$, $P < 0.001$). This result does not differ much from that calculated for *P. phocoena*.

A comparison of the results for the three species reveals that there is not much difference in the mean thickness of the dentinal layers in *P. phocoena* and *D. delphis*. In the latter species more layers are present. In *L. albirostris*, however, the mean thickness of the layers is much greater. They are about twice the thickness found in the species first mentioned. The same is true for *T. truncatus* and *G. melaena*. Here the mean thickness in the first four layers decreases from about 373 $\mu$m to 333 $\mu$m.

In *S. fluviatilis* the thickness of the first dentinal layer is about the same as in *P. phocoena*, (about 220 $\mu$m). However, the decrease in thickness in more gradual, so the thickness of the seventh layer is about 130 $\mu$m (fig. 6). After the deposition of seven or eight layers, the formation of the layers suddenly changes such that subsequent layers are narrow, very regular and uniform in appearance.

When examined under a higher magnification (fig. 7) it becomes clear that through the first seven or eight layers, the dentine tubules all run parallel to each other from the borderline with the cementum inwards to the pulp cavity. In older animals this regular pattern suddenly changes. At rather regular distances to each other the dentine tubules are coming together in one point, forming a brush-like structure. This point is often formed by a relatively large and dark odontoblast-like body. In the following layers the dentine tubules are no longer parallel to each other. There are now odontoblasts and fine granulae arranged in parallel rows, from which fine dendrite-like tubules go over a short distance in all directions

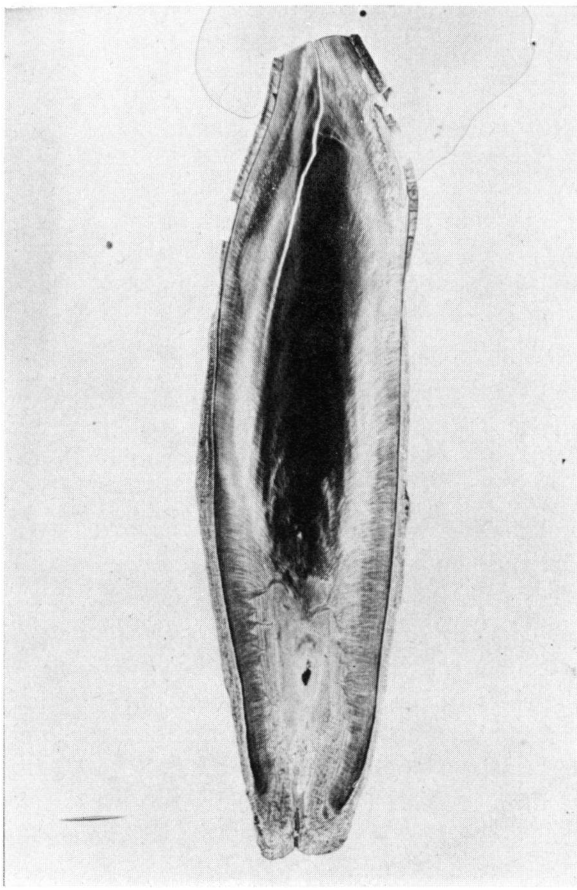

Fig. 6. Section of a tooth of *S. fluviatilis* showing the arrangement of the dentinal layers.

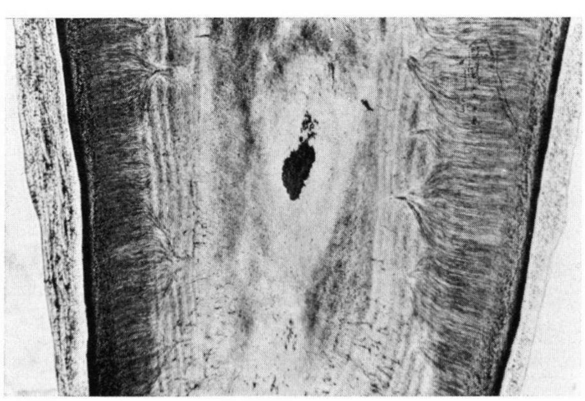

Fig. 7. Section of a tooth of *S. fluviatilis* showing the change in direction and arrangement of the dentinal tubules in the deeper layers of the dentine and the subsequent rows of granulae.

into the surrounding dentine. Under a low magnification this leaves the impression that fine dark lines are present. In all individuals of *S. fluviatilis* available for examination having over seven dentinal layers, this phenomenon was present. This was not found in the teeth of other species of odontocetes examined so far. This feature makes age determination in *S. fluviatilis* unreliable.

## RECORDS OF THE VARIATIONS IN DENSITY

In the dentine and often also in the cementum light transparent layers, separated by dark lines are visible in a more or less regular sequence. They resemble the features present in the earplugs of baleen whales (Purves, 1955, Van Utrecht & Van Utrecht-Cock, 1969). For *Balaenoptera physalus* (Linnaeus, 1758) it was demonstrated that records made of the reflecting capacity of the successive dark and light layers, visible in the bisected earplug, showed the same features as were found in the records of the variations in thickness of the baleen plates (Van Utrecht & Van Utrecht-Cock, 1969). In each individual animal both records are similar. This is self-evident because both structures are formed by epidermal tissue. The baleen plates are formed by the epidermis covering the roof of the mouth, while the earplug is formed by the epidermis covering the glove finger, a structure which projects over some distance into the external auditory meatus.

The records of the variations in thickness of the baleen plates of *B. physalus* show a regular pattern of peaks and hollows. It was shown that these repeated patterns are yearly increments in length of the baleen plate on which momentary variations in the mitotic activity of the epithelium forming the plates are superimposed. The growth of the plates is influenced by environmental (food, migration) and endogenous (e.g. sexual cycle) factors (Van Utrecht, 1966; Van Utrecht-Cock, 1966). The same is true for the earplugs (Van Utrecht & Van Utrecht-Cock, 1969). There is a difference between the records of the baleen plates of juvenile and sexual mature animals, and between the records of the plates of males and females, the latter caused by the sexual cycle.

This is particularly clear in the records of the baleen plates of females. Here characteristic peaks are present which can be related to ovulations (Van Utrecht-Cock, 1966).

Moreover, when series of records of baleen plates of various species are compared, differences between them become evident, i.e. the patterns are specific.

For the present study records are made of the variations in density visible in thin sections of teeth. This is done by means of a set of apparatus described by Van Utrecht (1971) and Van Utrecht & Schenkkan (1972). It consists of a microscope which has an adjustable slit and a LDR (light dependant resistance) over one of the oculars, while a low speed adjustable electromotor drives the turntable. The signal of the LDR is fed into a strip chart recorder.

The records made in this way clearly show the variations in density along the recorded part of the tooth as well in the cementum as in the dentine. However, a particular repetitive pattern, as present in the record of baleen plates and earplugs, is hard to discern. Even the records of the teeth of the various species of dolphins examined do not show marked differences. It is fairly impossible to devide these records into growth periods, as done in the records of the baleen plates. This is due to the decrease in thickness of the layers in the dentine, as described above. The width of the layers in the dentine rapidly decreases and never becomes reasonably constant. This is in contrast to what is found in the records of the baleen plates, where the growth periods are reasonably constant in length. So in the dentine the fine layers present in the growth layers become extremely packed. They are only distinguishable in the first three or four growth layers.

The difference in expression of growth features between teeth and e.g. baleen plates is most probably related to their origin. Both baleen plates and earplugs are solely formed by the epidermis. The teeth, however, originate from two different germinal layers, the ectoderm and the mesenchym. The enamel cap is formed by the ectoderm during the embryonal development. In the later stages the enamel organ is resorbed and no more enamel is formed or added. The dentine and cementum are formed by highly differentiated connective tissue originating from the mesenchym. Both are formed and added during practically the whole life of the animals.

In the records of the teeth of *P. phocoena* it was found that the numbers of layers, peaks and hollows, in the part of the records that represented the cementum was the same as the numbers of layers that could be counted by eye in the dentine. In the other species of odontocetes examined so far, the cementum showed a sequence of light and dark layers. However, in a great number of animals these layers are rather irregular and difficult to count. This is most probably related to the fact that the development of the cementum and the layers in it is greatly influenced by the mechanical load exerted on the teeth (see also Keil, 1966). In *Phoca vitulina* (Linnaeus, 1758), the Harbour Seal, a strong development of the cementum takes place around the lower end of the roots of the canines when the third dentinal layer is deposited. Before that time no cementum was present, which may indicate the influence of the mechanical load on the formation of cementum.

In the cementum of the teeth of *D. delphis*, *S. fluviatilis* and *L. albirostris* the layers are not well defined. They are also not as clearly defined in the records as was found for *P. phocoena*. In most cases the layers in the cementum had a wavy course and often varied in numbers from one place to another.

In *Kogia breviceps* (Physeteridae) the situation is different, though it is also an odontocete. In this species no enamel cap is formed, the teeth consist only of a core of dentine and a layer of cementum (fig. 8). The dentinal growth layers are added under an acute angle to the long axis of the tooth. In a longitudinal section they are present as chevrons, one placed over another. The root of the teeth remains open during life. The tissues in the pulp cavity remain intact and the addition of dentine layers is not hampered.

There is a slight decrease in thickness of the growth layers throughout life. However, in the oldest individual of this species which became available, with 32 layers in the dentine, the thickness of the last formed layer was such that also

Fig. 8. *K. breviceps.* Longitudinal section of a tooth showing the regular arrangement of the dentinal layers.

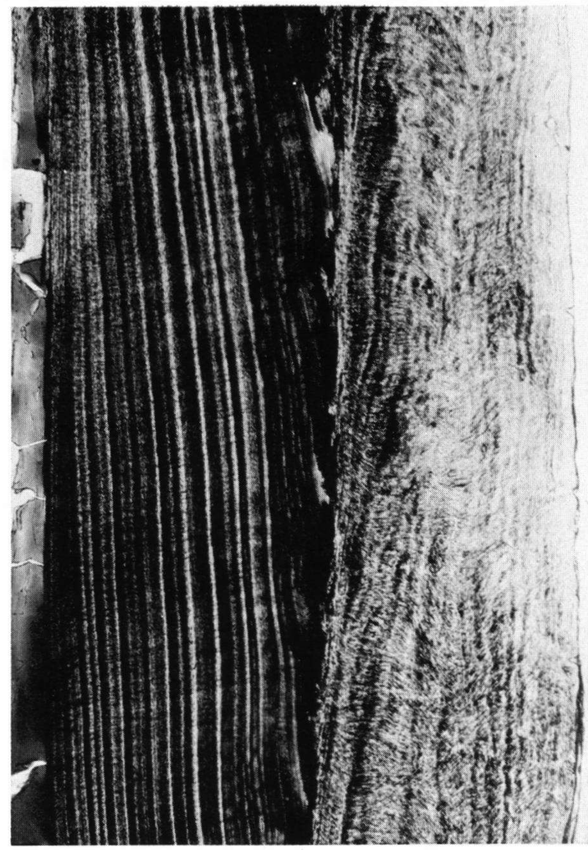

Fig. 9. *K. breviceps.* Part of the toath of fig. 8 under higher magnification, showing the nearly uniform thickness of the dentinal layers and the wavy course of the layers in the cementum at the right.

the secondary dark bands were easily discernible (fig. 9).

In the cementum of the teeth of *K. breviceps* layers are visible (fig. 9). From the present material it proved that counting of them is hardly possible, because they are very irregular in development and course. This is in particular in the cementum covering the outer curve of the teeth. The cementum at the inner curve of the teeth shows far more regular layers. However, here each layer does not cover the entire length in the cementum, they are placed one over another like shingles.

From the material available it proved that the teeth in *K. breviceps* increased in length during the formation of the first eight growth layers. This is in accordance with the results of the measurements taken from the skull, which showed an increase in dimensions during this period, and remaining constant thereafter. Further growth in length must be compensated by wear of the crown, which is facilitated as no enamel cap is present. In *K. breviceps* the period in which the growth in length of the teeth and the growth of the skull takes place, is about twice as long as in other species of cetaceans.

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