Review of the Formation
of Incremental Lines in Tooth Cementum
# of Terrestrial Mammals

by
HELEN GRUE & BIRGER JENSEN

Med et dansk resumé:
Oversigt over dannelse af vækstlinier i tændernes rodcement
hos terrestriske pattedyr

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DANISH REVIEW OF GAME BIOLOGY

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Introduction

The possibility of determining age of a mammal from the histological structure of its teeth is one of the most useful tools available for wildlife research and management. During the last 25 years, annual incremental lines in tooth cementum have been found in almost every group of mammals, terrestrial as well as marine (for references see KLEVEZAL & KLEINENBERG 1967, MADSEN 1967, SERGEANT 1967, MORRIS 1972, SPINAGE 1973, BOULIÈRE & SPITZ 1975, PUCEK & LOWE 1975, MORRIS 1978, KIMURA in prep.). Today the method is considered a routine tool in population studies.

Appositional growth resulting in development of incremental lines is found both in cementum and dentine, as well as in bones. In most species of terrestrial mammals, dentine structures normally may not be suitable for age determination, at least not beyond the first years of life (MORRIS 1972). Dentine is deposited within the tooth, gradually filling the pulp cavity, and thus space can be a limiting factor. In addition dentine more often than the cementum shows multiple accessory groups of lines which make interpretation difficult. Bone features can be useful for determining age in some species (for references see KLEVEZAL & KLEINENBERG 1967), but loss of features may occur within the bone tissue as well as on the external surface, caused by resorption and standard cleaning processes respectively. Thus structures in tooth cementum are normally preferable when present and available for study in a species. This review is therefore largely restricted to structures in root cementum and for practical reasons furthermore restricted to terrestrial mammals.

Even though the procedure of assigning age by means of cementum structures (cementum reading) is so valuable to mammalogy, the physiological processes leading to development of incremental lines in cementum and their regulation are almost unknown. Concepts adopted from human odontology suggest that incremental lines represent periods of arrested cementoblast activity. Retardation in cementum growth may then reflect a general slowing down in growth of organisms, caused for example by regular seasonal changes in the overall growth rate (KLEVEZAL & KLEINENBERG 1967). Nevertheless, critical investigations supporting such statements are still lacking, and if the method in question is to retain its present status as the most reliable one for age determination, both the internal and external factors which regulate development of cementum structures should be clarified. In addition, it should be known to what extent the presence of these factors is required to produce synchrony between incremental line deposition and seasons of the year. Investigation of these points can either be done experimentally by keeping animals under controlled conditions, or by comparing the nature of the cementum structures and time for their development with the changes in the environment to which wild populations are exposed. The present review is primarily based on the latter method.

For a number of species of terrestrial mammals from the Palaearctic region the authors examined cementum structures and time for their development and compared these to the biology and life conditions of the animals. Furthermore, literature dealing with age determination by means of incremental lines in root cementum of teeth was reviewed in order to collate the scattered information on the nature of cementum structures and especially

the time of year for their deposition. Rhytmic development of tooth cementum resulting in formation of incremental lines is generally accepted to be present in every species of terrestrial mammals possessing teeth with a closed root. It is not the intention here to present a complete list of the species for which presence of annual cementum structures has been reported; the review specifically aims to compile present knowledge of formation of cementum incremental lines and their regulation in terrestrial mammals. Furthermore it aims to present it in a way which will simplify comparison, indicate questions of importance concerning age determination and indicate questions which require answering if a better understanding of the processes leading to the formation of cementum incremental lines is to be reached.

Materials

Information on the nature of cementum incremental lines and the season for their development is based on three different sources:

1) Teeth made available by various persons and institutions, and prepared by one of the authors (HG). Most slides possessed by the authors (own material).

2) Prepared slides or cut teeth, borrowed from persons who primarily had them prepared for age determination (borrowed material).

3) Information from literature.

1) Own material:

Nyctalus noctula, 28 animals from Copenhagen, Denmark (Zool. Mus., Coph. - Hans Baagøe). Material utilized by BAAGØE (1977).

Canis familiaris, 18 domesticated animals from various localities in Denmark (authors' collection). Material utilized by GRUE (1976).
35 semi-domesticated animals from various localities in both West and East Greenland (Zool. Mus., Coph. - Chr. Vibe). Part of this material utilized by GRUE (1976).
47 semi-domesticated animals from various localities in West Greenland (State Veterinary Serum Lab., Coph. - J. Müller).
2 semi-domesticated animals from Godhavn, West Greenland (authors' collection).
6 semi-domesticated animals from Holsteinsborg, West Greenland (G.B.S., Kalø - Birger Jensen).

Alopex lagopus, 44 animals from various localities in West Greenland (Zool. Mus., Coph. - Chr. Vibe). Material utilized by GRUE & JENSEN (1976).
20 animals from a fur farm in Denmark (G.B.S., Kalø - Birger Jensen). Material utilized by GRUE & JENSEN (1976).

Vulpes vulpes, about 1000 animals from various localities in Denmark (G.B.S., Kalø - Birger Jensen). Part of this material utilized by JENSEN & NIELSEN (1968) and GRUE & JENSEN (1973).
20 animals from various localities in Holland (Res. Inst. for Nature Management, Arnhem - F. Niewold).

20 animals from outskirts of London, England (Dept. of Zool., Royal Holloway College, Univ. of London - Stephen Harris).

Ursus maritimus, 41 animals from Northeast Greenland (Zool. Mus., Coph. - Chr. Vibe).

Martes martes, 29 animals from various localities in Denmark (G.B.S., Kalø - Birger Jensen and Zool. Mus., Coph. - Hans Baagøe).

Martes foina, 222 animals from various localities in Denmark (G.B.S., Kalø - Birger Jensen).

Mustela erminea, 89 animals from various localities in Denmark (G.B.S., Kalø - Mette Fog and Birger Jensen). Part of this material utilized by FOG (1969).
96 animals from various localities in Sweden (Dept. of Ecology, Univ. of Lund - Sam Erlinge).

Mustela nivalis, 110 animals from various localities in Denmark (G.B.S., Kalø - Mette Fog and Birger Jensen). Part of this material utilized by FOG (1969).
75 animals from various localities in Sweden (Dept. of Ecology, Univ. of Lund - Sam Erlinge).

Mustela vison, 40 animals from a fur farm in Denmark (authors' collection).
21 animals from various localities in Norway (Zool. Mus., Oslo - Jørgen A. Pedersen).

Mustela putorius, 39 animals from various localities in Denmark (G.B.S., Kalø - Birger Jensen and Zool. Mus., Coph. - Hans Baagøe).

Meles meles, 232 animals from various localities in Denmark (Zool. Mus., Coph. - P. Valentin-Jensen).

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Lutra lutra, 95 animals from various localities in Denmark (G.B.S., Kalø - Birger Jensen). Material utilized by JENSEN (1964) and VAN BREE et al. (1966).

Felis silvestris, 12 animals from various localities in Slovakia (Inst. of Vertebrate Zool., Czechoslovak Acad. of Sci., Brno - Z. Kratochvil).

Felis catus, 132 domesticated animals from various localities in Bern Canton, Switzerland (Natural History Museum, Bern - Peter Lüps).

Capreolus capreolus, 94 animals from various localities in Denmark (G.B.S., Kalø - H. Strandgaard).
11 animals from Southeastern England (Donald and Norma Chapman).

Rangifer tarandus, 30 animals from West Greenland (G.B.S., Kalø - H. Strandgaard).

Cervus elaphus, 130 animals from various localities in Denmark (G.B.S., Kalø - Birger Jensen).

Cervus nippon, 30 animals from Frijsenborg, Jutland, Denmark (G.B.S., Kalø - Birger Jensen).

Dama dama, 14 animals from Southeastern England (Donald and Norma Chapman).

Of the following species less than 10 specimens have been sectioned; these are included in the discussion when appropriate: *Macropus agilis* (N.T., Australia), *Talpa europaea* (Denmark), *Erinaceus europaeus,* (Denmark), *Pteropus alecto* (N.T., Australia), *Pipistrellus pipistrellus* (Denmark), *Sciurus vulgaris* (Denmark), *Castor fiber* (Norway and Sweden), *Castor canadensis* (Finland), *Arvicola terrestris* (Denmark), *Rattus norvegicus* (Denmark - laboratory animals), *Muscardinus avellanarius* (Denmark), *Sicista betulina* (Denmark), *Canis lupus* (Ontario, Canada and West Greenland), *Canis dingo* (N.T., Australia), *Canis latrans* (Oklahoma, U.S.A.), *Nyctereutes procyonoides* (Finland and Denmark), *Procyon lotor* (Ontario, Canada), *Martes pennanti* (Ontario, Canada), *Taxidea taxus* (Oklahoma, U.S.A.), *Lutra canadensis* (Connecticut, U.S.A.), *Crocuta crocuta* (Kenya), *Lynx rufus* (Oklahoma, U.S.A.), *Equus caballus* (Denmark - domesticated), *Sus scrofa* (Denmark - domesticated and semi-domesticated - and Poland), *Odocoileus virginianus* (Connecticut,

U.S.A.), *Bos taurus* (Denmark - domesticated), *Bubalus bubalis* (N.T., Australia), *Syncerus caffer* (Kenya), *Rupicapra rupicapra* (Switzerland), *Capra cylindricornis* (U.S.S.R.), *Ovis musimon* (Europe), *Homo sapiens* (Denmark).

2) Borrowed material:

Sciurus vulgaris, 19 animals from various localities in Sweden (Grimsö Res. Lab. - Per Arne Lemnell).

Vulpes vulpes, 22 animals from various localities in Bern Canton, Switzerland (Veterinary Bacteriological Lab., Univ. of Bern - A. Wandeler).

Ursus maritimus, 83 animals from Svalbard (Norwegian Polar Res. Inst., Oslo - Thor Larsen).

Meles meles, 11 animals from various localities in England (Zool. Dept., Royal Holloway College, Univ. of London - P. Morris).

Lynx lynx, 337 animals from various localities in Norway (Game Res. Inst., Trondheim - Thor Kvam).

Alces alces, 18 animals from various localities in Norway (Norwegian State Game Res. Inst., Ås - Hans Haagenrud).

Rangifer tarandus, 195 animals from various localities in Norway - incl. 26 from Svalbard (Norwegian State Game Res. Inst., Ås - Eigil Reimers).

Cervus elaphus, 77 animals from various localities in Norway (Game Res. Inst., Trondheim - Rolf Langvatn).

Ovibos moschatus, 91 animals from East Greenland (Zool. Mus., Coph. - Hans Baagøe and Poul Henrichsen).

3) Information from literature:

Approximately 300 articles providing some information on age determination by means of cementum incremental lines have been reviewed with special reference to data on the season for development of cementum structures and factors influencing cementum development. Of these 125 contribute to the present work. However, the available data were often incomplete and did not allow detailed evaluation.

Methods

Teeth subjected to age determination can be processed in two different ways (for description of procedure see MORRIS 1972). Cleaved teeth or thin-sections prepared from undecalcified teeth are commonly used for large herbivores, while stained sections of decalcified teeth – usually processed according to standard histological

practice for soft tissue – are mostly used for smaller mammals where the cementum layer is thin. The latter method is however being increasingly used in larger species, as histological sections of small teeth (incisors) may give more accurate results than the undecalcified, thin-sections or polished surfaces of large teeth (molars).

To obtain information on the time of year for development of incremental lines in tooth cementum, the nature of the outermost layer on the root, i.e. the layer bordering the periodontal membrane, must be studied and correlated with time of death of the animal. In most species only histological sections are satisfactory for this purpose. If sections are relatively thin, less than 15 μ, and of an optimal technical standard an incremental line can be recognized during the actual process of apposition. The tendency of stain to accumulate round the edges of the sections can be confusing, but this is a minor problem for trained observers. In ground sections or thin-sections, however, the newly formed incremental line usually does not show up clearly until it is sealed off from the edge of the cementum layer, and thus more often recognizable only at a later state than in histological sections.

All teeth listed as *own material* (p. 4-5) have been processed at the same laboratory under constant guidance of one of the authors (HG). The general procedure was decalcification in 5% by volume HNO$_3$ (teeth kept in constant movement in order to minimize time of acid treatment), sectioning on a freezing-microtome, (thickness of sections varying from 6 to 12 μ depending on the species), staining with Mayers haemalun, blueing in 1% NaHCO$_3$, rinsing in tap-water, and mounting of coverslip with XAM, George T. Gurr. As far as possible the teeth were all treated in the same way to minimize the risk of differences in the final preparation due to different techniques. All teeth were sectioned longitudinally, usually incisors of ungulates and canines of other species.

Borrowed material was prepared at different laboratories and with slightly different techniques, but all teeth had been decalcified, cut longitudinally, stained and mounted according to standard histological methods.

Information from literature was based on all methods used for age determination by cementum incremental lines making comparison more difficult. Determination of the season for development of incremental lines is especially uncertain in undecalcified teeth and in transversely cut decalcified teeth.

Information on season for development of incremental lines has been used no matter which tooth was studied. Today selection of the tooth most suitable for age determination is merely considered a technical question, as the number of annual lines is usually the same in every undamaged tooth in the same animal when the time of formation of the first line is taken into account.

A varying terminology has been used to describe incremental lines, partly because the appearance of the lines depends on the technique used. This can cause some confusion and in the present paper the terms outlined below will be used. *Incremental lines:* All structures in the cementum layer which in stained sections of decalcified teeth appear as dark lines and in undecalcified thin-sections as thin lines of a different optical density than the surrounding tissue. These lines can normally be classified into three groups. *Primary lines:* these are generally well-defined and appear in a regular sequence. *Secondary lines:* these are all less well-defined lines found in all species and formed in a more or less regular sequence during the year. In males of some ungulates a secondary line can appear especially well-defined and is often called a

rut line. In juveniles a well-defined line can appear outside the normal season for formation of the primary line. This secondary line may be termed a juvenile line and may be comperable to the structure described especially in the dentine in some seals where it is called a weaning line (e.g. LAWS 1962). *Resorption lines:* these are the irregular lines resulting from reparative apposition processes. They are most frequently found in the apical part of the root in ungulates.

Time for development of the first incremental line

DECIDUOUS TEETH

Incremental lines in deciduous teeth have rarely been recorded in literature on cementum reading. Firstly, this may be due to the fact that many species shed the deciduous dentition or part of it so early in life that it is not present when young animals pass through the first season where line development normally occurs for the species in question. Secondly, to look for incremental lines in deciduous teeth with reference to age determination has not been necessary, as other and more simple methods have been available e.g. development of the secondary dentition.

McEVAN (1963) found a uniform calcified cementum zone in the incisor of a 3 month old calf of *Rangifer tarandus* and in the incisor of a calf 8 months old one "rest line" had been added to the cementum in close proximity to the fibrous periodontal membrane. TURNER (1977) found an incipient primary line in i_1 of *Ovis canadensis* 7-9 months of age, and in fawns of *Odocoileus hemionus columbianus* deciduous incisors show primary lines at age 7 to 9 months (BUNNELL pers. comm.). HITCHINS (1978) found cementum lines in the deciduous premolar of *Diceros bicornis* but they were extremely difficult to count. Furthermore close-lying, highly mineralized incremental lines – of the secondary type (authors' comment) – have been noted in the cementum of deciduous molars in 9-15 weeks old domestic *Sus scrofa* from Norway although they are ge-

nerally absent (FURSETH 1970). In a few instances cementum incremental lines have also been discerned in the acellular cementum in human deciduous teeth but were not seen in the cellular part (FURSETH 1967).

To consider the background for development of incremental lines, it is of interest to know whether primary lines occur in deciduous teeth just as in the permanent teeth. With reference to this, deciduous teeth of *Vulpes vulpes, Cervus elaphus, Cervus nippon* and *Ovibos moschatus* have been examined.

In *Vulpes vulpes* where permanent dentition is fully erupted at an age of approximately 7 months, i_3 and c from an animal killed in July at an age of about 4 months showed a thin homogenous layer of cementum. As the normal period for line development in permanent teeth is April-September, an incremental line in formation might already be expected in the deciduous teeth, but could not be detected. The ungulate species live through one or more periods for primary line development with at least part of the deciduous dentition in function. *Cervus elaphus* and *Cervus nippon* shed the first incisor when the animals are approximately 15 months old, and the last premolar when approximately 24 months old. In *Ovibos moschatus* the first incisor is shed when the animal is 24 months old and here pm_4 can still be found on top of the protruding permanent tooth at an age of approximately 36 months (HENRICHSEN pers. comm.). Distinct incremental lines were seen. In *Cer-*

vus elaphus (Plate 1A) and *Cervus nippon* one in i_1 and two in pm_4 just before shedding. In *Ovibos moschatus* the i_1 and pm_4 showed two (Plate 1B) and three incremental lines, respectively.

These observations suggest that cementum incremental lines generally occur in deciduous as well as in permanent teeth. Furthermore that they are formed as long as the tooth is attached in the alveolus during the period for line development, and that the first line appears when the animal passes through this period for the first time. Thus the number of lines present in deciduous teeth roughly corresponds to the age of the animal in years, generally somewhat less than a full year or full two years etc.

PERMANENT TEETH

It is generally accepted that cementum development in most species is initiated shortly before or just at the time of eruption of teeth, and age at eruption must therefore be taken into account when using cementum structures for determining age. Nevertheless, cementum development prior to eruption has been reported and can for some species be important for correct age determination. The season for development of the apical part of the root, i.e. closing of the root foramen, is also important, as it may determine whether the first complete incremental line will be developed during the animal's first or second season with erupted, permanent teeth.

In many carnivore species living in the Palaearctic, permanent canines erupt during the animal's first autumn and are thus fully erupted with at least a partly-closed root during the normal period for development of incremental lines. As cementum development in these species starts about the time of incipient eruption the first incremental line in permanent teeth is

formed when the animals are 6 to 18 months old. This is illustrated in Fig. 1a for a species with lines being formed during winter *(Mustela erminea)* and in Fig. 1b for a species with lines being formed during summer *(Vulpes vulpes)*. Similar results have been found by the authors for: *Alopex lagopus* (farm animals), *Martes martes*, *Martes foina*, *Mustela putorius*, *Mustela vison* (farm animals), *Mustela nivalis*, and *Meles meles*, all from Denmark, and is reported in literature for *Alopex lagopus*, *Martes zibbelina*, and *Mustela vison* all from U.S.S.R (KLEINENBERG & KLEVEZAL 1966), for *Vulpes vulpes*, England (HARRIS 1978), *Procyon lotor*, Illinois, U.S.A. (GRAU et al. 1970), *Meles meles*, Sweden (AHNLUND 1976). In *Canis mesomelas* from Transvaal, South Africa, LOMBAARD (1971) found that the first incremental line began forming at an age of about 10 months (p. 142). Nevertheless when determining age Lombaard added one year to the number of incremental lines counted, which indicates that only fully formed lines were included in the count.

In species where cementum formation is initiated at eruption of permanent teeth and where time for this coincides with the normal period of incremental line development, no distinct line will be formed during the first period. This is illustrated for *Lynx lynx* from Norway in Fig. 1c, where the first complete primary line in the canines is seen when the animals are 1¾–2¼ years old. A line will already appear in the first year in some but not all specimens; this is easily distinguished as incomplete as it does not continue round the root apex, but actually this is the first primary line. As it does not show up clearly in all specimens, it may be most practical not to count it for age determination in any specimens of this species. This brings it in accordance with findings for *Lynx rufus* from Wyoming, U.S.A. (CROWE 1972) and

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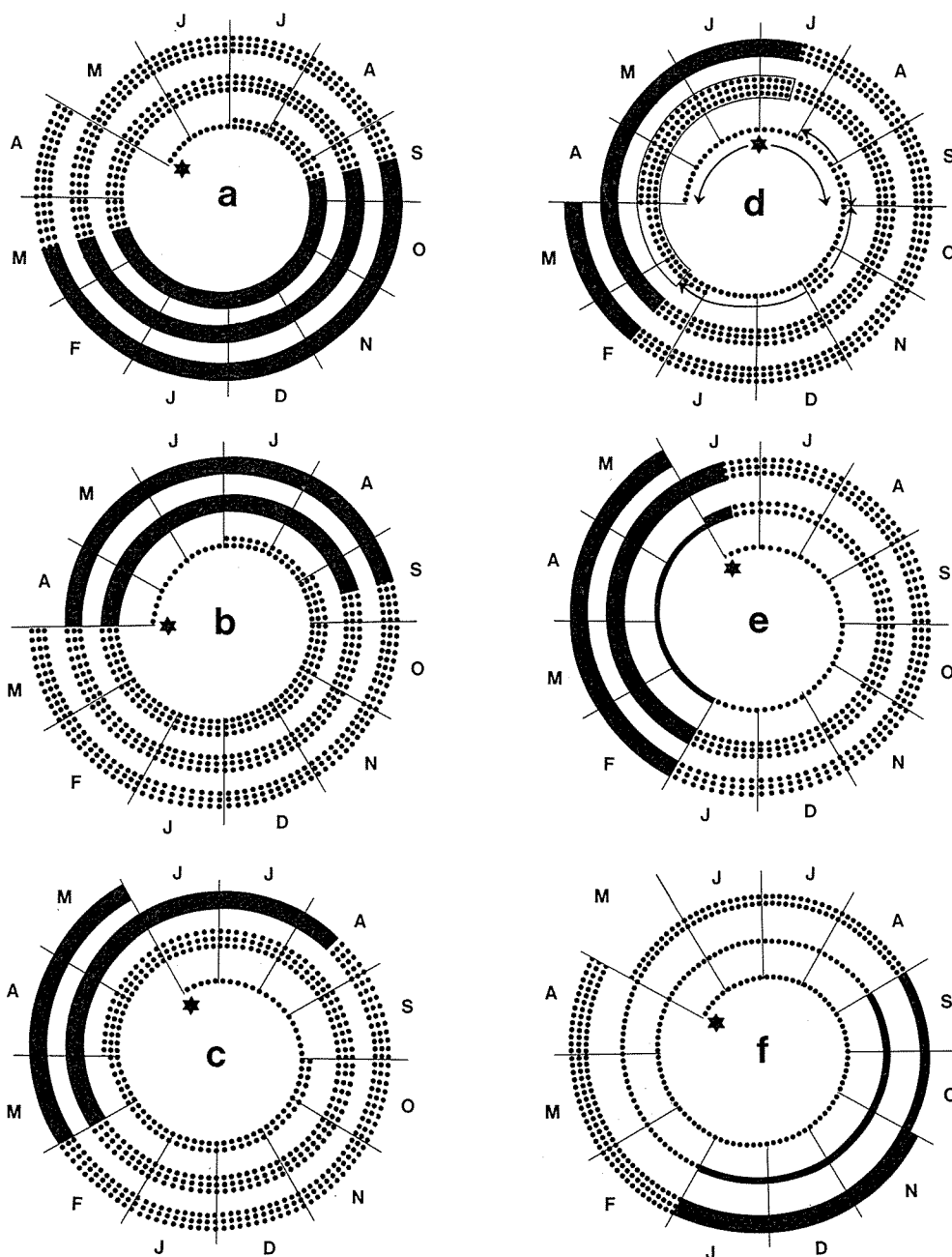
Fig. 1. Diagram illustrating development of primary incremental lines in relation to permanent tooth development in canine of four carnivores and first incisor of two ungulates. a: *Mustela erminea (Denmark)*, b: *Vulpes vulpes* (Denmark), c: *Lynx lynx* (Norway), d: *Felis catus* (Switzerland), e: *Cervus elaphus* (Denmark), f: *Ovibos moschatus* (Greenland). Asterisk = time of birth, dots = period for development of light-staining cementum, and solid bars = period for development of primary incremental line. The single row of dots and narrow bars indicate permanent tooth not yet visible, double rows of the same indicate erupting permanent tooth, and three rows of dots and broad bars indicate fully-erupted permanent tooth.

Arkansas, U.S.A. (FRITTS & SEALANDER 1978). In the latter species the apical root foramen closes at about 13-18 months of age, and the first incremental line is formed at about 20-23 months of age, i.e. late during the second winter of life of the animal.

In canines of *Canis latrans* from Montana and Wyoming, U.S.A., LINHART & KNOWLTON (1967) did not observe incremental line formation until the animals had reached an age of 20-23 months. In the same species from North Dakota, U.S.A., ALLEN & KOHN (1976) found developing incremental lines during the first winter of life of the animals. In *Canis latrans* from Alberta, Canada, NELLIS et al. (1978) found the first incremental line appearing at 20 months of age, i.e. second winter of life. According to LINHART & KNOWLTON (1967) and NELLIS et al. (1978) eruption of permanent canines – and presumably initiation of cementum development (authors' comm.) – occurs in early winter in the first year of life of the animal. As winter is the normal period for line development in this species the situation may be similar to that described for *Lynx lynx*. When time for line formation and tooth development nearly coincide a slight difference in these periods in different specimens or populations may determine whether a more or less complete primary line is formed already in the first year of life of the animal.

In *Taxidea taxus*, Southeast Wyoming, U.S.A., initiation of the first incremental line in the canines is postponed until the animal's second year of life (CROWE & STRICKLAND 1975). Both in this North American species and in the European *Meles meles* young are born about the month of March and permanent canines are erupted about the month of July. However in *Taxidea taxus* incremental lines are formed in late summer and consequently the first line is not formed until the animal is about 18 months old, while in *Meles meles*

incremental lines are formed in winter and the first line is formed when the animal is about one year old.

The species mentioned so far have a rather restricted breeding season which means that the age when the first primary incremental line is initiated can be regarded as roughly the same for every member of a population. *Mustela nivalis* is an exception, as it may produce two litters per year and give birth from late spring to early autumn. The lengthy breeding season is of minor importance as the rapid development from juvenile to adult for this species brings the last-produced litter just as far in dental development as the first one, before the normal period for primary line development. Similar observations have been noted for several species of rodents by KLEVEZAL & KLEINENBERG (1967) as far as cementum structures are concerned.

In species which usually breed more than once a year and where growth is slower, the age when the first incremental line appears may vary as much as half a year. This is illustrated for *Felis catus* from Switzerland in Fig. 1d. In this species eruption of permanent canines is completed at an age of 6 months (HABERMEHL 1975) and cementum development starts about the time of eruption. Animals born during spring therefore possess fully erupted permanent teeth with a partly or completely closed root and a relatively well developed cementum layer during the normal period for primary line development. The first incremental line is thus formed when animals are approximately 1 year old. In animals born in autumn, however, permanent canines have just erupted and have an open root during normal period for line development; formation of a distinct incremental line is apparently prevented. Consequently the first primary line in autumn-born young will appear during the second period for line development, when

the animals are approximately 1½-2 years old.

Canis familiaris (sledge dogs) in Greenland and *Lutra lutra* in Denmark have no definite breeding season, and birth of young has been reported from all seasons of the year. However a definite period for development of incremental lines has been observed (Fig. 2) and age for development of the first primary line is therefore assumed to vary between ½ and 1½ year.

As shown above for some carnivores, time of tooth eruption in relation to the period where incremental lines are formed may be important for a correct age determination because initiation of cementum coincides with eruption. In at least some ungulates initiation of cementum development and time for eruption does not coincide, and both cementum and incremental lines in the cementum may in some species appear before the tooth erupts.

This is illustrated for *Cervus elaphus* from Denmark in Fig. 1e. By the time I_1 is fully erupted – at an age of approximately 15 months (Von Raesfeld 1957) – one incremental line is already present in the cementum. Similarly a primary line was observed in a newly erupted I_1 of *Cervus nippon*. Development of incremental lines before eruption was also found in *Ovibos moschatus* from Northeast Greenland as illustrated in Fig. 1f. I_1 is fully erupted at an age of approximately 2½ years (Poul Henrichsen pers. comm.). At that time one

fully-formed incremental line is seen plus the beginning of a second, bordering the periodontal membrane. These observations indicate the presence of a well-developed root already at an age of roughly 1¼ years. In literature development of incremental lines in unerupted teeth has been reported in *Rangifer tarandus* both from Norway (Reimers & Nordby 1968) and from Canada (Miller 1974 a & b). Initiation of cementum development prior to tooth eruption has been noted in literature for *Alces alces* (Sergeant & Pimlott 1959, Wolfe 1969), *Capreolus capreolus* (White 1974), *Odocoileus virginianus* (Gilbert 1966), *Ovis aries* (Saxon & Higham 1968), and *Ovis canadensis* (Turner 1977).

In the ungulate species investigated in the present study the first primary line is easily distinguished from the succeeding line as it does not continue round the root apex. This has also been mentioned in literature, e.g. for *Rangifer tarandus* (Miller 1974 a & b).

Based on different criterias younger animals are usually omitted before the cementum reading method is used for age determination. Considering the examples cited it is recommended that some young animals are included when using this method, to assess more precisely the age when cementum formation begins and to establish whether incremental lines are developed prior to tooth eruption.

Time of year for incremental line formation

Information on the time of year for development of cementum structures, derived from our own material, from the borrowed material and from literature, has been surveyed and classified according to the degree of accuracy involved.

1. When data throughout the year were available for a species, a diagram was prepared showing for each month the number of animals with a developing primary incremental line bordering the periodontal membrane, as a percentage

11
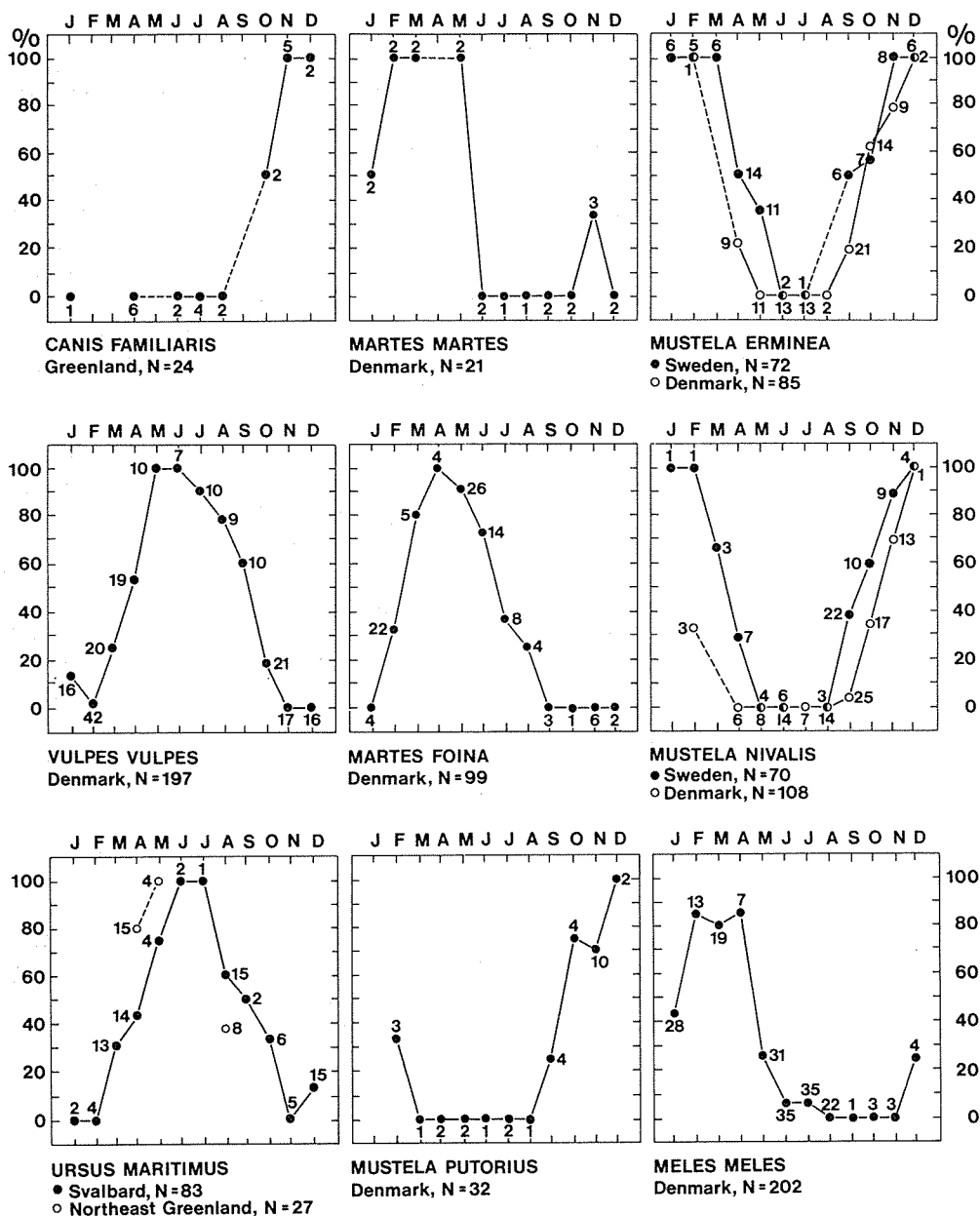
Fig. 2. Time of year for development of primary incremental lines in 17 terrestrial mammals. For each month the number of specimens showing a developing incremental line is plotted as a percentage of the total number

of the total number of animals available for the particular month (Fig. 2).

2. Where data were restricted to specific

seasons, the nature of the cementum being formed when the animal died is illustrated by symbols (Fig. 3), following

12
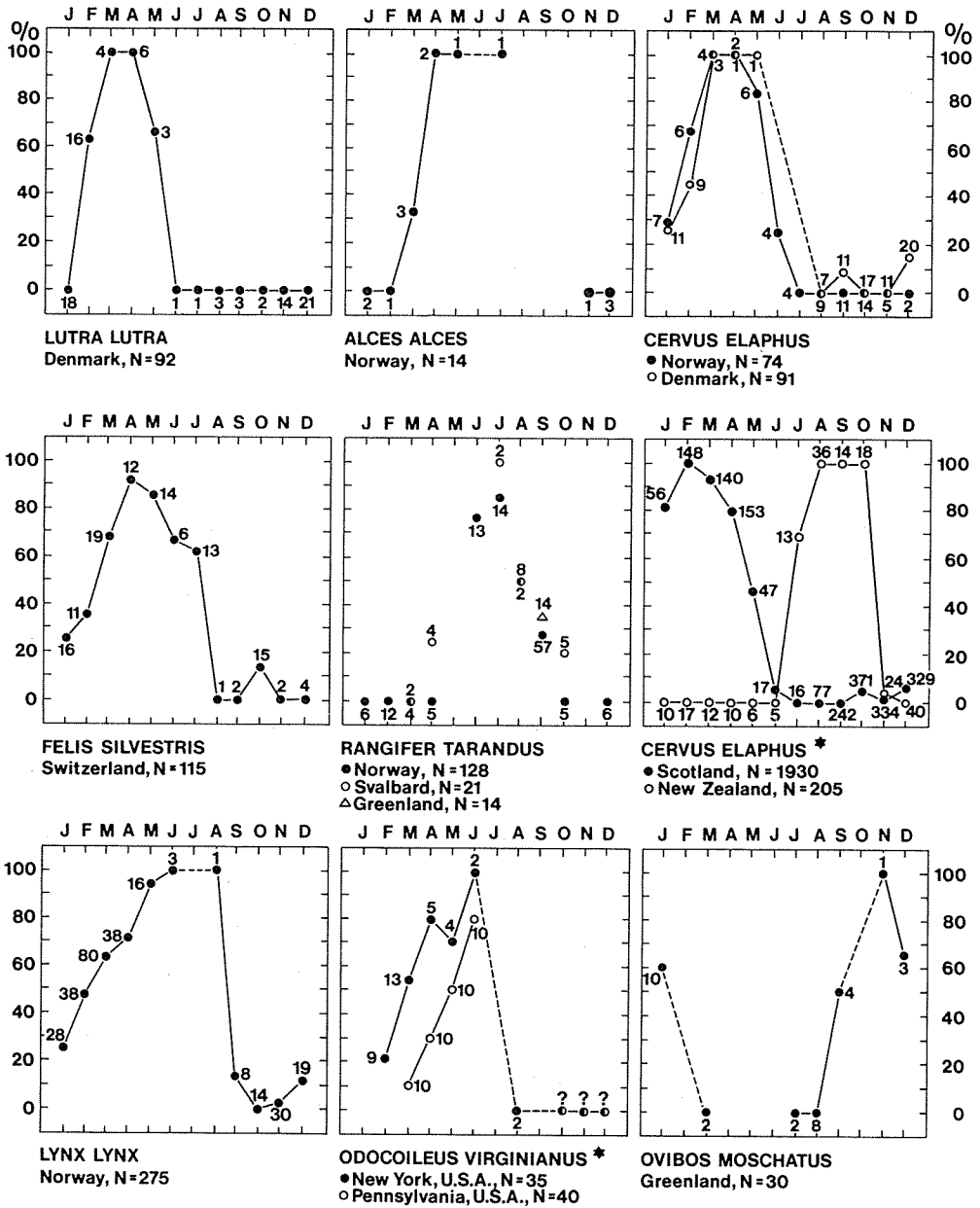
available for that month. Asterisk marks information from literature - *Cervus elaphus*, Scotland (MITCHELL 1967) and New Zealand (DOUGLAS 1970), *Odocoileus virginianus* (SAUER 1973).

the approach of KLEVEZAL & KLEINENBERG (1967, p. 24). Results derived from literature, however, sometimes rest on indications only. Data from Fig. 2 are incorporated in order to facilitate comparison.

Reference	Technique	No. of spec.	Country	Species	J F M A M J J A S O N D
1	H	40	U.S.S.R.	*Sorex araneus*	
2	H	28	Denmark	*Nyctalus noctula*	
1	H	10	U.S.S.R.	*Myotis myotis*	
1	H	25	U.S.S.R.	*Castor fiber*	
2	H	4	Norway	*Castor fiber*	
1	H	83	U.S.S.R.	*Apodemus agrarius*	
1	H	63	U.S.S.R.	*Rattus norvegicus*	
1	H	25	U.S.S.R.	*Ondatra zibethica*	
1	H	23	U.S.S.R.	*Cricetus cricetus*	
2	H	42	Greenland	*Canis familiaris*	
3	T	235	Ontario, Canada	*Vulpes vulpes*	
4	H	?	England	*Vulpes vulpes*	
2	H	16	Holland	*Vulpes vulpes*	
5	H	197	Denmark	*Vulpes vulpes*	
6	H	50	New York, U.S.A.	*Vulpes fulva var. silver*	
1	H	30	U.S.S.R.	*Alopex lagopus*	
7	H	20	Greenland	*Alopex lagopus*	
7	H	20	Denmark	*Alopex lagopus*	
8	H	101	Alaska, U.S.A.	*Ursus arctos*	
9	H	27	Wyoming, U.S.A.	*Ursus arctos*	
10	H	522	Canada	*Ursus arctos*	
11	H	8	Hokkaido, Japan	*Ursus arctos yesoensis*	
2	H	83	Svalbard	*Ursus maritimus*	
2	H	27	Greenland	*Ursus maritimus*	
12	H	61	Illinois, U.S.A.	*Procyon lotor*	
2	H	21	Denmark	*Martes martes*	
2	H	206	Denmark	*Martes foina*	
1	H	?	U.S.S.R.	*Martes zibbelina*	
2	H	32	Denmark	*Mustela putorius*	
13	H	259	Sweden	*Mustela vison*	
2	H	40	Denmark	*Mustela vison*	
14	H	37	Holland	*Mustela erminea*	
2	H	71	Sweden	*Mustela erminea*	
2	H	85	Denmark	*Mustela erminea*	
2	H	68	Sweden	*Mustela nivalis*	
2	H	108	Denmark	*Mustela nivalis*	
2	H	201	Denmark	*Meles meles*	
15	H	80	Wyoming, U.S.A.	*Taxidea taxus*	
2	H	92	Denmark	*Lutra lutra*	
2	H	118	Switzerland	*Felis catus*	
2	H	275	Norway	*Lynx lynx*	
16	H	140	Wyoming, U.S.A.	*Lynx rufus*	
1	H	13	U.S.S.R.	*Equus hemionus*	
17	T	110	England	*Capreolus capreolus*	
2	H	14	Norway	*Alces alces*	
18	H	999	Canada	*Rangifer tarandus*	
2	H	124	Norway	*Rangifer tarandus*	
2	H	21	Svalbard	*Rangifer tarandus*	
2	H	14	Greenland	*Rangifer tarandus*	
19	H	16	Colorado, U.S.A.	*Odocoileus hemionus*	
20	H	37	Brit. Col., Canada	*Odocoileus hemionus*	
21	H	35	New York, U.S.A.	*Odocoileus virginianus*	
21	H	40	Pennsylvania, U.S.A.	*Odocoileus virginianus*	
2	H	74	Norway	*Cervus elaphus*	
2	H	91	Denmark	*Cervus elaphus*	
22	T	1930	Scotland	*Cervus elaphus*	
23	T	22	Canada	*Cervus canadensis*	
1	H	?	U.S.S.R.	*Cervus nippon*	
2	H	19	Denmark	*Cervus nippon*	
2	H	14	England	*Dama dama*	
2	H	30	Greenland	*Ovibos moschatus*	
24	I	97	Canada	*Bison bison*	
25	H	?	Rhodesia	*Tragelaphus strepsiceros*	
26	T	205	New Zealand	*Cervus elaphus*	
27	T	93	New Zealand	*Dama dama*	

3. For some species, only general statements or just suggestions about the time of year for development of the different cementum structures were available. These are listed in Table 1.

In the authors' own material in Fig. 2 juvenile animals have been omitted. Before processing the teeth, part of the young animals were separated from older ones based on tooth replacement (ungulates) or pulp cavity size measured on microradiographs (carnivores) cf. GRUE & JENSEN (1976). Furthermore, for each species a certain date was chosen, after which root development in alle young animals should enable the initiation of an incremental line to be seen, and young animals from before that date were omitted. This exclusion of juveniles can be important, as it may change the shape and position of the curves in Fig. 2 if young animals with an open root and only a relatively thin cementum layer around the root are recorded as having no incremental line under formation. For *Cervus elaphus* from New Zealand, DOUGLAS (1970) omitted animals less than 18 months of age and MITCHELL (1967) in his material from Scotland included only "stags and hinds". However, for the two samples of *Odocoileus virginianus* from Pennsylvania and New York, U.S.A. (SAUER 1973) no information on exclusion of young animals was provided.

It is not known how long the formation of a primary line takes in a single individual. Fig. 2, however shows that in a certain species within a restricted area, lines may be formed over more than half a year but in only one to three months do the mainpart of the animals show an incremental line as the outermost layer in the cementum. There are even species where a hundred percent is never reached in any month *(Meles meles, Felis catus)*.

Each curve represents material from a relatively restricted area, but generally the material has been collected unevenly over a number of years and this may affect the curves somewhat.

Presently an evaluation of minor differences in shape and position of the curves for the same species is difficult. Only in *Cervus elaphus* is there a clear example of difference in time for the formation of the primary lines. While they are formed in most of the individuals from Scotland in January-April formation may take place a little later in Norway and Denmark (March-May) but in New Zealand it takes place in August-October. This is in accordance with the time difference in seasons of half a year between the northern and southern hemispheres.

In literature the primary incremental lines have often been called winter lines but this can be most misleading, as they are formed in different periods of the year in different species even in the same area. As an example, there are in any given month of the year at least one of the eight free-living carnivore species investigated from Denmark with more than fifty percent of the material forming a primary line (Fig. 2). A similar seasonal difference among other species and in other areas is indicated in Fig. 3 and Table 1.

Fig. 3. Time of year for development of incremental lines in 41 terrestrial mammals. Continuous line = period with developing incremental line, broken line = light-staining cementum being deposited. H: histological sections, T: thin-sections or cleaved teeth. References: 1: KLEVEZAL & KLEINENBERG (1967), 2: Present study, 3: JOHNSTON & BEAUREGARD (1969), 4: HARRIS (1978), 5: GRUE & JENSEN (1973), 6: MONSON et al. (1973), 7: GRUE & JENSEN (1976), 8: RAUSCH (1969), 9: CRAIGHEAD et al. (1970), 10: PEARSON (1975), 11: INUKAI & KADOSAKI (1974), 12: GRAU et al. (1970), 13: GERELL (1975), 14: VAN SOEST & VAN BREE (1970), 15: CROWE & STRICKLAND (1975), 16: CROWE (1972), 17: AITKEN (1975), 18: MILLER (1974 b), 19: ERICKSON & SELIGER (1969), 20: THOMAS & BANDY (1973), 21: SAUER (1973), 22: MITCHELL (1967), 23: FLOOK (1970), 24: NOVAKOWSKI (1965), 25: SIMPSON & ELDER (1969), 26: DOUGLAS (1970), 27: BAKER(1973).

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Species	Country	No. of specimens	Technique	Timing of cementum layers	Reference
Northern hemisphere					
Sciurus vulgaris	Sweden	39	H	L: spring-summer	LEMNELL (1973)
Sciurus carolinensis	Virginia, U.S.A.	228	H	I: winter L: summer	FOGL & MOSBY (1978)
Spermophilus beecheyi	California, U.S.A.	22	H	I: winter L: summer	ADAMS & WATKINS (1967)
Castor canadensis	Maryland, U.S.A.	63	T	I: winter L: summer	LARSON & van NOSTRAND (1968)
Castor canadensis	Canada	42	T	I: winter L: summer	van NOSTRAND & STEPHENSON (1964)
Canis latrans	Wyoming, U.S.A.	186	H	I: winter	LINHART & KNOWLTON (1967)
Vulpes vulpes	Denmark	133	H	I: June-Sept. L: start Sept./Oct.	JENSEN & NIELSEN (1968)
Ursus spp.	Canada	29	T	I: end of summer L: summer	MUNDY & FULLER (1964)
Ursus americanus	New York, U.S.A.	109	H	I: winter L: summer	SAUER et al. (1966)
Ursus americanus	Brit. Columbia, Canada	13	H	I: fall-winter L: spring-early summer	STONEBERG & JONKEL (1966)
Meles meles	England	232	H	I: start Oct./Nov. L: start March/April	FARGHER & MORRIS (pers. comm.)
Lontra canadensis	Ontario, Canada	482	H	I: winter L: summer	STEPHENSON (1977)
Capreolus capreolus	Poland	200	H	I: winter L: summer	SZABIK (1973)
Capreolus capreolus	England	25	T	I: winter	WHITE (1974)
Capreolus capreolus	Germany & Rumania	51	T	I: winter L: vegetation period	ALMASAN (1972)
Alces alces	Alaska, U.S.A.	68	T	I: summer, fall, early winter L: winter	GASAWAY et al. (1978)
Alces alces	New Foundland, Canada	64	T	I: winter-spring L: summer-fall	SERGEANT & PIMLOTT (1959)
Alces alces	Isle Royale, U.S.A.	140	T	I: winter-early spring L: summer-fall	WOLFE (1969)
Rangifer tarandus	Canada	100	H	I: winter L: Feb./Aug.	McEWAN (1963)
Rangifer tarandus	Norway	29	H	I: winter-May L: summer	REIMERS & NORDBY (1968)
Odocoileus hemionus	Brit. Columbia, Canada	40	H	I: winter L: spring-summer	LOW & COWAN (1963)
Odocoileus virginianus	Michigan, Minnesota, U.S.A.	16	T	I: winter L: summer	RANSOM (1966)

Species	Country	No. of specimens	Technique	Timing of cementum layers	Reference
Odocoileus virginianus	Michigan, U.S.A.	10	H	I: late fall-winter L: summer	Gilbert (1966)
Odocoileus virginianus	North America	377	H	I: March/April (presumed) L: Nov./Jan. (presumed)	Lockhard (1972)
Cervus elaphus	Central Europe	40	T	I: winter L: Jan.-fall	Almasan & Rieck (1970)
Cervus canadensis	Colorado, U.S.A.	218	H	I: fall-winter (presumed) L: spring-summer (presumed)	Keiss (1969)
Cervus canadensis	Arizona, U.S.A.	35	H	I: winter-spring L: summer-fall	Smith (1970)
Cervus nippon	U.S.S.R.	121	H	I: winter L: summer	Prisjazhnjuk (1968)
Antilocapra americana	Montana, Wyoming, U.S.A.	110	H	I: fall-winter L: spring-summer	McCutchen (1969)
Ovis dalli	Alaska, U.S.A.	129	T	I: fall (before rut)-spring (lambing period)	Hemming (1969)
Ovis canadensis	North America	166	H	I: just prior to rut - 1 month after (=fall)	Turner (1977)

Southern hemisphere

Species	Country	No. of specimens	Technique	Timing of cementum layers	Reference
Desmodus rotundus	Argentina	2	H	I: July	Linhart (1973)
Canis mesomelas	Transvaal	407	H	I: fall-winter L: spring-summer	Lombaard (1971)
Cervus elaphus	Fiordland, New Zealand	34	T	I: late winter-early summer L: late summer-early winter	Smith (1974)
Syncerus caffer	Uganda	148	H	I: dry season (2 per year)	Grimsdell (1973)
Syncerus caffer	Tanzania	91	H	I: dry season (2 per year)	Sinclair (1977)
Kobus defassa	Uganda	108	H	I: dry season (2 per year)	Spinage (1967)
Gazella granti	Tanzania	101	H	I: dry season (2 per year)	Spinage (1976b)
Antidorcas marsupialis	Transvaal	100	H	I: winter L: summer (Oct./March)	Rautenbach (1971)
Ovis aries	New Zealand	15	T	I: winter L: summer	Saxon & Higham (1968)
Ovis aries	New Zealand	55	T	I: winter L: spring	Rudge (1976)

Table 1. Season for development of incremental lines in 28 terrestrial mammals. I: incremental line, L: light-staining cementum, H: histological sections, T: thin-sections or cleaved teeth.

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As shown on p. 10, knowledge of the time of year for incremental line formation may in some species be important for a correct age determination. In addition it may be essential for checking the number of primary lines formed per year. It can now be accepted generally that one primary line is laid down every year in Arctic and Temperate regions but it seems too early to generalize about line formation in Tropical regions. Further studies of species from the Tropics would help to solve this problem.

It should be noted that knowledge of the season of formation is fundamental when the season of death for an animal is deduced from the stage of line formation e.g. as it has been done recently in archaeological studies (SAXON & HIGHAM 1968, KAY 1974, SPIESS 1976, BOURQUE et al. 1978).

Intra- and interspecific variation in incremental lines

A number of factors have been suggested as being responsible for the development of incremental lines and the observed synchrony between seasons of the year and the time of development of these lines (for a review see MORRIS 1972, SPINAGE 1973). For practical reasons such factors will be discussed here under five headings, but it must be emphasized that these are often difficult to separate, partly because the factors are not independent of each other, and partly because information on the animals' environmental conditions is often insufficient.

It is helpful to consider first general characteristics of incremental lines because they can appear differently in different stained sections of decalcified teeth. When working with only a small number of specimens and species, it can be difficult to decide to what extent the differences found are due to techniques employed or to true intra-and interspecific variation. In the present study, variation caused by technique is probably negligible (cf. p. 6) but it is still difficult to give any measure of the true variation. This is especially a problem when the influence of environmental conditions on the character of the incremental lines is to be evaluated. However, the use of a total number of 50,000 sections from 3,700 specimens representing over 50 species has provided a wide frame of reference of the present work.

Growth of the cementum layer of mammalian teeth is appositional and generally considered to function as a process uplifting the tooth from below to counteract abrasion from above. This functionally determined growth of cementum is of relevance in the examination of incremental lines, as these are more widely separated when the cementum layer is well-developed. An example of a functionally determined vigorous cementum formation on the unstressed side of a root apex is shown in Plate 1G where the stress arises from the mesial drift of the tooth.

MITCHELL (1967) and WHITE (1974), for *Cervus elaphus* and *Capreolus capreolus* respectively, mention that growth of the cementum layer is proportional to the wear. SERGEANT & PIMLOTT (1959) for *Alces alces* and AITKEN (1975) for *Capreolus capreolus* demonstrated an almost linear relationship between the number of incremental lines and thickness of the cementum. Similarly ZANDER & HÜRZELER (1958) found for *Homo sapiens* a linear relationship between age and thickness of the cementum layer. In *Ursus arctos* a sudden reduction in the annual apposition is a definite feature of the cementum pattern (PEARSON 1975) but it seems to occur at dif-

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ferent ages between 5 and 12 years (MUNDY & FULLER 1964, RAUSCH 1969, CRAIGHEAD et al. 1970).

In connection with the present study apposition of cementum with development of primary incremental lines was observed in the scarcely functional upper canines of *Cervus elaphus* and *Capreolus capreolus* and similar observations were reported for *Cervus canadensis* by SELIGER et al. (1969). As mentioned on p. 11 apposition of cementum in teeth not yet erupted has been found in several species and incremental lines may occur. In teeth which never erupt apposition of cementum with development of primary lines may also occur. This was found in vestigal canine teeth in *Ovibos moschatus* from Clavering Island and Dove Bay in North-east Greenland (HENRICHSEN pers. comm.). The number of lines in the canines was in accordance with the number found in the erupted incisors of the same animal. Furthermore apposition of cementum was observed in a non-functional, broken canine of *Vulpes vulpes* (Plate 1F). Judging from the size of the pulp cavity and the thickness of the dentine, the overall growth of this tooth had stopped at an early stage, and the remains of the tooth were concealed in the jaw. Nevertheless, the number of primary lines in its root cementum was in accordance with the number found in an erupted tooth (PM_3). These examples indicate that apposition of cementum is not entirely conditioned by use, but is also a result of general growth with age.

Where to count the incremental lines is an important practical question. In the majority of species investigated during the present study, primary lines appear most distinct close to the cementum - enamel interface (cervical region). Here the primary lines are even, and secondary lines are seldomly observed. When many lines are present counting can be difficult, however, because the cementum layer here is usually very thin. In carnivores in particular the most recently formed layers cannot always be distinguished in the cervical region, and as far as possible structures in the apical region of the root should be studied. Among ungulates a large number of specimens have disturbed cementum formation in the apical area and layers here can be less distinct. Usually therefore the coronal half of the root must be used for interpretation (cf. Plate 2 E & F). In cheek teeth of ungulates a relatively thick cementum layer may be deposited in the angle of the roots. This cementum layer is normally studied when using cleaved teeth or thin-sections for age determination, but because of the large size of the tooth it is less suitable for histological sections, and here in addition the cementum structures often appear as broad and more diffuse layers.

Both transverse and longitudinal sections of decalcified teeth have been used for counting incremental lines. A transverse section can show incremental lines more clearly than a longitudinal one. In most cases however, longitudinal sections are preferable for all species as they make it possible to follow the lines all along the root. This gives a better opportunity for correct judgement of the number of lines and their character, and for observing the developing cementum structures at the earliest stage possible.

The actual size of the tooth is of minor importance regarding distinctness of incremental lines, well defined lines being present in both a 5 mm long canine tooth from *Nyctalus noctula* and 80 mm long canine from *Ursus maritimus*. On the other hand the development of the cementum layer as such is of major importance, and examples of the variability in cementum structures can be seen in Plates 1-4. In *Mustela erminea* and *Mustela nivalis* the canine is very slender with a well-developed cementum layer and distinct

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lines in the apex but not along the lateral walls of the root (Plate 3 E & F). In *Lynx lynx* and *Vulpes vulpes* thickness of the cementum layer along the sides of the root increases with age, and here the lines are well defined (Plate 2 A & B).

A decreasing thickness of annual additions to the cementum with increasing age may in some cases affect the possibility of counting incremental lines and especially for assessing whether an incremental line is under formation or not. The age at which this is first seen varies from species to species. For instance in *Ursus americanus* 27 distinct layers have been observed (FREE & SAUER 1966) and a specimen has been aged 32½ years from cementum layers (SAUER 1975). In *Lynx lynx* the lines could easily be separated even up to 15 years of age, while in canines from *Pipistrellus pipistrellus* it was hardly possible with the technique used here to distinguish more than 4 layers. Due to the thinness of the annual addition in *Meles meles* and *Lutra lutra* it was difficult to assess whether an incremental line was under formation when the number of primary lines exceeded about 8. In most cases however the latter did not prevent counting of the number of lines present even in older animals.

The character of the lines varies somewhat in different species, but generally they are smooth and distinct as e.g. in *Lynx lynx* (Plate 2A). In canines of *Meles meles*, however, they are wavy in the apex but straight on the lateral walls of the root (Plate 2C). In canines of *Felis catus* cementum structures appear more or less as zones (Plate 1E), and this is even more pronounced in the very thick cementum layer in molars of *Castor fiber* (Plate 2D).

The varying contrast with which the lines stand out from the homogeneous, cellular and acellular cementum in different species cannot at the moment be related to either of the two types of cementum. It has simply been noted that in some species the lines appear very distinct, for instance in *Lynx lynx* and *Martes foina*, and in others very faint, for instance in *Martes martes* and to some degree in *Meles meles.*

In most species, primary lines in the cementum can be distinguished and counted, but secondary lines appear in all the species examined. For example in *Ursus maritimus* both from Greenland and Svalbard it was difficult to distinguish between primary and secondary lines. In *Capreolus capreolus* from Denmark and from England (Thetford forest) it was only in some animals possible to assess the number of primary lines and in dogs from Denmark kept as pets this was not possible at all (Plate 4A).

A primary line followed annually by a secondary line has been observed (p. 29). Such "double lines" were especially frequent in *Mustela vison* from fur-farms in Denmark and in *Felis catus* from Switzerland (Plate 1E).

Cementum formation may be disturbed in teeth which have been broken, mechanically damaged in other ways or where inflammation has caused necrosis of the periodontal membrane (Plates 2 B & F). Usually they can be recognized from the irregular line formation and resorption lines. Care must be taken when using such teeth for age determination, and it is better to discard them.

The patterns of the incremental lines in various undamaged teeth from the same specimen usually look alike; this phenomenon has also been noted in literature. It suggests that there can be a certain individually distinctive character that appears in some lines or in the whole pattern of lines, and therefore nothing can be gained by sectioning an additional tooth from a specimen where interpretation was difficult in the first place. For *Ursus americanus* WILLEY (1974) states "Indistinct

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annulations appear to be more characteristic of the bear itself than the sophistication of the slide preparation".

The time of year incremental lines are formed in various teeth of the same individual seems also to be the same, though it was noted by HARRIS (1978) for *Vulpes* *vulpes* from England that lines may sometimes be distinguished earlier in one tooth than in another. Whether the time for initiation and the duration of the period of development of primary lines varies in the same individual from year to year is apparently not known.

VARIATION IN RELATION TO TAXONOMY

Incremental lines have been found in members of all the larger mammalian orders, and there is reason to believe that they occur in all species where a suitable basis is provided by the morphology of the teeth and the mode of life of the animal. Based on the 52 species examined here and on information in literature there does not appear, either in the character of the lines or in the time of year they are formed, to be any factor which can be directly related to the taxonomic position of the species.

In Carnivora, for example, even and wavy incremental lines and groups of lines occur (p. 20), together with distinct or indistinct lines (p. 20). Comparisons within the 12 species of Carnivora, in particular, but also within the 5 species of Cervidae all from Scandinavia examined here do not suggest close systematic relationship to be of direct importance for the character of incremental lines (cf. Plates 1-4, especially Plate 3). On the other hand, the shape of a tooth and its position in the jaw is of importance for cementum development and thus for formation of incremental lines. From these relationships there is in some cases an indirect relationship between the appearance of the incremental lines and the taxonomic position of the species.

In some cases distinct incremental lines were observed although it was impossible to discover a relationship between the age of the animal and the number of lines. This was the case for humans (present study) and dogs kept as pets in Denmark (GRUE 1976). In both cases, however, there is reason to believe that the absence of a seasonal environmental influence has resulted in irregular line formation, with the presence of many secondary but no primary lines (Plates 4A & B). The same is true of several examples known from literature, but it seems that with the possible exception of man, all species mentioned in literature do form incremental lines in synchrony with the seasons in other parts of their range, or else a closely related species does so. Such is the case for *Trichosurus vulpecula* and *Perameles nasuta*, Australia (KINGSMILL 1962), *Odocoileus hemionus*, California, U.S.A. (CONNOLLY et al. 1969), *O. virginianus gymnotis*, Venezuela (BROKX 1972), *Aepyceros melampus*, South Africa and Tanzania (GRAFTON in SPINAGE 1971) and *Ammotragus lervia*, New Mexico, U.S.A. (OGREN 1965). For some populations, only a slight

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relationship was found between the number of lines and age of individuals, such as in *Meles meles*, Cornwall and Gloustershire, England (FARGHER & MORRIS, pers. comm.), *Cervus elaphus*, Rhum, Scotland (LOWE 1967), *Capreolus capreolus*, Cranborne Chase, England (PRIOR 1968), Thetford forest, England (present study), Denmark (present study), and *Ovis aries*, New Zealand (RUDGE 1976).

There is great variation in the time of formation of primary lines (Figs. 2 & 3 and Table 1) and even in different species within the same taxonomic group living in the same region, the formation of primary lines may occur at different times of year (Figs. 2 & 3). Therefore season for line formation cannot be associated direct-

ly with the systematic affiliations of the species concerned. However, there may again be an indirect relationship between the time of formation of incremental lines and the taxonomic position of a species, as closely related species often share much the same mode of life and thus the same environmental situation for the formation of incremental lines. As an example it is presumably the environmental conditions in general and not taxonomic relationships that in Denmark are the reason that most *Mustela putorius*, *Mustela erminea* and *Mustela nivalis* form incremental lines during November-January, *Martes martes*, *Martes foina*, *Meles meles* and *Lutra lutra* in February-March, and *Vulpes vulpes* in May-August.

VARIATION IN RELATION TO AGE AND SEX

A decrease in the rate of cementum deposition usually occurs with increasing age, but generally this does not affect the formation of primary incremental lines. KLEVEZAL & MINA (1973) found that primary lines in *Canis lupus* and *Alces alces* were less distinct in young animals than in adult and sexually mature animals. However, in the species investigated in the present study generally no such difference was found.

In fish, it has been found that age and sexual maturity both influence the time of formation of annual rings in otoliths (WILLIAM & BEDFORD 1974). However, for terrestrial mammals it is difficult to gain sufficient material to determine whether the same is true for them. Not only should the total number of individuals be large, with various age groups of both sexes adequately represented in each year of collection, but also material should be collected from a specific population.

For *Vulpes vulpes*, *Martes foina*, *Meles meles* and *Lutra lutra*, all from Denmark, the time of formation of primary lines was examined within each age group, and no apparent difference was found. The four species mentioned become sexually mature in their first or second year. In contrast to that, *Lynx lynx* from Norway is first sexually mature at an age of 3-4 years. However, even in the latter species no difference was found in the time when incremental line formation was initiated in young or older animals.

In the present study as a whole, no indication was found of any age-dependent difference in the character of primary incremental lines, nor in the time of formation of lines for those species included in Fig. 2. Present evidence suggests that formation of incremental lines shows no consistent relationship with age.

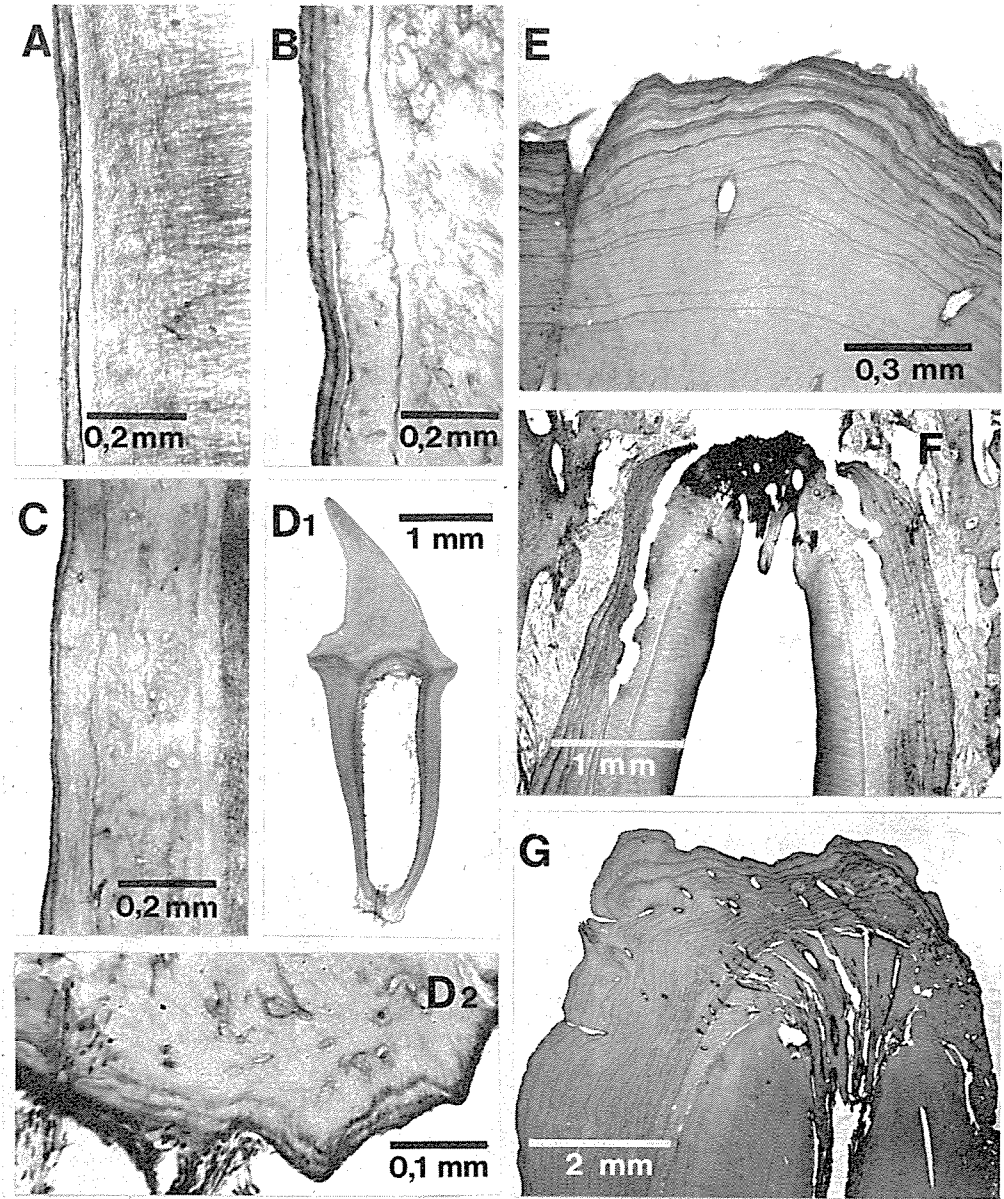No difference related to sex could be found in the character of primary incre-

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Plate 1.

A:	Cervus elaphus	♂ (401)	Denmark	30/1	1958	i_1	1 line	estm. age 8 m
B:	Ovibos moschatus	♂ (3763)	Greenland	18/1	1975	i_1	2 lines	estm. age 1 y 8 m
C:	Cervus elaphus	♂ (347)	Denmark	25/2	1957	I_1	2 lines	estm. age 1 y 9 m
D:	Nyctalus noctula	♂ (2512)	Denmark	15/2	1956	C	3 lines	—
E:	Felis catus	♀ (6229)	Switzerland	8/3	1974	C	9 lines	estm. age 9½ y
F:	Vulpes vulpes	♀ (LLB 1299)	England	7/12	1974	C	6 lines	estm. age 6 y 9 m
G:	Taxidea taxus	—	Oklahoma, U.S.A.	—		C	17 lines	—

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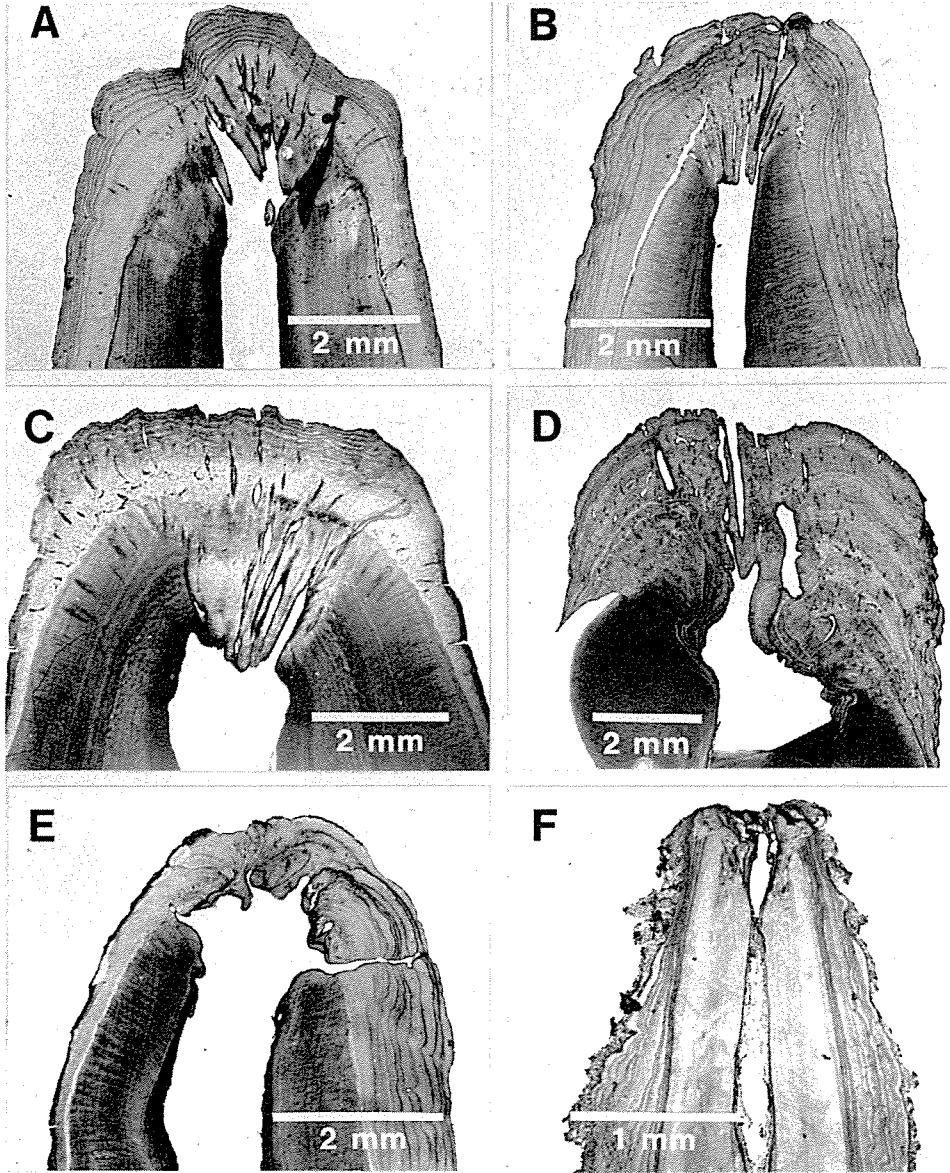
Plate 2.

A: Lynx lynx	♂ (4006-73)	Norway	10/1 1973	C	8 lines	estm. age 9 y 7 m
B: Vulpes vulpes	♂	Denmark	—	C	9 lines	—
C: Meles meles	♂ (4152)	Denmark	17/7 1952	C	9 lines	estm. age 9 y 4 m
D: Castor fiber	♂ (6)	Norway	12/5 1975	M₁	13 lines	estm. age 13 y
E: Cervus elaphus	♀ (423)	Denmark	9/10 1958	I₁	9 lines	estm. age 9 y 4 m
F: Rangifer tarandus	♀ (544)	Greenland	24/9 1977	I₁	7 lines	estm. age 7 y 3 m

24

1 mm
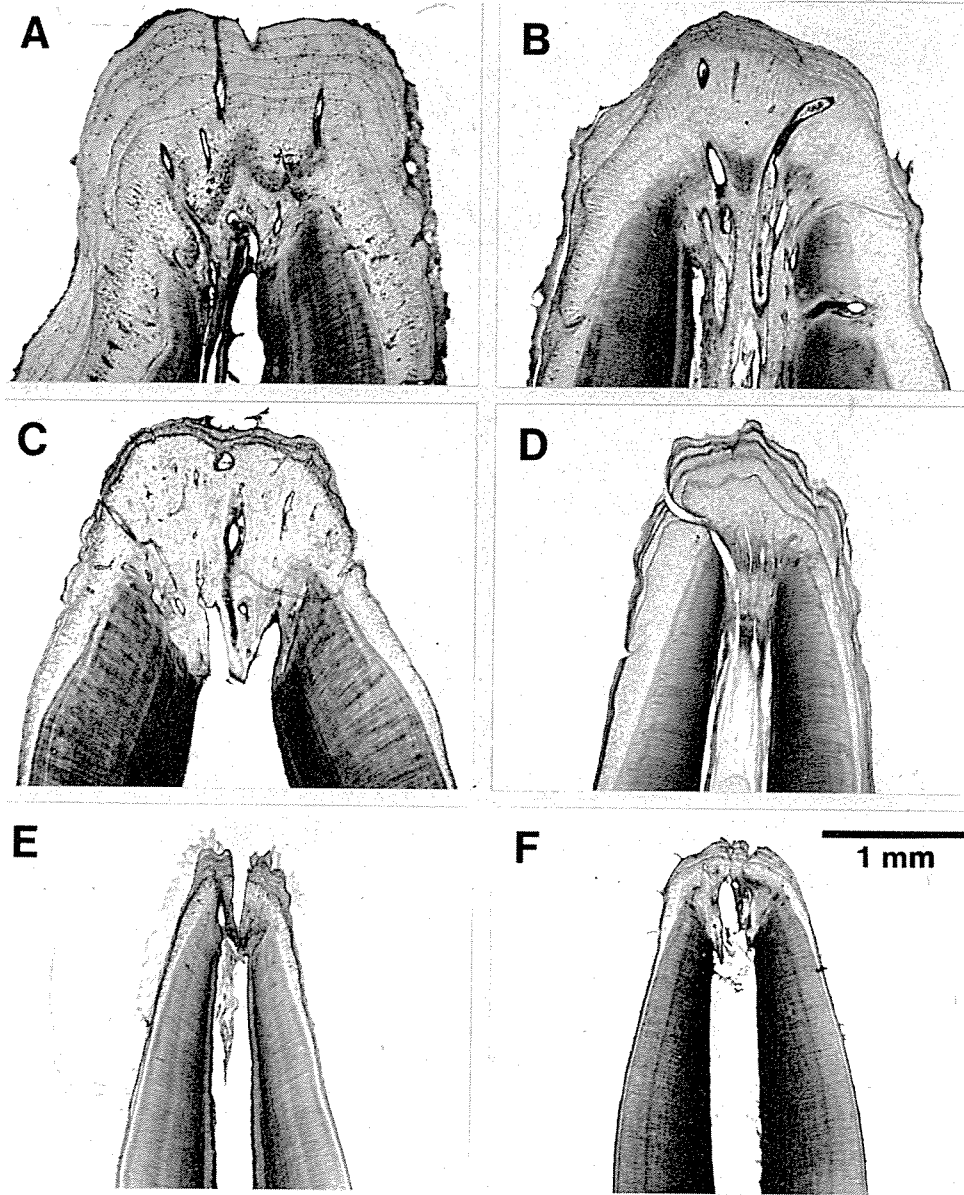
Plate 3.

A:	Martes foina	♂ (238)	Denmark	28/2	1977	C	4 lines	estm. age 4 y 11 m
B:	Martes martes	♂ (206)	Denmark	7/9	1970	C	4 lines	estm. age 4 y 6 m
C:	Mustela putorius	♂ (1239)	Denmark	14/10	1969	C	2 lines	estm. age 2 y 6 m
D:	Mustela vison	♂ (S2499)	Denmark (farm)	April	1975	C	4 lines	known age 4 y 11 m
E:	Mustela erminea	♀ (116)	Denmark	25/6	1961	C	5 lines	estm. age 5 y 1 m
F:	Mustela nivalis	♀ (93)	Denmark	11/6	1961	C	4 lines	estm. age about 4 y

25
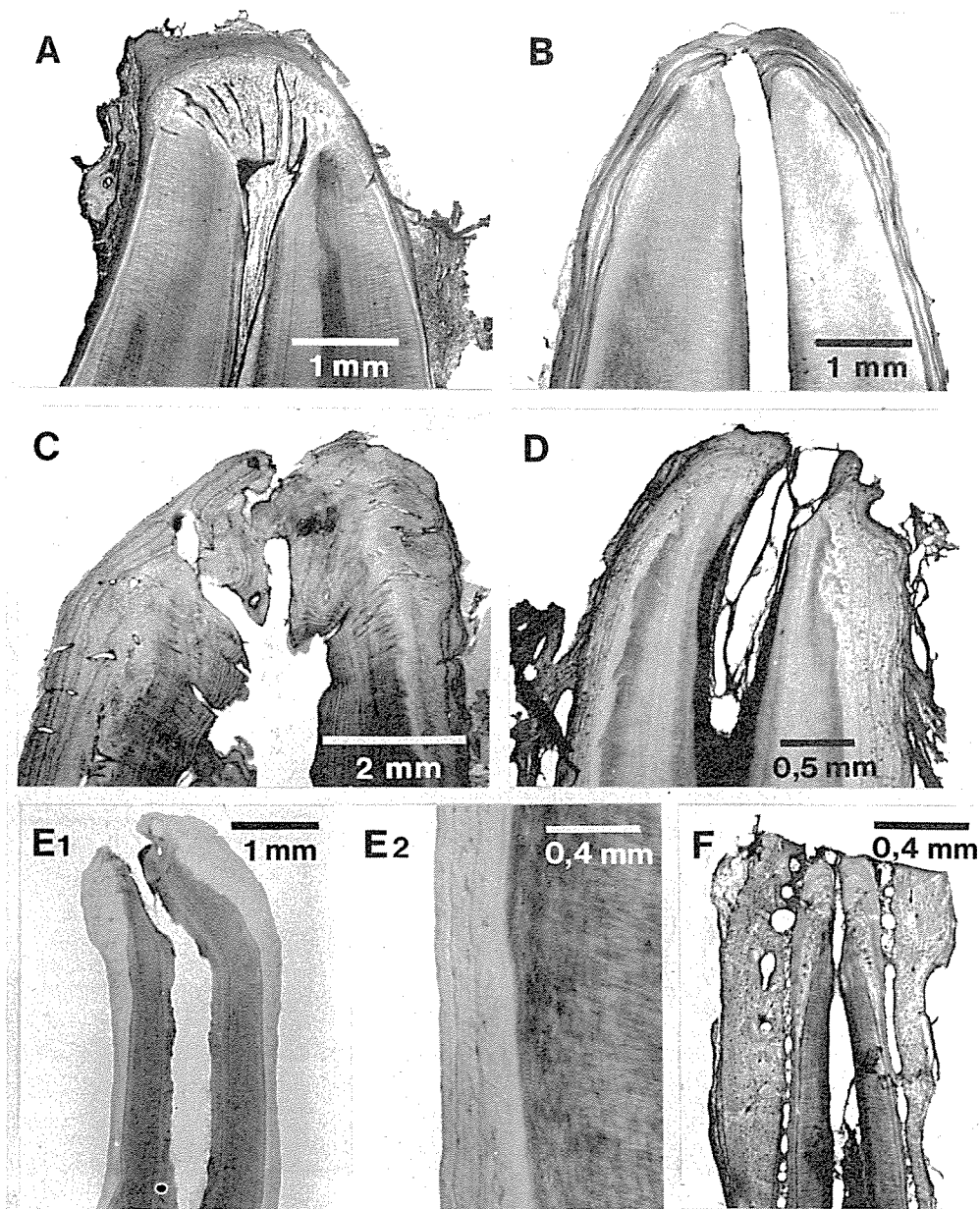
Plate 4.

A:	Canis familiaris	♂	Denmark	5/12 1975	I₃	—	known age 13 y 3 m
B:	Homo sapiens	♀ (2-76)	Denmark	July 1976	PM₁	—	known age 46½ y
C:	Bos taurus	♀ (1-77)	Denmark	May 1977	I₁	5 lines	—
D:	Capreolus capreolus	♂ (27-68)	Denmark	12/11 1968	I₁	6 lines	known age 4 y 5 m
E:	Erinaceus europaeus	♂ (11)	Denmark	22/4 1976	—	2 lines	estm. age 2 y
F:	Talpa europaea	♀ (641)	Denmark	20/4 1977	—	4 lines	estm. age 4 y

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mental lines in any of the many species studied (p. 4-5), and the time of line formation in the species included in Fig. 2 showed no significant variation in period for development of primary lines between males and females. However, possible minor differences in time of line formation in the two sexes cannot be treated conclusively for any species on the basis of the present material collected over a number of years and from several localities.

In literature statements regarding a similar character of primary lines in males and females have been made for various species: *Vulpes fulva*, New York, U.S.A. (MONSON et al. 1973), *Capreolus capreolus*, England (WHITE 1974), *Rangifer tarandus*, Canada (MILLER 1974 a & b), *Odocoileus virginianus*, New York, U.S.A. (SAUER 1973), *Kobus defassa*, Uganda (SPINAGE 1967), but no comments

on time of line formation in the two sexes seem to exist.

According to literature, secondary incremental lines appearing as regularly as primary ones have been found in various ungulate species, sometimes occurring more frequently in males. This has led to the suggestion that they could possibly be caused by the rut; they will be further discussed in connection with the reproductive cycle (p. 27) and condition (p. 34). ALMASAN & RIECK (1970) also stated that in males of *Cervus elaphus* from Central Europe the depositions in the cementum "Ablagerungen in der Zementschicht - die Alterszonen" are much more uniform than in females. No differences could be observed between males and females in the present material of *Cervus elaphus* from Denmark and Norway.

VARIATION IN RELATION TO REPRODUCTIVE CYCLE

Since primary incremental lines seem to occur in a similar way in deciduous and permanent teeth and in the latter in sexually immature as well as mature animals, it is indicated that in general the breeding cycle does not form the basis for the existence of such lines. Furthermore as primary lines seem to be formed at roughly the same time in males and females the rut or heat would appear to be the only factor in the breeding cycle which in general could influence the time of year for their development.

In order to gain an impression of the way in which the time of formation of primary incremental lines is related to the time of mating and birth in our own material of carnivore and ungulate species, these factors are shown diagrammatically in Fig. 4. The period given for line formation is based on Fig. 2, p. 12-13, while the

times of mating and birth are based on literature. From the figure it is evident that for the species given, there is no general coincidence between the time of mating and the time of formation of primary lines. In the case of females, the duration of the gestation and lactation periods varies from species to species, but these factors cannot be related to the time of formation of primary lines any more than the time of birth itself.

In particular it can be emphasized that while the breeding cycles of the carnivore species mentioned are very different, this has apparently no influence on the formation of primary incremental lines. As an example (cf. Fig. 2), the period for line formation in *Canis familiaris* and *Lutra lutra* which can give birth throughout the year is just as sharply defined as in *Felis catus* and *Mustela nivalis*, where births nor-
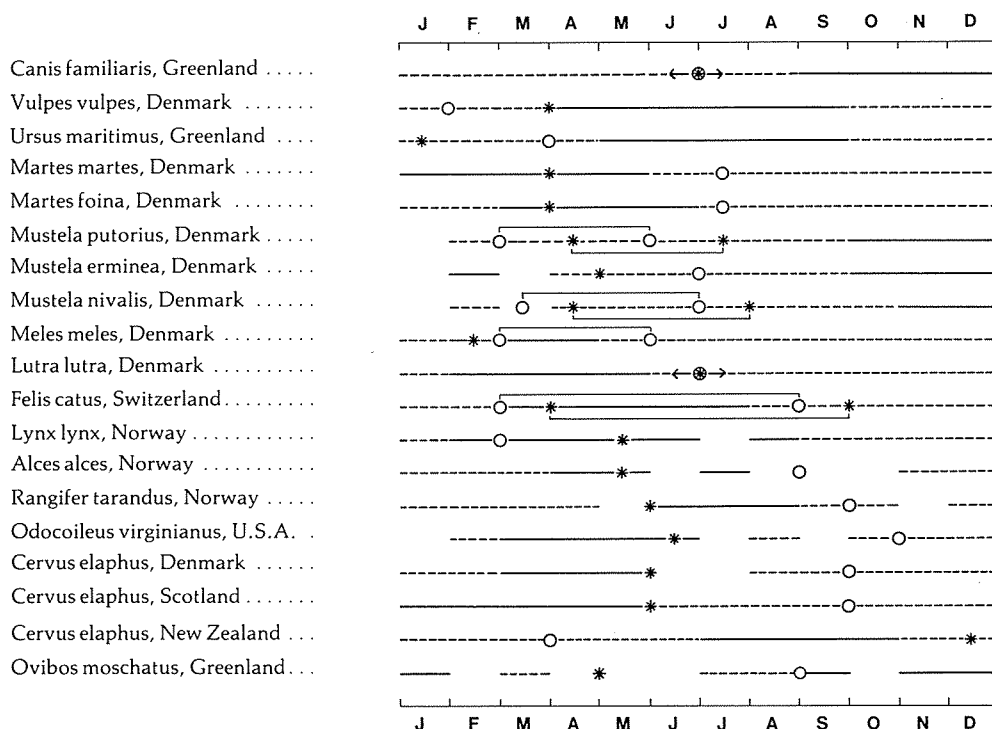
27

Fig. 4. Time of year for development of primary incremental lines compared to period of mating (o) and birth (★) for the species shown in Fig. 2. Continuous line = period with developing incremental line, broken line = light-staining cementum being deposited.

mally take place within a 6-month period, and in *Martes foina* and *Vulpes vulpes*, where births occur within two months of the year. In southern Africa SIMPSON (1972, 1973) also found a close similarity in appearance and time of formation of incremental lines in *Tragelaphus strepsiceros* with a restricted breeding season and *Tragelaphus scriptus* with an indeterminate breeding season. It is also evident from Fig. 4 that in Denmark line formation occurs at about the same time in *Mustela putorius*, which has one litter per year without extended gestation, as in *Mustela erminea* which has one litter annually, normally with extended gestation, and as in *Mustela nivalis*, which can produce two litters annually and does not have an extended gestation period. Line

formation in *Meles meles* occurs a little later than in the above three species, and while birth takes place within a short period of the year, copulation can take place over a long period. It might also be mentioned here that in four castrated males of *Felis catus* from Switzerland line formation did not deviate from that of non-castrated males (present study), and that INUKAI & KADOSAKI (1974) mentioned incremental lines in a castrated male *Ursus arctos* from Japan.

KLEVEZAL & MINA (1973) reached a similar conclusion that in adult animals, neither the sex of the individual nor the changes in its physiological condition associated with its sex (such as rut or gestation) had any effect on the character of the annual cementum layer.

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Although the formation of primary lines cannot be associated with heat or oestrous, it is still possible that not only these factors but also growth of the embryo, birth and lactation subject the female animal to physiological stress which is reflected in formation of secondary lines. However, a distinction must be made here between the more or less clear secondary lines, the formation of which does not appear to be governed by any common factor, even in a well-defined population, and the more distinct and regularly occurring secondary lines.

The former category has been observed in both males and females and in the majority of species examined so far, including all those examined in the present study. The number of these lines varies from individual to individual, and often from year to year, and it does not seem likely that a common factor exists which can be related to their formation.

The second category has been observed in both males and females in a range of species which are systematically very different, and such lines are described in literature as double, divided or split lines. In this study they have been observed both in carnivores and ungulates, occurring almost equally frequently in males and females. Such "double lines" are illustrated in Plates 1E and 2F, in females of *Felis catus* from Switzerland and *Rangifer tarandus* from Greenland, respectively. They were especially common in *Mustela vison* reared on fur farms in Denmark.

For females it has not been possible in the material studied to associate occurrence of the regular secondary lines with any feature of the reproductive cycle. Nor could an association be found with any of the different breeding cycles in carnivores mentioned above. In *Felis catus* for example regular secondary lines were common but rare in *Mustela nivalis* and both species may give birth to two litters during a period of half a year. Furthermore distinct and regular secondary lines were found in farm animals of *Mustela vison* which had not been mated. Similarly KLEVEZAL & MINA (1973) found double lines in both barren and pregnant females of *Marmota baibacina* in U.S.S.R. Only AITKEN (1975) mentions an occasional occurrence of an extremely narrow secondary line in *Capreolus capreolus* from England as possibly associated with lactation.

In males of several ungulate species regular occurrence of secondary lines has in literature been associated with rut. As they are however absent in many populations or do not occur in all mature males in a population the phenomenon may be more a question of condition than of a general reproductive cycle (see also p. 39).

In literature, the occurrence of double lines has been mentioned without reference to sexual differences, e.g. in *Antilocapra americana*, Montana and Wyoming, U.S.A. (McCUTCHEN 1969), *Odocoileus virginianus*, Michigan, U.S.A. (GILBERT 1966), *Cervus canadensis*, Colorado, U.S.A. (KEISS 1969). LOCKARD (1972) examining *Odocoileus virginianus* from 15 American states found divided annual lines in 39% of the females, but in only 28% of the males.

A more detailed analysis of the occurrence of secondary incremental lines is needed but difficult to perform. Based on the scattered data available it seems justified however to conclude that the reproductive cycle alone does not cause a regular formation of secondary lines.

VARIATION IN RELATION TO CLIMATE AND REGION

Climate is one factor which frequently has been mentioned as a potential regulator of the formation of incremental lines. However, this has usually been as an incidental comment, when differences in the distinctness of the lines have been observed in age determination work, and in general no further analysis has been attempted as to which climatic factors might be directly or indirectly responsible.

Considerable difficulty is associated with obtaining material which can indicate the influence of climate in a satisfactory manner. Due to individual variation, a large number of teeth is required, originating from widely different areas for which reliable information on both the climate and condition of the animals throughout the year is available for the same period. Furthermore, for reasons of comparison, sectioning of teeth and interpretation of the resulting slides should be carried out by the same laboratory.

In the present study, no material was examined which could relate the distinctness and season of year for formation of incremental lines to climate and region in a satisfactory manner. However, in the following section, comments in literature concerning distinctness of lines is first presented, and then the results of the present study are treated including time of year for line formation.

Trichosurus vulpecula. PEKELHARING (1970) found clearly defined layering within the cementum structure both in specimens from areas in New Zealand with a marked variation in temperature of the summer and winter season and in specimens from Adelaide, South Australia with a Mediterranean climate and not subjected to a similar marked seasonal variation.
Desmodus rotundus, Santiago Del Estero, Northern Argentina and Rio Grande Do Sul, Southern Brazil. No differences are mentioned in distinctness of lines between specimens from the two areas (LORDet al.

1976). – From Mexico and Argentina, the northern and southern extremities of the geographical range of the species, no comments were made on line distinctness in relation to region, although it was stated that lines in some cases were not well-defined (LINHART 1973).
Sorex araneus, Apodemus agrarius, Apodemus flavicollis, Moscow and Kurisches Haff (55°N, 21°E), U.S.S.R. Annulation in individuals from the Moscow region, with a moderate continental climate, was more uniform than in individuals from the Baltic Sea coast with an oceanic climate (KLEVEZAL & MINA 1973).
Castor canadensis, Wisconsin, U.S.A. and Ontario, Nova Scotia, Newfoundland, Canada. Cementum layers were least distinct in animals from Wisconsin, and age determination based on these gave more variable results in both Wisconsin and Ontario materials compared to materials from the two other regions (VAN NOSTRAND & STEPHENSON 1964).
Ursus americanus, Vermont, U.S.A. Cursory examination of the geographical location of kill of bears exhibiting poor annulations revealed no apparent bias (WILLEY 1974).
Canis latrans, Southern Texas, New Mexico, Colorado, Oregon, and Wyoming, U.S.A. (free-living and captive-raised animals). No comments offered about differences in line distinctness (LINHART & KNOWLTON 1967). – Considerable variation was noticed in the degree of clarity and definition of annuli in specimens collected from different geographical areas; teeth from Atascosa County, Texas, were especially difficult to interpret (ROBERTS 1978).
Alces alces. MARKGREN (1969) mentioned that cementum layers are usually quite distinct in Swedish moose at least in those from Northern Sweden. Specimens from Norway (present study) and Poland (DZIECIOLOWSKI 1976) could be aged from incremental lines.
Cervus nippon. Age could be determined from incremental lines in specimens from Denmark (present study), Germany (UECKERMANN & SCHOLZ 1971, BRIEL 1979), the Far East (PRISJAZHNJUK 1968) and Japan (OHTAISHI 1978) and lines were also present in specimens from New Zealand (DOUGLAS 1970). No comments were included on line distinctness.
Cervus elaphus. On the Isle of Rhum off the west coast of Scotland, LOWE (1967) failed to find a clear correlation between number of lines and age of animal in 53.6% of 28 animals of known age examined. He suggested that seasonal variation in the oceanic climate prevailing there is too small to produce distinct primary lines. This species could be aged from incremental lines in Scotland (MITCHELL 1967), Nor-

way and Denmark (present study), Sweden (AHLÉN 1965) and Central Europe (ALMASAN & RIECK 1970, HELL et al. 1971, UECKERMANN & SCHOLZ 1976, BRIEL 1979).

DOUGLAS (1970) observed clear lines in teeth of individuals from New Zealand, and SMITH (1974), from knowledge of individuals from Fiordland, New Zealand, emphasized that distinct lines are formed even in animals living in areas where the annual variation in temperature does not exceed 10°C. He suggested that a large temperature variation in itself is not necessary for the regular and orderly deposition of cementum annuli.

Odocoileus hemionus, from Hopland, California, U.S.A., failed to show clear incremental lines, although the same species from Colorado, U.S.A., and British Columbia, Canada, possessed distinct lines, and it was suggested that in Hopland the winter may not be severe enough to induce the production of distinct annulations (CONNOLLY et al. 1969). – Primary lines have been useful as age criteria in animals from Colorado, U.S.A. (ERICKSON & SELIGER 1969) and British Columbia, Canada (LOW & COWAN 1963, THOMAS & BANDY 1973).

Odocoileus virginianus. Having investigated stocks from Michigan, U.S.A., and Nova Scotia, New Brunswick, Ontario and British Columbia in Canada, GILBERT (1966) suggested that age determination from cementum lines is applicable to most if not all specimens in the northern range of this species. Confer also GILBERT & STOLT (1970). – Deer from the Upper Peninsula of Michigan, U.S.A., from a wildland habitat where winter food commonly is in short supply, usually showed a more distinct annuli formation than deer from Iowa, U.S.A. (SOHN 1967). – Investigating stocks from 15 states in U.S.A. and one Canadian province, LOCKARD (1972) pointed out a variation in clearness of incremental lines, as lines in the teeth of animals from southern states lay closer together, and were more difficult to interpret, than those in teeth from animals from northern and northwestern states.

Odocoileus virginianus gymnotis from Venezuela, often showed poorly defined annuli, and the number of annuli did not always correspond exactly to the age of the animals. In this area of the Southern hemisphere, one dry season is evident, and the species may reproduce at any time of year (BROKX 1972). – *Antidorcas marsupialis* from Transvaal, South Africa, compared with *Odocoileus virginianus*, from Montana, U.S.A., revealed that annulations in the teeth of the former species were less distinct (well-defined and clear) than in the American species (RAUTENBACH 1971). The suggestion offered for this discrepancy in line distinctness is that the more severe winter conditions endured by the American species induce formation of well-defined lines. Here, how-

ever, the author was comparing two different species. *Equus burchelli* from South Africa showed fairly clear annual rings in contrast to animals from East Africa (SMUTS 1974).

In the present study, it was possible to perform a more detailed comparison of material from different and limited areas, for four species living in the wild: *Vulpes vulpes, Mustela erminea, Mustela nivalis* and *Cervus elaphus*. For *Vulpes vulpes*, the material came from Southern Jutland, Denmark (55°N, 09°E), the Arnhem region of Holland (52°N, 06°E), and the London area of England (51.3°N, 0.1°W). In these three areas, the annual average temperatures are 8.1, 9.3, and 10.4°C respectively, lowest average monthly temperatures are −0.1, 1.7, and 4.0°C respectively, and highest average monthly temperatures 16.4, 17.0, and 17.5°C respectively. The material was compared further with borrowed slides of fox teeth from the Berne canton in Switzerland. The material of both *Mustela erminea* and *Mustela nivalis* was from Southern Jutland, Denmark (55°N, 09°E) and the Revinge area in Scania, Sweden (55° 45'N, 13° 30'E), with respective temperatures as treated above 8.1 and 5.9, −0.1 and −4.3, and 16.4 and 16.9°C. The material of *Cervus elaphus* was from Western Jutland, Denmark (55° 40'N, 08° 10'E), and Songli in Norway (63°N, 09°E), with respective temperatures as above of 8.2 and 6.1, 0.5 and −3.0, and 16.2 and 15.0°C respectively. In these four species it was not possible in any single case to determine any significant differences in the distinctness of the incremental lines present.

In individuals of *Ursus maritimus* from Svalbard and North-eastern Greenland respectively it was not possible to observe differences in the distinctness of lines. In *Rangifer tarandus* from Norway (Ottadal, Rondane and Hardangervidda) and from Svalbard, the distinctness of incremental lines was more or less the same. On the

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other hand, the pattern of the lines was less clear in individuals of the same species from Holsteinsborg in East Greenland. However, the 20 specimens examined from this region lived in a heavily overgrazed area, and it is possible that the observed differerence is due to nutritional conditions (cf. p. 36). In *Alopex lagopus,* living wild in Greenland and as a farm animal in Denmark respectively, a slight difference in distinctness of primary lines was observed, and it was suggested that climatic differences rather than conditions of captivity were the cause (GRUE & JENSEN 1976). In a few individuals examined of *Castor fiber* from Jämtland in Northern Sweden, the primary lines were more distinct than in a few of the same species from Southern Norway. The greatest difference in distinctness of incremental lines was observed between specimens of *Canis familiaris* from Greenland (sledge dogs) and Denmark (dogs kept as pets). The former group developed clear primary lines, corresponding in number to the age of the animal in years, while in the latter group no primary lines could be discerned although many irregular secondary lines were visible (GRUE 1976). However, in this case, other differences than climatic ones also affect the mode of life of the dogs in the two regions, and it is difficult to decide which factor is responsible for the difference (cf. p. 37).

From literature and the present study, it can thus be stated that primary incremental lines occur in the root cementum of teeth of terrestrial mammals in all the climatic zones of the Northern hemisphere, from the Arctic to the Subtropic and from coastal areas with mild oceanic climates to areas with a markedly continental climate. However, the majority of the species examined originates from the northern temperate zone. In the fewer species examined from the Southern hemisphere (particularly from East and South Africa

and New Zealand), primary lines were generally also found. In areas where dry and rainy seasons occur, a seasonal variation in the formation of incremental lines was found, corresponding to that found in areas with a change from summer to winter. However, in areas with two dry seasons annually, two lines appear to be formed each year.

First, if the distinctness of primary incremental lines is compared in different species from different climatic zones of the Northern hemisphere, it cannot be generally stated that incremental lines in species from the Polar zone, e.g. *Alopex lagopus, Ursus maritimus, Ovibos moschatus* and *Rangifer tarandus* are substantially more distinct than in those from the Temperate zone, e.g. *Vulpes vulpes, Martes foina, Lynx lynx, Alces alces* and *Cervus elaphus.*

Next, if a range of different species within a limited geographical area (Denmark) is considered, both species forming distinct primary lines and some species forming indistinct lines were found among the 10 species of carnivores examined. Similarly, a difference was found in the three deer species examined from Denmark, as both *Cervus elaphus* and *Cervus nippon* have distinct lines, while those of *Capreolus capreolus* are indistinct. It can thus be said that in different species from the same geographical area, there can be a considerable difference in the degree of distinctness of incremental lines.

Finally, comparing distinctness of incremental lines in specimens of the same species from different parts of its range it appears from the literature mentioned p. 30-31 that lines appear less distinct in populations from areas with small seasonal variations in climate than in populations living in areas with marked seasonal variations. This has particularly been emphasized by KLEVEZAL (1973) and KLEVEZAL & MINA (1973), and it was concluded that in ani-

mals belonging to different taxonomic groups (insectivores, rodents, and ungulates), and in animals which are quite different in their ecology, a tendency towards greater variability in the nature of the annual layers is observed, the less continental the climate.

In tropical mammals, where the scanty literature deals only with African species, there appears to be a tendency for cementum structures to appear clearly, while primary lines can be difficult to discern. Thus in *Gazella granti* excessively large numbers of cementum lines were observed which were difficult to interpret, and in *Syncerus caffer* lines generally appeared diffuse and difficult to interpret (SPINAGE 1976 a & b).

In spite of a broad trend suggesting that climatic extremes affect line formation, at present there does not appear to exist adequate information to evaluate to what degree clarity of primary lines is influenced by seasonal variations in the climate.

From Figs. 2 & 3 and Table 1, it is evident that there is great variation in the time of formation of primary incremental lines, but more detailed information is only available for a few species (Fig. 2).

If different species from different climatic regions in the Northern hemisphere are compared, no general relationship is apparent between climatic region and time of formation of lines. Both in northern and more southernly occuring species, some form lines during the winter period, while in others spring – summer is the time of line formation.

Furthermore, if species from a limited geographical area (Denmark) are compared as to season of formation of primary lines (Fig. 2) some species *(Mustela putorius, Mustela erminea, Mustela nivalis)* form incremental lines during autumn–winter, others during winter–spring *(Martes martes, Martes foina, Meles meles, Lutra lutra)*, and yet others during spring–summer *(Cervus elaphus, Vulpes vulpes).*

Finally, if the time of line formation is compared in specimens collected from different parts of the range of a single species, it appears in general to be synchronous, but divergences exist. The time of formation of the primary line is about the same in Denmark and Sweden for both *Mustela erminea* and *Mustela nivalis* (Fig. 2). The same is true for *Vulpes vulpes* from Denmark and Holland. In *Cervus elaphus* (Fig.2) from Scotland, Norway and Denmark, formation of the primary line occurs in the first half of the year, occurring a little earlier in animals in Scotland compared to those in Norway and Denmark. In New Zealand, the species forms primary lines 6 months later, in agreement with the seasonal displacement of 6 months between the Northern and Southern hemispheres (cf. p. 15). A similar displacement in the time of line formation occurs between *Dama dama* from England (present study) and New Zealand (BAKER 1973) (Fig. 3).

M. Douglas, Christchurch informed us (in litt. Nov. 1978) that in New Zealand the time of year, layers are deposited in deer, varies with species, but generally the translucent layers (primary incremental lines) are laid down during the Southern hemisphere winter–spring period, July to October.

For the few species of ungulates investigated from the equatorial parts of East Africa in which bi-modal dry seasons occur, the time of year for development of the two yearly incremental lines appears to coincide with the dry seasons.

Alces alces and *Rangifer tarandus* (Fig. 2 & Table 1) provide examples of intraspecific variation in the time of line formation which is not easily explained. In *Alces alces* from Newfoundland, Canada (SERGEANT & PIMLOTT 1959) and from Isle Royale, Michigan, U.S.A. (WOLFE 1969),

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the material used suggested that the formation of translucent cementum (primary incremental lines) occurs during the winter–spring period. In animals from Norway however, formation of the primary line begins in March and continues at least to July (present study, Fig. 2). Lastly, the formation of translucent cementum (primary incremental lines?) in animals from Alaska, U.S.A. occurs during summer, autumn and early winter (GASAWAY et al. 1978).

In *Rangifer tarandus* from Canada, McEWAN (1963) and MILLER (1974 a & b) found developing incremental lines in winter, while REIMERS & NORDBY (1968) give the period as winter–May. In the authors' own material of *Rangifer tarandus* from Greenland, 40% of the animals from September showed a developing incremental line, and in the borrowed material from Svalbard and Norway, more than 50% of the animals from June–August possessed a developing primary line (Fig. 2). The material from Norway is part of that utilized by REIMERS & NORDBY (1968).

It must however be emphasized that some of the information concerning the time of year for formation of primary lines obtained from literature must be treated with reservation. This is particularly true of the information in Fig. 3 and Table 1, which, as mentioned on p. 13, was often suggested from a weak basis, and time periods cited merely suggestions. However, it was considered useful in the present study to include all available information, partly to illustrate that intraspecific variation in the time of formation does exist, but also to emphasize the necessity of a more accurate dating of the formation of primary lines.

VARIATION IN RELATION TO CONDITION OF THE ANIMAL

In a wider context, the condition of an animal, including its growth, is the result of many external and internal factors, the individual effects of which are difficult to isolate. Very often incremental lines are believed to occur during periods when the overall growth rate of the organism is reduced, and for this reason the formation of primary lines has been related to periods in which life conditions are at a minimum, e.g. in arctic and temperate areas during winter, and in tropical and subtropical areas during the dry season. Similarly, secondary lines are believed to be a reflection of periods during which minor physiological stress causes short-term changes in growth rate (MORRIS 1972).

The information available concerning seasonal variation in the condition of a species in a given area is often scattered and of a very general character. Furthermore changes in condition are frequently so closely related to climatic changes in an area, that any influence of these individual factors is very difficult to isolate. It is however possible to attempt a rough comparison of life conditions, in particular the availability of food, in a range of different species and in specimens of a single species from different areas, with the appearance of incremental lines and the time of their formation. As in the previous section information from literature concerning distinctness of lines is first outlined briefly, followed by the results of the present study, and finally the time for line formation is discussed.

Eptecicus fuscus and *Lasionycteris noctivagans*, a hibernating and a migrating species respectively, collected in Alberta, Canada, both showed distinct incremental lines (SCHOWALTER et al. 1978).

Vulpes fulva. No differences were noted between teeth of captive and wild Red Fox with the possible exception of increased clarity of layering in the wild specimens (MONSON et al. 1973).

Ursus americanus kept in Zoos in New York state showed no consistent cementum pattern compared to wild animals (SAUER et al. 1966). – In a 28 year old captive specimen from Ontario, Canada, which denned each year, FREE & SAUER (1966) were however able to count 27 lines in the cementum. – Absence of annuli was reported by RAUSCH (1969) for a 2½ year old captive animal which had been fed every day and remained active.

Ursus arctos from Wyoming, U.S.A. showed no relationship between time of year for development of primary lines and low nutritional level (CRAIGHEAD et al. 1970). – Six known age captive specimens from Japan showed primary lines in accordance with age (INUKAI & KADOSAKI 1972).

Panthera leo. No difference was found between the basic pattern of deposition in free ranging and captive specimens from South Africa (SMUTS et al. 1978).

Alces alces. MARKGREN (1969) found layers nearly absent or very indistinct in two of three Swedish zoo-animals compared to free-living.

Capreolus capreolus. Comparing literature different populations in Europe seem to differ remarkably in cementum pattern (PRIOR 1968, BLAZYS 1971, ALMA-SAN 1972, SZABIK 1973, WHITE 1974, AITKEN 1975, BRIEL 1979 and present study p. 36). – In England AITKEN (1975) found clearly defined bands in animals from Thetford Chase, Norfolk, while animals from Cheddington, Dorset, were characterized by poorly defined bands. Probably climatic factors were not directly involved since the seasonal temperature range for the two areas only differ by 1-2°C. Inferior quality of the Thetford animals may render them more susceptible to nutritional stress during winter.

Cervus elaphus from Scotland showed a pattern of cementum growth over the year that corresponded more with that of body growth and condition than with other features of the annual life cycle. Furthermore animals from an area where they had only the available natural forage showed more distinct annulations than animals from an area where they were given extra winter feeds (MITCHELL 1967).

Rangifer tarandus. In North-central mainland Canada MILLER (1974 a & b) found no sex-linked difference in the initiation of primary incremental lines although rutting male Caribou lost body weight and fat reserves from October to December while female Caribou often made slight gains in weight and fat reserves during that period.

Odocoileus virginianus, New York and Pennsylvania, U.S.A. Annulus formation occurs from February through June. This period coincides with a period when low levels of serum phosphate, alkaline phosphatase and protein, and high levels of serum calcium occur in captive white-tailed deer. The changes in these serum parameters occur during a period when the deer have voluntarily reduced food intake and are loosing body weight as stored energy is catabolized for heat production (SAUER 1973).

Giraffa camelopardalis in the Transvaal Lowveld, South Africa has only once a year a major nutritional depression, in the late dry season. It is suggested that only one dark staining incremental layer per year is due to a nutritional effect as found in immature animals. A second band which forms in most years in some adults with no selection for sex, is likely to be associated with the endocrinology of reproduction or lactation (HALL-MARTIN 1976).

Ovis aries from Ruakura Animal Research Center, New Zealand had restricted food intake in winter even when fodder was available at summer levels. They showed growth rings in the cementum and it was suggested that these reflect, in part, a basic metabolic rhytm which is strengthened by seasonal changes in the environment (SAXON & HIGHAM 1968). – RUDGE (1976) in New Zealand found lines in known-age domestic sheep kept under normal pastoral conditions with ample food throughout the year. However, even in the best sample the age estimates were wrong by more than one year for 23%.

Syncerus caffer. GRIMSDELL (1973) concluded that the level of nutrition has a major influence on cementum growth in this species in equatorial regions such as the Queen Elizabeth Park in Uganda. It is not possible to involve photoperiodism as a causative factor in these regions because day length does not vary, nor would temperature seem to be important as the maximum difference between monthly maxima and minima in the Queen Elizabeth Park only amounts to 2°C.

As mentioned on p. 32, it is not generally true to say that primary lines in species from Polar regions of the Northern hemisphere are considerably more distinct than in species from the Temperate zone. For the majority of species, seasonal variation in the availability of food is most pronounced under Arctic conditions, and thus this factor does not appear to be the only decisive one. However, for a better understanding of this situation, more knowledge is needed of incremental line formation in species which live in climatic zones with very much less seasonal variation in availability of food, e.g. in tropical rain forests.

Comparison of species within a limited area (Denmark) indicates that in the majority, clearly delimited primary lines are formed. There are however quite considerable differences in the distinctness of lines even between species which have relatively similar feeding biology. This is true, for example, of *Martes martes* compared with *Martes foina*, and *Capreolus capreolus* compared with *Cervus elaphus* and *Cervus nippon*. Altogether, it is very difficult to discern any relationship between the distinctness of primary lines of the 14 different free-living species from Denmark examined, and the degree of variation in the condition of health during the year caused by their different modes of life.

In comparisons of free-living populations of the same species from different areas, information on variation in food availability is often lacking. For the material (mentioned on p. 31) of *Vulpes vulpes, Mustela erminea, Mustela nivalis* and *Cervus elaphus*, there is no reason to believe that food conditions were considerably different in each area, and as mentioned on p. 31, no significant difference in the distinctness of lines was observed. Concerning the material from Holsteinsborg, Greenland, of *Rangifer tarandus*, it is however known that for some years the area has been steadily overgrazed, and that the general condition of the animals was extremely poor. The majority of these individuals possessed a very diffuse line structure compared to conspecifics from Norway.

It should be mentioned that the majority of the Danish species investigated were collected from many parts of the country. However, for *Cervus elaphus* and *Capreolus capreolus*, it was possible to compare material from three and two limited populations respectively, viz. from the areas of Oksbøl, Klosterheden, and Rold, and from Kalø and Borris. In both species, some difference in the distinctness of in-cremental lines was observed in populations from the different areas. However, the 15-30 individuals examined from each population do not form an adequate basis for estimating more accurately which factors may have caused this difference, but it is known that the growth and environmental conditions of the populations are quite dissimilar.

As mentioned p. 35 cementum pattern in *Capreolus capreolus* seems to differ remarkably in different populations in Europe. Cementum structures were reported to be applicable for age determination in animals from Lithuanian S.S.R. (C) (BLA-ZYS 1971), Germany and South Rumania (M_1 and M_2) (ALMASAN 1972), Southeastern Poland (I_1) (SZABIK 1973), Northumberland, England (M_1) (WHITE 1974) and from Thetford Chase, England (M_1) (AITKEN 1975). However in animals from Cranborne Chase, England (M_1) (PRIOR 1968), Cheddington, England (M_1) (AITKEN), Nepten-Brauersdorf, Germany (M_1) (BRIEL 1979) and in known age animals from Kalø and Borris, Denmark (I_1) (present study) cementum structures could not be used for age determination. Furthermore I_1 of 11 animals from Thetford Chase, England, were cut by the present authors. Cementum structures in these were found to be as indistinct as in the animals from Denmark and judged not to be safely applicable for age determination. This is thus in contrast to the finding of AITKEN (1975) in animals from the same locality.

In hibernating species and species with a period of greatly reduced activity definite seasonal changes occur in the amount of food consumed. However, in species with this mode of life, the occurrence of particularly well-delimited primary lines does not appear to be a general event. This is the case for example, in genuine winter hibernants in Denmark such as *Pipistrellus pipistrellus, Nyctalus noctula* and *Erina-*

ceus europaeus, along with *Meles meles* which shows reduced winter activity.

Seasonal variation in the conditions of life for domestic animals and those in zoological gardens is reduced in some respects. In the present study, cementum structures were compared in a few species exposed to different degrees of domestication, ranging from stray animals through those reared on fur-farms and in cattle-sheds to pets kept mainly indoors.

In *Felis catus* from Switzerland, primary lines were distinct, while secondary lines occurred frequently (Plate 1E). These cats were killed as strays, but the majority contained food in their stomachs provided by humans, and should be considered as pets rather than as free-living animals. In wild living *Felis silvestris* from Czechoslovakia no similar occurrence of secondary lines was observed. Amongst the fur-bearers, *Alopex lagopus* and *Mustela vison* from farms in Denmark were examined. They were kept outside in open cages, having access to adequate food throughout the year. Primary lines were particularly distinct in both species. For *Alopex lagopus* a comparison of primary lines in farm animals from Denmark and free-living in Greenland revealed that the lines in the latter group were slightly more distinct (GRUE & JENSEN 1976). In this case, however, climatic conditions might have some influence (cf. p. 32). For *Mustela vison* a regular occurrence of secondary lines in both sexes was more frequent in Danish farm animals than in free-living animals from Norway. Dairy cows *(Bos taurus)* in Denmark kept inside during winter and allowed to graze in fields during summer showed relatively distinct primary lines occurring in numbers corresponding to the age of the animal in years. However, the frequent occurrence of secondary lines could make age determination difficult. Only two specimens of domestic pig *(Sus scrofa)* were examined.

Both showed primary lines corresponding to those found in a wild boar from a deer park. The domestic pigs had been kept inside throughout their lives, whereas the wild boar lived outside, but was fed. In all three incremental lines appeared rather faint. In four free-living boars from Poland the lines however appeared slightly more distinct. In *Canis familiaris* kept as pets in Denmark, very irregular incremental line formation was observed, which did not allow separation of primary lines and consequent age determination (Plate 4A). However in sledge dogs from Greenland, which are subjected to marked seasonal variation in life conditions both in respect to climate and food, clearly delimited primary lines were observed (GRUE 1976).

Although variation in the amount of food throughout the year is normally less for captive animals than for free-living ones, variation in the composition of the food will often still occur. Even if this source of variation is no longer present, primary incremental lines may still be formed, as was observed for *Mustela vison* reared in a fur farm on a uniform diet (GRUE unpublished).

Altogether, there appears to be a tendency towards an increase both in the number and in the clarity of secondary lines, the less captive animals are exposed to seasonal variation in environmental factors. It is however as yet not clear which factor, when it is absent, causes the seasonal rhythm in the formation of incremental lines to become blurred or disappear completely.

In this connection, man can be considered. In individuals from areas in which the standard of living has very much lessened the annual variation in climate and food conditions, the formation of incremental lines has been observed, but it was not possible to isolate primary lines. As yet no humans whose conditions of life involve

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exposure to great seasonal variation appear to have been examined.

Evaluation of the distinctness of incremental lines is made more difficult both as a result of individual variation and of variation in development of the complete cementum layer in different species, and consequently it will always be subjective. However, the time of year during which the primary incremental lines are formed can be determined rather more accurately.

On a regional basis, there is a fair agreement between the time of formation of primary lines (Figs. 2 & 3 and Table 1) in relation to changes in food available during the year, but there is doubt as to whether a causal relationship exists. In Palaearctic regions lines are formed in winter–spring in the majority of species, generally the period when access to food is at a minimum. Similarly, most species from the Southern hemisphere probably form primary lines during the winter period in this hemisphere. In animals living in areas with seasonal shift between wet and dry periods, development of primary lines seems to occur during the dry period, with one line being formed per year in areas with a single dry period and two lines in areas with two dry periods.

In considering different species from a relatively small region, it is however difficult to claim the existence of a direct relationship between periods with scarcity of food and the period in which primary lines are formed. Such a relationship can hardly be true for the carnivorous animals from Denmark examined (Fig. 2). In *Mustela erminea* and *Mustela nivalis* for example, line formation begins in the last few months of the year when relatively sufficient food in the form of small rodents should be available, and in *Vulpes vulpes* it mainly occurs during May–August, when there is no reason to believe that there is any scarcity of food. The same could probably be said for *Lynx lynx* from Norway (Fig. 2).

In the case of *Alces alces* from Norway and *Cervus elaphus* from Scotland, Norway and Denmark, the period of formation of primary lines in spring (Fig. 2) coincides with the period when the condition of the animals is at its poorest.

For *Rangifer tarandus* the information available concerning the time of formation of primary lines in different areas is hardly precise enough to be linked with environmental conditions. It should however be mentioned that the authors found that primary lines in *Rangifer tarandus* from Norway, Svalbard and Greenland were formed during summer (Fig. 2), while in *Ovibos moschatus* in Greenland they appear to be formed in winter (Fig. 2). In these very species, both of which are herbivores living under the same extreme conditions of climate, line formation could be expected to occur at the same time of year, which is not the case.

In the case of genuine hibernants and species with reduced activity during part of the year, very little information concerning the time of formation of primary lines is available. Thus there is presently little justification for relating line formation to activity and hence condition. It is merely noted that in *Meles meles* from Denmark, formation of the primary line occurs during the inactive period (Fig. 2), while in *Taxidea taxus* from Wyoming, U.S.A., it is formed during the active period (CROWE & STRICKLAND 1975), (Fig. 3). MUNDY & FULLER (1964), for *Ursus arctos* in Canada, and STONEBERG & JONKEL (1966) for *Ursus americanus* from British Columbia, Canada, both state that formation of the primary line begins before the animal enters its den, while PEARSON (1975) states that for *Ursus arctos* from Canada, most of the primary line is formed during dormancy. CRAIGHEAD et al. (1970) mention that in *Ursus arctos* from Wyoming, U.S.A., formation of the primary line is completed before the animals reach the

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term, even when the species considered come from only a small geographical area.

Based on the assumption that primary lines are formed in winter it was appropriate to consider the conditions of life to which animals are exposed in winter as a causative factor. Amongst other reasons, the great variation which is now known to occur in the time of line formation shows that the situation is not that simple. Of course it may be suggested that the formation of primary lines is induced by conditions of life during e.g. the winter period, only to take place later. However, this implies such variation in the length of the latent period even in closely-related species from the same geographical area, that the suggestion is unreasonable.

Variation in the character and time of formation of incremental lines is described, mainly on the basis of material available for the present study. From the results presented here and information from literature it is evident that the formation of both primary and secondary incremental lines is a general phenomenon in terrestrial mammals. The taxonomic position of the species can only indirectly affect the character of the lines, through the morphology of the teeth (p. 21). Similarly, neither the sex and age of animals, nor their reproductive cycle appear to have any direct effect, at least in the case of formation of primary lines (p. 22 and 27).

It is generally agreed that incremental lines arise as a result of variation in the growth rate of the cementum layer. KLEVEZAL (1970) even states that cementum record both seasonal and age determined features of individual growth and that an analysis of this record permits a study of the various aspects of mammal growth from birth to death under natural conditions.

Probable causative factors of discontinuous cementum growth include both endogenous and exogenous factors.

Amongst the latter, seasonal change in environmental temperature or in photoperiod may be particularly mentioned but have as yet not been thoroughly investigated. The cementum pattern has also been taken as reflecting changes in metabolism of the animal. This again should reflect such features as variation in feeding habits, changes in parathyroid activity and/or variation in vitamin D levels. Physiological stress in connection with breeding, moulting, or in certain species hibernation, has also been mentioned. The hypothesis which has gained greatest support relates incremental line formation to a decrease in overall growth rate, linked to seasonally unfavourable conditions of life. As early as 1962 LAWS also mentioned the possibility that formation of the incremental line was related to several factors, which might vary in importance according to the species and type of annual cycle.

In recent years there has been an increasing tendency to emphasize the importance of endogenous rhythms, and that such rhythms can be inherited is mentioned by SPINAGE (1973) and KLEVEZAL & MINA (1973). However, in the present study, differences were observed in the pattern of lines in siblings of *Mustela vison* from fur farms and free-living *Vulpes vulpes*, eartagged as cubs and later recovered.

Until now, the formation of incremental lines has almost exclusively been investigated by relating the character of lines and their time of formation to naturally occurring variations in the conditions of life of different species. However, a few experimental workers (SAUER 1973, KLEVEZAL & MINA 1973, GRUE unpublished), have underlined the complexity of incremental line formation.

The main impression gained is that the formation of primary incremental lines is governed to a considerable degree by an internal rhythm, and that it is part of the

lowest nutritional level of the year. Teeth from *Ursus maritimus* are generally difficult to interpret. Adult females do not differ in that respect from adult males and young animals though adult females exhibit a more pronounced seasonal change in bodyweight in connection with denning and bearing of cubs (LÖNÖ 1970, present study).

As mentioned on p. 27 and 29, the regular occurrence of secondary lines in male ungulates has been related to rutting season (rut lines). This has been described for several species, e.g. in *Cervus elaphus*, Scotland (MITCHELL 1967), *Cervus canadensis*, Canada (FLOOK 1970), *Odocoileus hemionus*, British Columbia, Canada (LOW & COWAN 1963), *Odocoileus virginianus*, Michigan and Minnesota, U.S.A. (RANSOM 1966), *Capreolus capreolus*, Poland (SZABIK 1973), and *Rangifer tarandus*, Ottendalen, Norway (REIMERS & NORDBY 1968). In the last mentioned work it is indicated that rut lines may sometimes appear as a phenomenon mediated through nutrition in association with the reproductive cycle, as the food intake of male animals is often reduced during the rut. However, the regular occurrence of secondary lines seen most frequently in males does not appear to be a general phenomenon in deer populations. Thus in the present study they were not observed in any of the cervid species examined.

A hypothesis may also be mentioned here, put forward in connection with a study of *Tragelaphus strepsiceros* in Rhodesia, to explain the occurrence of two primary lines per year in African bovids, as well as the occurrence of rut lines in some male cervids (SIMPSON & ELDER 1969). According to these authors, one line is formed during the period of poor feeding, and the other, the so-called "breeding line", in connection with reproduction. It is further suggested that in temperate areas where winter nutritional stress is pronounced, the relatively broad "winter line" may mask the second or "breeding line" in the males of some species, or completely incorporate the "breeding line" in females, for in these the period of pregnancy would be concomitant with the period of winter stress.

As mentioned on p. 29, regularly occurring secondary lines have been observed in both sexes in a range of carnivores and ungulates. There is reason to believe that their occurrence is related to environmental conditions. However, until more detailed analyses of the occurrence and time of year for formation in particular are available there is hardly evidence enough to point out any factor which alone or together with others, can be responsible for the regular formation of secondary lines sometimes observed.

Conclusion

Both for correct age determination and for discussion of which factors affect the formation of incremental lines it is necessary to know at which time of year primary lines are formed. Until now more detailed information on this point has only been available in very few cases.

Based on the first scattered observations from species in the Palaearctic region, and by analogy with annual rings in trees, the formation of primary lines was believed in general to occur in winter, and the term winter lines gained acceptance. Since then several examples of line formation outside the winter period have been found, but the term itself has remained unchallenged. Figs. 2 & 3 and Table 1 however illustrate the misleading nature of the

animal's whole growth and metabolic rhythm. External conditions, and in particular those which directly or indirectly affect growth and physiological condition, can then modify line formation, but only in extreme cases can they obscure the rhythm through the formation of secondary lines, or obliterate it entirely. This is e.g. found in species exposed to different degrees of domestication.

Certainly a greater understanding of the formation of incremental lines can be reached now only through wide-ranging physiological studies of metabolism. Ne-vertheless game biology can still contribute by providing accurate descriptions of incremental lines, and of their time of formation in different species and under different conditions. This is especially required from regions and climatic zones from which few or no studies are presently available. In addition the continuation of such descriptions is a necessary prerequisite for the practical application of counting incremental lines as a method of age determination. The method has a sound theoretical basis, but in practice it must be used critically.

Appendix – Recommendations

In the present work, cementum structures have been studied in 3.700 individuals, representing 52 species of terrestrial mammals. This material provided a wide opportunity to compare the formation of incremental lines in both closely-related species and in larger taxonomic groupings. In this way some idea has been gained of the intra- and interspecific variation occurring, which would scarcely have been possible from the normal use of incremental lines for age determination, in which often a single, or very few species, are studied. During the work with the authors' material and in extracting information from literature, the importance of several practical points in studying incremental lines became apparent. To aid future work on the formation of incremental lines, and in particular determination of age, some general recommendations are offered. It must however be emphasized that the importance given to each individual point should depend upon the background and purpose of each particular study.

1. Which tooth to use:

1.1 Only undamaged teeth should be used. – Where teeth have been broken or mechanically damaged in other way, or where inflammation has caused necrosis of the periodontal membrane, cementum formation may be disturbed, and the pattern of incremental lines obscured.

1.2 Primary lines are recognizable in all teeth with arrested longitudinal growth. – Even in teeth that are partly non-functional or do not erupt lines are formed, as cementum deposition takes place also in these teeth throughout the life of the animal.

1.3 Choice of tooth depends upon size and form, and on the thickness of the cementum layer. – In order to distinguish each incremental line from its neighbour a certain thickness of cementum is required, but if the layer is too thick, the seasonal pattern of incremental lines may be obscured. For each species, it is therefore advisable to judge from experiment which tooth is the most suitable.

2. Which method to use:

2.1 Purpose of investigation as well as size of tooth available determines choice of method. – To investigate the time of year for development of primary lines, stained sections of decalcified teeth are required. For age determination from features of small teeth the same method is required, but for species with sufficiently large teeth, half-ground teeth or thin-sections of undecalcified teeth may be used.

2.2 Comparison of cementum structures in sections prepared according to different preparation techniques. – Cementum structures are readily comparable in half-ground teeth and thin-sections of undecalcified teeth, when direction of the light under which preparations are viewed is

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taken into account. Since optical density and staining characteristics of the organic matrix are not directly comparable, care must be taken when correlating structures in preparations of undecalcified teeth and stained sections of decalcified teeth.

2.3 Longitudinal (sagittal) sections should be used. – Incremental lines may be readily discerned in transverse sections, but the possibility of misjudging the number of primary lines present in this type of section is considerable. The number may either be overestimated due to difficulties in distinguishing between secondary and primary lines when just one level of the root is exposed, or underestimated as the last-formed layer may not be present at certain levels. In longitudinal sections incremental lines can be followed and compared over the entire length of the root.

2.4 Only sections from the center of the tooth should be used. – Ideal medial sections are difficult to obtain as roots are usually somewhat curved, but it is essential to select sections exposing the root foramen.

2.5 Technical standard of preparations. – To assess the time of year for development of primary incremental lines, sections of an optimal technical standard are essential. If incremental lines are merely used to separate individuals into age-groups, the technical standard required may be less than optimal. The uncertainty which may arise should however be carefully considered in relation to the work involved and to other possible methods of age determination.

3. Interpretation and calibration:

3.1 Start of cementum development. – Knowledge of the time when cementum development commences is essential for correct age determination. In most species investigated this coincides with eruption of the tooth, but in at least some ungulates cementum development and formation of incremental lines prior to tooth eruption has been noted.

3.2 Closing of the root. – The time of closing of the root in relation to season for development of primary lines can be important. It may determine whether or not a complete primary incremental line is formed when an animal passes for the first time through the season for primary line development.

3.3 Primary versus secondary lines. – As a check of the possibility for distinguishing between primary and secondary lines and of the observers ability to do it, comparison with material of known age is essential. Where known-age material is

lacking, comparison with young animals aged by other criteria can often be useful. Care should be taken not to include a possible juvenile line, or the dentine - cementum border, in the primary line count.

4. Season for development of primary incremental lines:

4.1 Checking the number of primary lines formed per year. – Assessment of time of year for development of primary lines will show whether one or more lines are formed each year. This is especially important in connection with studies of animals from Tropical and Sub-tropical regions.

4.2 Separation into age groups. – Knowledge of the time of year when primary lines are formed is a prerequisite for correct age determination. In species which bear their young over a large part or over the whole of the year and in specimens where the time of death falls within the usual period for primary line formation intraspecific variation in the time of birth and line formation respectively makes it possible that animals belonging to the same age group possess a different number of primary lines. Thus, individuals born early in the season may have one line more than those born late and individuals in which the line formes early in the period may have one newly-formed primary line more than those in which the line formes late.

4.3 Information on season of death. – Once assessed, knowledge of time of year for primary line development may give clues as to the season of death in other materials (recent and subfossil), but only within the same species occurring under the same climatic conditions.

5. Presentation of data:

5.1 Material. – Locality, number examined of the two sexes and the different age classes and distribution of collecting over the year should be given.

5.2 Method. – Quality of preparations is an important factor. Not only the technique used should be mentioned but all details in preparation technique should be shortly summarized.

5.3 Illustrations. – Photomicrographs may be valuable for illustrating incremental lines and their formation. They should always be accompanied by complete information on locality, date of death, sex and estimated or known age, tooth shown and scale used.

Acknowledgements

Dansk resumé

Aldersbestemmelse af pattedyr udfra histologiske tandstrukturer er et af de vigtigste hjælpemidler ved populationsundersøgelser indenfor vildtforskning og vildtforvaltning. Skønt metoden i dag benyttes rutinemæssigt, har man ringe kendskab til hvilke faktorer, der betinger og regulerer dannelsen af vækstlinier i tænderne.

På grundlag af histologiske præparater af tænder fra 3.700 individer repræsenterende 52 arter, samt oplysninger i litteraturen, er sammenstillet en oversigt over dannelsen af incrementallinier i tændernes rodcement hos terrestriske pattedyr.

Incrementallinier kan dannes i såvel mælketænder som de blivende tænder. Hos de fleste arter dannes den første incrementallinie i en tand i den første sæson for liniedannelse efter tandens frembrud. Liniedannelse kan dog hos nogle arter finde sted inden tandfrembrud, og tidspunktet for rodlukning i den frembrudte tand kan påvirke dannelsen af den første linie (fig. 1).

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I arktiske og tempererede områder synes alle undersøgte arter i princippet at danne én primær vækstlinie om året, men hos nogle arter kan det være vanskeligt at skelne primære fra sekundære. Fra områder med mindre årstidsvariation eller f.eks. to årlige tørtider foreligger ikke tilstrækkelige undersøgelser til en generel konklusion. Under hensyntagen til ovennævnte forhold vil det i de fleste tilfælde være muligt at foretage en rimelig sikker aldersbedømmelse af et individ udfra antallet af primære incrementallinier, men såvel erfaring som en god teknisk kvalitet af præparater er væsentlig (jvf. Recommendations p. 41-42).

Tidspunktet af året, hvor dannelsen af primærlinier finder sted, er illustreret i fig. 2 og 3 samt tabel 1. Det fremhæves på grundlag heraf, at dannelsestidspunktet varierer fra art til art, og at det er vildledende at betegne den primære incrementallinie som en vinterlinie.

Den inter- og intraspecifikke variation i primærliniernes karakter og dannelsestidspunkt diskuteres i relation til de undersøgte arters systematiske stilling (p. 21), alder og køn (p. 22), forplantningsforhold (p. 27) og de klimatiske forhold (p. 30) samt dyrenes kondition (p. 34).

På det foreliggende grundlag er det ikke muligt at pege på en enkelt faktor eller et faktorkompleks som den regulerende mekanisme. Hovedindtrykket er, at dannelsen af primærlinier er baseret på en indre rytme, og at de er et led i dyrets hele vækst- og stofskifterytme. Ydre forhold, og især de, der direkte eller indirekte påvirker vækst og kondition, kan påvirke liniedannelsen, men kun i ekstreme tilfælde kan de sløre den ved dannelse af sekundærlinier eller helt ophæve den. En yderligere forståelse af de regulerende mekanismer forudsætter nu eksperimentelle fysiologiske undersøgelser over incrementalliniedannelsen.

Резюме на русском языке

Определение возраста млекопитающих по гистологическим структурам зубов служит одним из важнейших пособий при исследованиях популяций в связи с изучением и охраной дичи. Хотя этот способ нынче применяется шаблонно, имеется мало знаний о факторах, которыми обусловлено и регулируется образование ростовых линий в зубах.

На основании гистологических препаратов зубов от 3.700 особей, представлявших собой 52 вида, а также литературных сведений, здесь составлен обзор образования ростовых линий в корневом цементе зубов сухопутных млекопитающих.

Ростовые линии могут образоваться как в молочных, так и в постоянных зубах. У большинства видов первая ростовая линия образуется в зубе в первом сезоне образования линий после прорезывания зуба. Однако, образование линий у некоторых видов может происходить и до прорезывания зубов, и время закрытия корня прорезавшегося зуба может повлиять на образование первой линии (фиг. I).

В местностях арктической и умеренной зоны кажется, что у всех исследованных видов в основном образуется по одной первичной линии в год, но у некоторых видов может быть трудно отличить первичные от вторичных. Из местностей с менее значительной разницей между временами года, или например с двумя годичными засухами, не имеется достаточных исследований для общего вывода. Принимая в учет эти обстоятельства, в большинстве случаев бывает возможно с приемлемой степенью надежности определить возраст особи по числу первичных ростовых линий, но для этого важны как опыт, так и хорошее техническое качество препаратов (см. «Рекомендации», стр. 41-42).

Время года, в котором происходит образование первичных линий, иллюстрировано в фиг. 2 и 3, а также в табл. I. На основании этого подчеркивается, что момент их образования у разных видов неодинаков, и что неправильно называть первичную ростовую линию зимней линией.

Междувидовые и внутривидовые вариации характера и момента образования первичных линий обсуждаются в связи с систематическим положением исследованных видов (стр. 21), возрастом и полом (стр. 22), условиями размножения (стр. 27) и климатическими условиями (стр. 30), а также с физическим состоянием животных (стр. 34).

На имеющейся в распоряжении основе невозможно указать на один определенный фактор или комплекс факторов как служащий регулирующим механизмом. Общее впечатление сводится на то, что образование первичных линий основано на внутреннем ритме, и что они являются звеном общего ритма роста и обмена веществ животного. Внешние условия, и в особенности те, которые непосредственно или посредственно воздействуют на рост и физическое состояние, могут повлиять на образование линий, но только в крайних случаях замаскировать его образованием вторичных линий или совершенно предотвратить его. Для более ясного понимания регулирующих механизмов теперь необходимы экспериментальные физиологические исследования образования ростовых линий.

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