Mandibular dentition and horn development as criteria of age in the Dall sheep Ovis dalli Nelson

James E. Hemming
The University of Montana

Follow this and additional works at: https://scholarworks.umt.edu/etd
Let us know how access to this document benefits you.

Recommended Citation
Hemming, James E., "Mandibular dentition and horn development as criteria of age in the Dall sheep Ovis dalli Nelson" (1967). Graduate Student Theses, Dissertations, & Professional Papers. 6503.
https://scholarworks.umt.edu/etd/6503

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact scholarworks@mso.umt.edu.
MANDIBULAR DENTITION AND HORN DEVELOPMENT AS CRITERIA
OF AGE IN THE DALL SHEEP, Ovis dalli Nelson

by

JAMES E. HEMMING

B.S. University of Montana, 1961

Presented in partial fulfillment of the requirements
for the degree of

Master of Science in Wildlife Technology

UNIVERSITY OF MONTANA

1967

Approved by:

[Signatures]

Chairman, Board of Examiners

Dean, Graduate School
ACKNOWLEDGMENTS

I am indebted to Dr. Robert L. Rausch, Arctic Health Research Center, Anchorage, Alaska, for his continuing assistance and encouragement and especially for donating the bulk of the specimen material used in this study and for his constructive criticism of this manuscript. The research was done under the guidance of Dr. Philip L. Wright, Department of Zoology, University of Montana, who offered many helpful suggestions during the research and preparation of the manuscript. Dr. Robert S. Hoffmann and Dr. William B. Rowan, Department of Zoology, University of Montana, also provided helpful suggestions. Mr. Richard Baker, Stella Duncan Institute, University of Montana, generously assisted in fluorescence microscopy and photomicrography. The radiograms were prepared by Mrs. Betty Cerino, Health Service, University of Montana. Several skulls and other materials from wild Dall sheep were provided by biologists of the Alaska Department of Fish and Game and the University of Alberta. Mr. Robert M. Shelden and Mr. F. Russell Lockner, Department of Zoology, University of Montana, translated papers from Russian and German to English. Mr. Ronald Stoneberg, Department of Zoology, University of Montana, provided suggestions regarding histological technique. I am especially grateful to my wife, Eunice, for her continued support and encouragement throughout the course of this study.

To these persons, as well as to others not individually named, I express my sincere thanks.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>INTRODUCTION</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>MATERIALS AND METHODS</strong></td>
<td>3</td>
</tr>
<tr>
<td>- Horns</td>
<td>4</td>
</tr>
<tr>
<td>- Tooth replacement</td>
<td>8</td>
</tr>
<tr>
<td>- Cementum annuli</td>
<td>9</td>
</tr>
<tr>
<td><strong>RESULTS AND DISCUSSION</strong></td>
<td>12</td>
</tr>
<tr>
<td>- Aging by horn rings</td>
<td>12</td>
</tr>
<tr>
<td>- Horn-curl</td>
<td>19</td>
</tr>
<tr>
<td>- Aging by eruption of teeth</td>
<td>20</td>
</tr>
<tr>
<td>- Aging by increments in the dental cementum</td>
<td>27</td>
</tr>
<tr>
<td>- Longevity</td>
<td>34</td>
</tr>
<tr>
<td><strong>SUMMARY</strong></td>
<td>37</td>
</tr>
<tr>
<td><strong>LITERATURE CITED</strong></td>
<td>39</td>
</tr>
<tr>
<td>FIGURE</td>
<td>PAGE</td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
</tr>
<tr>
<td>1. Horns of a 4 year-old ram showing annual rings and other corrugations</td>
<td>5</td>
</tr>
<tr>
<td>2. Internal horn anatomy of a 5 year-old ewe</td>
<td>5</td>
</tr>
<tr>
<td>3. The Taylor Horn-curl Protractor</td>
<td>7</td>
</tr>
<tr>
<td>4. Radiograms of Dall sheep mandibles</td>
<td>10</td>
</tr>
<tr>
<td>5. Graph of length of annual horn segments in Dall sheep ewes</td>
<td>14</td>
</tr>
<tr>
<td>6. Graph of length of annual horn segments in Dall sheep rams</td>
<td>14</td>
</tr>
<tr>
<td>7. Graph of length of annual horn segments in bighorn sheep rams</td>
<td>15</td>
</tr>
<tr>
<td>8. Graph of growth patterns in horns of Dall sheep</td>
<td>16</td>
</tr>
<tr>
<td>9. Graph of growth patterns in horns of bighorn sheep</td>
<td>16</td>
</tr>
<tr>
<td>10. The horns of lambs</td>
<td>17</td>
</tr>
<tr>
<td>11. The horns of yearlings</td>
<td>17</td>
</tr>
<tr>
<td>12. Graph of horn-curl in rams</td>
<td>22</td>
</tr>
<tr>
<td>13. The incisiform dentition of Dall sheep</td>
<td>23</td>
</tr>
<tr>
<td>14. Internal anatomy of the first incisor and fine structure of the dental cementum</td>
<td>29</td>
</tr>
<tr>
<td>15. Fluorescence photomicrographs showing cementum increments of 7 and 10 year-old Dall sheep</td>
<td>32</td>
</tr>
<tr>
<td>16. Graph of incisor width in relation to age</td>
<td>36</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. The periods of eruption of deciduous and permanent teeth</td>
<td>21</td>
</tr>
<tr>
<td>2. Eruption sequence of permanent mandibular dentition in the genus <em>Ovis</em></td>
<td>27</td>
</tr>
</tbody>
</table>
INTRODUCTION

The purpose of this study is to establish valid criteria which may be used by other workers to accurately age specimens of Dall sheep (*Ovis dalli*).

Three methods of determining age are explored in this report; annual growth patterns of the horns, annual growth patterns of the teeth, and tooth replacement and attrition. Until recent years age determination in wild artiodactyls has often been based upon tooth replacement and wear (Severinghaus, 1949; Robinette et al., 1957). However, it has been established that the teeth of artiodactyls of the same species from different areas exhibit different wear patterns within the same age class i.e., wear patterns may be quite area specific within the same species. There may also be inconsistencies due to variation in the subjective judgments of observers (Severinghaus and Cheatum, 1956; Robinette et al., 1957; Ryel et al., 1961). An attempt to study the succession of tooth wear i.e., the loss of infundibula and state of attrition of individual cusps and/or teeth in Dall sheep revealed individual variation so great as to prove the technique undesirable for purposes of aging this species.

The sequence of tooth eruption and replacement for Dall sheep has not been described, except in a very general way by Murie (1944). Data on tooth succession and replacement for the bighorn sheep (*Ovis canadensis*) have been presented by Cowan (1940), Demming (1952), Taber (1963), and Taylor (1962). Chernyavskii (1962a) presented a detailed description of tooth development in the Siberian snow sheep (*Ovis nivicola*).
Techniques for the study of annual increments in the dentine or cementum were first described by Scheffer (1950) and Laws (1952, 1953) in their respective studies of northern fur seals (Callorhinus ursinus) and elephant seals (Mirounga leonina). Similar techniques were applied to North American cervids such as moose (Alces alces) by Sergeant and Pimlott (1959); caribou (Rangifer tarandus) by McEwan (1963); mule deer (Odocoileus hemionus) by Low and Cowan (1963); white-tailed deer (O. virginianus) by Gilbert (1966) and Ransom (1966). Among wild North American bovids only the bison (Bison bison) has been examined for the presence of annual increments in the cementum of the teeth (Novakowski, 1965). The above workers have shown that cementum is deposited on the roots in the form of alternating translucent and opaque layers, with one translucent and one opaque layer representing one year's growth.

In some bovids the annual rings or transverse grooves around the horn, at the terminus of each annual segment, have been used as criteria of age. Various workers have suggested that one horn ring is laid down each year in such species as the chamois (Rupicapra rupicapra) (Couturier, 1938), Dall sheep (Dixon, 1938; Murie, 1944; and others), bighorn sheep (Cowan, 1940), and mountain goat (Oreamnos americanus) (Brandborg, 1955). However, it was not until 1965 that such an hypothesis was supported by statistically sound data in a study of the Himalayan thar (Hemitragus jemlahicus, Bovidae) by Caughley (1965) and by the use of known-age animals in a study of bighorn sheep by Geist (1966)
In most cases data from the horns of trophy animals such as Dall sheep, cannot be obtained from hunters. Since animals harvested by hunters are a good source of data it is important that criteria of age be derived from specimens which may be readily obtained from sportsmen. The mandible is one of the easiest items to collect from hunter-killed trophies; therefore, the main emphasis of this study is placed on mandibular dentition.

I have also compared age-specific characters of species of Ovis having ranges adjacent to O. dalli in the present work.

MATERIALS AND METHODS

All but 11 of the specimens utilized for this study were obtained from Nunamiut Eskimo hunters from the central Brooks Range, Arctic Alaska. At the request of Dr. Robert L. Rausch the skulls or mandibles and horns from Dall sheep harvested for food were saved and carefully labeled with sex, date and location. In this manner 118 specimens were collected between 1950 and 1966, an average of 7 per year. Dall sheep do not play an important role in the economy of the Nunamiut, but they are hunted when caribou are scarce (Rausch, 1951). Ten more specimens from various locations in south central Alaska were provided by biologists of the Alaska Department of Fish and Game, including one known-age animal, and a known-age 5 day-old lamb was obtained from the University of Alberta. Bones were cleaned by means of dermestid beetles and
bleached in hydrogen peroxide. After cleaning, all bones and horns were
dried thoroughly before being measured.

Birth dates for Dall sheep from the literature fall between 5 May
and 28 June (Sheldon, 1930; Dixon, 1938; Murie, 1944; Rausch, 1951). Since
the frequency distribution of births is not known the median date, 1 June,
was used.

Horns

The horns of 89 Dall sheep, 37 males and 52 females, were used for
this phase of the study. Careful examination of the external morphology
of the horns revealed the exact nature of annual segments and made it
possible to differentiate between annual rings and other corrugations
of the horns (Fig. 1). The validity of annual ring counts was checked
with a series of horns which were sawn lengthwise with a band saw, a
technique reported by Rausch (1951). The internal morphology revealed
the exact location of annual rings (Fig. 2).

In addition a series of measurements were routinely taken. These
included: circumference at the base; circumference at each annual
ring; length of the annual segments; length of the frontal surface;
distance between tips; degree of curl. The length of the frontal
surface and the length of each annual segment was determined by measuring
around the spiral on the frontal surface of the horn from the orbital
corner to the tip. A steel tape, a meter-long piece of 50 lb test
monofilament fishing line and a meter stick were used to take horn
Figure 1—Horns of a 4 year-old ram showing annual rings and other corrugations. White lines indicate the exact location of the annual rings.

Figure 2—Internal horn anatomy of a 5 year-old ewe. Note 5 dark annual rings.
measurements. Fishing line proved more accurate for measuring circumference of the horns than a steel tape. All measurements were recorded to the nearest millimeter. The degree of curl for rams was determined with the aid of a Taylor Horn-curl Protractor (Fig. 3). This device is a modification of the type originated by Taylor (1962).

The apparatus consists of an alignment disc of plexiglass, 40 cm in diameter, a 6 inch diameter plastic 180° protractor, a plexiglass angle arm, and a plywood mounting stand. The alignment disc is scribed with two perpendicular lines which meet at the center of the disc and extend to the outer edge, and with concentric circles scribed at 2 cm intervals. The alignment disc and protractor are drilled at the center and the angle arm at one end to accommodate the mounting bolt. These are attached to the slotted vertical bar of the mounting stand by a bolt and wing nut, in such a manner that the unit may be moved or locked to any point on the vertical axis and the components may be rotated independently. To measure the degree of curl the skull of a ram is placed behind the protractor with the long axis parallel to the alignment disc and the vertical bar of the mounting stand bisecting the circle formed by the horns. The alignment disc and protractor are then centered on the circle formed by the horns. It should be noted here that in most cases the horns do not form a perfect circle and the exact form is subject to individual variation.
Figure 3--Diagram of the Taylor Horn-curl Protractor.
so in each case the horns must be properly centered within the scribed
circles of the alignment disc, so as to conform to the circle which
most closely matches the diameter of the horns. The horns and
protractor are viewed from a distance of approximately 10 feet to
determine the degree of curl. The orbital corner of each horn was
considered 0°. Any of the perpendicular lines of the alignment disc
may be aligned with the orbital corner of the horn, and the angle
arm is aligned with the tip of the horn. By positioning the base
line of the protractor on the perpendicular closest to the horn tip,
the degree of curl can be measured.

Tooth Replacement

The terminology of dentition is derived from Riney (1951) and
Sisson and Grossman (1953). Symbols for deciduous teeth will be
preceded by a capital "D". The eruption of maxillary teeth occurs
at essentially the same time as the corresponding mandibular teeth,
but only mandibular dentition is considered in the present evaluation.

Routine measurements of the teeth were taken, including maximum
width and height above the level of the alveolus and length of the
mandibular and incisiform tooth rows. All measurements were taken
with dial type dividers and a steel scale graduated in half millimeters.
The teeth of Dall sheep are hypsodont and as the crown is worn off
the tooth continues to erupt throughout the life of the individual.
Measurements of the height of the tooth above the level of the
alveolus are of little value since the extent of exposure remains more
or less constant throughout life. The radiograms in Figure 4 show the reduction in length of teeth due to continuous eruption and wear.

The sequence of tooth replacement was determined by visual examination of the cheek teeth and incisors. A tooth was considered to be erupting if any portion was visible above the level of the alveolus of the cleaned skull. Radiograms proved useful in determining when new permanent teeth were beginning to form within the alveoli (Fig. 4). In 50 of 129 specimens there was evidence of tooth replacement activity. By comparing specimens of unknown age with two specimens of known age and by counting the annual rings in the horns it was possible to estimate the age of each specimen to the nearest month, providing the date at death was known.

Cementum Annuli

The first incisor \( I_1 \) was chosen as the most suitable tooth for a study of annual increments in the cementum. This tooth is easily removed from the mandible, is the first of the replacement dentition to erupt, and it erupts shortly after birth. The \( I_1 \) was removed from the mandible by carefully cutting away the bone or by soaking the jaw in tap water for 12-24 hours. In valuable museum specimens it was possible to remove \( I_1 \) by soaking and then by cutting off only the lower half of the root, the remainder of the tooth was returned to the skull and glued in place.

Several techniques were tried to determine the simplest method of detecting annual changes in the fine structure of the
Figure 4—Radiograms of Dall sheep mandibles 3/5 x natural size.
A. Jaw of 1 ½ month-old lamb. The rooted deciduous premolars DP₂ - DP₄ and M₁ show distinctly. Note 3 cusps on DP₄. B. Jaw of 4 month-old lamb. M₂ is just beginning to form. C. Jaw of 10 month-old lamb. M₂ is well formed, but does not extend above the level of the alveolus.
D. Jaw of 13 month-old animal. M₂ has erupted and M₃ is just beginning to form. E. Jaw of 16 month-old animal. F. Jaw of 20 month-old animal. Permanent premolars P₃ and P₄ are developing beneath the deciduous teeth. G. Jaw of 26 month-old animal. M₃ has erupted from the alveolus. H. Jaw of 28 month-old animal. P₃ and P₄ extend above the level of the alveolus, but DP₃ and DP₄ have not been shed. P₂ is beginning to form. I. Jaw of 33 month-old animal with complete molariform dentition. J. Jaw of 6 year-old adult.
cement. In all cases individual teeth were first imbedded in plaster of Paris, using a plastic ice-cube tray as a mold. This allowed easy manipulation of the specimen and prevented unnecessary chipping during sectioning. The block containing the tooth was clamped to an adjustable table mounted just below a Dremel Moto-tool, to which was attached a 1-inch-diameter Dental Diamond Wheel. To cool the specimen during sectioning a jet of water was directed to the specimen from a small water tank mounted near the saw. A rubber squeeze-bulb served to force water from the tank. By using this technique it was possible to obtain sections 1 or 2 mm in thickness. The sections were reduced to a thickness of 50 to 75 microns by grinding on water proof carborundum abrasive paper, grit No. 320 and 400 respectively, using the Frost Technique (Frost, 1958). In this way sections with a thickness of 50 microns were made in less than 10 minutes.

Since the thickness of the cementum layer varies from place to place on the root of the tooth, sagittal sections proved to be the most reliable.

Some sections were decalcified with nitric acid and stained with Ehrlich's hematoxylin and eosin, while others were mounted unstained and undecalcified. Mounted sections were examined with a compound microscope using both white transmitted light and polarized light. Neither of these techniques gave satisfactory
results. Decalcifying and staining also proved quite time consuming. The procedure finally adopted involved using the sections of unstained, undecalcified material. This is a rapid process requiring approximately 30 minutes from the time the tooth is removed from the skull until the section is mounted on a slide. Thin sections prepared as described above were washed, by shaking, in a vial of distilled water to which several drops of liquid detergent had been added. Sections were then rinsed, by shaking, in a vial of distilled water. Subsequently, sections were dehydrated by immersion for periods of 5 minutes successively in 70% ethanol solution, and in absolute ethanol. The mounted sections were examined with a Carl Zeiss Standard GFL fluorescence microscope. The lamp was equipped with an Osram high-pressure mercury burner. Excitation filter III with barrier filters 53 on the upper rotary disc and 47 on the lower rotary disc gave the best results. Optimum magnification was 160X. The fluorescing part of the cement appeared bright and pale green in color, against a dark background. The annual increments appeared as alternating fluorescent and dark bands with one fluorescent band and one dark band representing one year's growth.

RESULTS AND DISCUSSION

Aging by Horn Rings

Caughley (1965) in his study of Hemitragus, pointed out that
aging by horn rings has considerable advantages over aging by indices derived from characters that change continuously with age because they represent a quantitative change with age i.e., they have no natural variation if the class interval is set at one year. When aging by the use of horn rings the only source of error is the misidentification of horn rings.

The horns of Dall sheep consist of a bony core covered with a permanent corneous sheath. Horns begin to develop when lambs are approximately 4 months old. The horny sheath continues to grow throughout the life of the animal, but it attains the greater part of its length during the second and third summers (Figs. 5 and 6). Taylor (1962) reported that bighorn sheep show maximum growth during the second summer (Fig. 7). The basal circumference and length in Dall sheep horns increase in size at essentially the same rate (Fig. 8). The horns of bighorn sheep rams show a greater rate of increase in basal circumference than length, but the effects of "brooming" distort the results in older age classes (Fig. 9). Lambs cannot be sexed from the horns (Fig. 10), but after the first year the horns of males are characterized by large bases, while the horns of females are very slender and only slightly enlarged at the base (Fig. 11). The surface of the horns bear corrugations, the so-called "ornamental rings" or sulci, and transverse grooves with loosened edges called horn rings.
Figure 5--Length of annual horn segments in Dall sheep ewes.

Figure 6--Length of annual horn segments in Dall sheep rams.
Figure 7—Length of annual horn segments in bighorn rams. Data from Taylor (1962).
Figure 8--Growth patterns in the horns of Dall sheep. Dots represent females and circles represent males.

Figure 9--Growth patterns in the horns of bighorn sheep rams. Data from Taylor (1962).
Figure 10—Left. Skull of a 9 month-old male lamb. Right. Skull of a 10 month-old male lamb. The horns of female lambs fall between the two extremes shown here.

Figure 11—Left. Skull of a yearling ram. Right. Skull of a yearling ewe.
The annual ring is the result of temporary interruption of growth during winter. All horns collected from October through January were quiescent. In February, one specimen in a sample of 18 had a new annual ring. By May new annual rings and growing horn segments were evident in all horns. Growth appears to be most active in early summer and by the end of September growth has essentially ceased. If we assume a birth date of 1 June it is obvious that the annual ring forms from 1-3 months before that date. Therefore an animal not yet 5 years old may show 5 horn rings and 6 horn segments. In late fall this animal with 6 complete horn segments will be 5\(\frac{1}{2}\) years old.

To the untrained observer it may be difficult to distinguish between annual rings and other corrugations of the horn, especially in females and old animals. The unique character of the annual ring is that it forms a deep continuous groove with loosened edges, whereas the other corrugations consist of smoothly rounded ridges and grooves (Fig. 1).

The horn tips of Dall sheep are rarely "broomed", as are bighorn sheep, but after 5 years of age they may show considerable wear. In some cases the first year horn growth may be almost completely worn away, but only 13 specimens were found in which the first annual ring could not be seen. In these specimens I judged the first visible annual ring as terminating the second horn segment. However, in most
cases, even if the loosened edges have worn away the presence of the ring is indicated by a swelling in the vicinity of the annual ring. No specimens were found in which the second annual ring was completely obliterated by wear. In horns which have been sawed lengthwise, the location and number of annuli is obvious. Figure 2 shows the sharp boundary separating old and new growth, resulting in a cone-shaped layer separating each annual segment. This gives the appearance, in the sectioned horn, of a series of cones stacked one upon the other, each representing one annual segment. A count of horn rings provides a convenient index of age to the nearest year. If the date of death and the median lambing date is known, an animal can be assigned an age to the nearest month.

Horn-curl

Since various state game agencies have assigned a value of 270° ("three/quarter curl") as the minimum a ram must have in order to be legally harvested, I thought it appropriate to attempt to relate the degree of curl to the age of the individual. A sample of 23 rams revealed great individual variation within each year class, but by the age of 57 months all animals had exceeded a curl of 270° (Fig. 12). The youngest animal to achieve this curl was 41 months old. Taylor (1962) reported that bighorn sheep rams achieved a 270° curl by the age of 41 months. Individual variation in curl, within the same age
class, was found to be too great to be of value as a criterion of age.

Aging by Eruption of Teeth

The deciduous dentition is essentially complete at birth. The formula for this dentition of Dall sheep is \( \text{DI} \, \frac{0}{3}, \, \text{DC} \, \frac{0}{4}, \, \text{DP} \, \frac{3}{3} \). The deciduous incisors and incisiform canines are much smaller than their permanent successors and have a distinct neck at the junction of the crown and root. The deciduous incisors and canines are shown in Figure 13, A. The canines persist longer than any of the other deciduous teeth. Upper and lower first premolars are lacking in both deciduous and permanent dentition. Permanent premolars were counted in 63 mandibles, excluding those which had been damaged, immature animals with incomplete permanent dentition, and aged animals in which secondary loss of teeth had occurred. The \( P_2 \) was absent from 5 specimens.

The \( DP_2 \) and \( DP_3 \) have 2 roots, but \( DP_4 \) has 3 roots (Fig. 4, A). Permanent premolars \( P_2 \) and \( P_3 \) have a single root, but \( P_4 \) has a double root. The \( DP_4 \) may be easily distinguished from the permanent representative by the presence of 3 cusps (Fig. 4, A), whereas in the permanent tooth there are only 2 cusps (Fig. 4, I). This character allows immediate separation of animals 2\( \frac{1}{2} \) years old or younger from the older age classes.

The timing of tooth replacement activities is sufficiently
consistent to precisely indicate the age of Dall sheep in their first 4 years of life (Table 1). No differences in the timing of replacement events was observed between rams and ewes.

Table 1. The periods of eruption of the teeth as determined from the mandibles of 50 Dall sheep.

<table>
<thead>
<tr>
<th>TEETH</th>
<th>DECIDUOUS</th>
<th>PERMANENT</th>
</tr>
</thead>
<tbody>
<tr>
<td>I₁</td>
<td>At birth or first week</td>
<td>13-16 months</td>
</tr>
<tr>
<td>I₂</td>
<td>At birth or first week</td>
<td>25-28 months</td>
</tr>
<tr>
<td>I₃</td>
<td>At birth or first week</td>
<td>33-36 months</td>
</tr>
<tr>
<td>C</td>
<td>At birth or first week</td>
<td>45-48 months</td>
</tr>
<tr>
<td>P₂</td>
<td>At birth or first week</td>
<td>27-32 months</td>
</tr>
<tr>
<td>P₃</td>
<td>At birth or first week</td>
<td>25-30 months</td>
</tr>
<tr>
<td>P₄</td>
<td>At birth or first week</td>
<td>25-30 months</td>
</tr>
<tr>
<td>M₁</td>
<td></td>
<td>1-4 months</td>
</tr>
<tr>
<td>M₂</td>
<td></td>
<td>8-13 months</td>
</tr>
<tr>
<td>M₃</td>
<td></td>
<td>22-40 months</td>
</tr>
</tbody>
</table>

The post-embryonic development of the dentition takes place in the following manner:

Five days, known-age (l)*. All deciduous incisors and canines extend above the level of the alveoli, but only DI₁ appears to have reached its final position. The tips of DP₂ are visible and extend above the level of the alveolus. The DP₃ and DP₄ appear functional. The tips of M₁ have not yet reached the level of the alveolus. There is no sign of M₂ or M₃.

One and one-half months (l). The deciduous teeth of the incisiform tooth row have all reached their final position. The deciduous premolars

*The number of specimens examined is indicated in brackets.
Figure 12--The degree of horn-curl in Dall sheep rams.
Figure 13--Incisiform dentition of Dall sheep.  A. Deciduous incisors and incisiform canines. B. 18 month-old animal with one pair of permanent incisors (I₁). C. 30 month-old animal with 2 pair of permanent incisors (I₁ and I₂). D. 35 month-old animal with 3 pair of permanent incisors (I₁-I₃). E. 47 month animal with permanent dentition.
have reached their final position. The tips of $M_1$ extend above the level of the alveolus. There is a swelling of the bone at the base of $M_1$ on the buccal surface of the mandible.

Four months ($t_4$). The $M_1$ has reached its final position. The $M_2$ begins to develop within the alveolus.

Five months ($t_1$). Swelling of the bone at the base of $M_1$.

Eight months ($t_1$). The tips of $M_2$ are visible within the alveolus and extend to the level of the alveolus. Swelling of the bone at the base of $M_2$. The infundibula of $DP_3$ have been lost.

Ten months ($t_2$). The tips of $M_2$ extend slightly above the level of the alveolus. Swelling of the bone at the base of $M_2$.

Eleven and one-half months ($t_1$). The $M_2$ extends well above the level of the alveolus, but has not reached its final position. Swelling of the bone at the base of $M_2$.

Thirteen months ($t_3$). The $M_2$ has reached its final position. The $M_3$ begins development within the alveolus. The $DI_1$ may be in the process of replacement by its permanent successor.

Sixteen months ($t_7$). The $I_1$ has reached its final position.

Seventeen months ($t_1$). No obvious change.

Eighteen months ($t_1$). No obvious change.

Nineteen months, known-age ($t_1$). The anterior cusps of $M_3$ are developing, but do not extend above the level of the alveolus.
Twenty months (2). No obvious change.

Twenty-one months (1). No obvious change.

Twenty-two months (2). The anterior cusps of $M_3$ extend slightly above the level of the alveolus. The anterior infundibula of $DP_4$ have been lost.

Twenty-three months (2). No obvious change.

Twenty-five months (2). Two cusps of $M_3$ extend above the level of the alveolus. Swelling of the bone at the base of $M_3$. Below the deciduous premolars, the developing dental crowns of $P_3$ and $P_4$ may be seen. The replacement of $DI_2$ is taking place.

Twenty-eight months (7). The $DP_3$ and $DP_4$ are being replaced by permanent premolars. Below $DP_2$ the dental crown of $P_2$ may be seen. The $I_2$ has reached its final position.

Thirty months (2). The $P_3$ and $P_4$ have reached their final position. The posterior or third cusp of $M_3$ now extends above the level of the alveolus.

Thirty-two months (1). The $P_2$ has reached its final position.

Thirty-three months (1). The $DI_3$ is being replaced.

Thirty-five months (1). The $I_3$ extends well above the level of the alveolus, but has not yet reached its final position.

Forty months (2). All cusps of $M_3$ have reached their final position.
Forty-five months (3). The deciduous canines are being replaced.

Forty-seven months (2). The dentition is complete. The permanent canines have reached or have nearly reached the level of the entire incisiform tooth row.

If horns cannot be obtained the stage of eruption of permanent teeth is a useful alternate criterion of age during the first four years of life. For such animals harvested in the fall, one, two, and three year olds will have one, two, and three permanent incisors respectively on each half of the mandible.

The sequence of eruption of permanent mandibular dentition among closely related species of *Ovis* may be seen in Table 2. Some confusion has resulted from studies of *O. canadensis*. This may be due to Cowan (1940) apparently combining data on eruption from *O. canadensis* and *O. dalli*. Cowan stated "By the age of thirty-six months first the third premolars (DP3) and then the second premolars (DP2) have been replaced by their permanent representatives". Taylor (1962) studied known-age animals and found no differences in the timing of replacement of DP2 and DP3.

It is interesting to note that P2 and P3 precede I2 in the bighorn sheep, but follow I2 in argali, snow, and Dall sheep and in bighorn sheep P4 is the last of the premolars to erupt while in snow and Dall sheep P2 is the last to erupt. *Ovis canadensis,*
O. dalli, and O. nivicola belong to the subgenus Pachyceros Gromova, and are thought to be derived from argali-like ancestors (Stokes and Condie, 1961; Chernyavskii, 1962b). However, the differences described above may not be too surprising since Ovis canadensis has apparently been separated from Ovis dalli and Ovis nivicola for a much longer period than the latter have been from each other. Stokes and Condie (1961) reported that argali-like sheep migrated across the Bering Straits to North America in the early Pleistocene and were then separated into northern and southern groups by periodic ice sheets of the upper Pleistocene which allowed canadensis and dalli to evolve. The northern group was divided at the close of the Pleistocene by inundation of the Bering-Chukchi platform giving rise to Ovis nivicola in Siberia. The taxonomic status of dalli and nivicola has not been settled. For example Chernyavskii (1962b) considers them to be distinct species while Rausch (1963) considers them to be conspecific. Another consideration is the hypothesis presented by Cowan (1940) who stated "The similarity of the environmental conditions under which dalli and nivicola have evolved may have been such as to foster somewhat parallel changes from the parent stock. At the same time the vastly different environment provided by the arid badlands and mountain ranges can easily be imagined as likely to foster the development of the southern population, canadensis, along somewhat different lines".
Table 2. Eruption sequence* of permanent mandibular dentition in the genus Ovis.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>SEQUENCE OF ERUPTION</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovis ammon**</td>
<td>M₁ M₂ I₁ M₃ I₂ [P₂ P₃ P₄] I₃ C</td>
<td>Habermehl (1961)</td>
</tr>
<tr>
<td>Ovis canadensis</td>
<td>M₁ M₂ I₁ M₃ P₂ P₃ I₂ P₄ I₃ C</td>
<td>Demming (1952)</td>
</tr>
<tr>
<td>M₁ M₂ I₁ M₃ (P₂ P₃) I₂ P₄ I₃ C</td>
<td>Taylor (1962)</td>
<td></td>
</tr>
<tr>
<td>Ovis dalli</td>
<td>M₁ M₂ I₁ M₃ I₂ (P₃ P₄) P₂ I₃ C</td>
<td>This study</td>
</tr>
<tr>
<td>Ovis nivicola</td>
<td>M₁ M₂ I₁ M₃ I₂ (P₃ P₄) P₂ I₃ C</td>
<td>Chemyavskii (1962)</td>
</tr>
</tbody>
</table>

*Square brackets enclose symbols for teeth where it was not possible, from the publications cited, to establish their order of eruption relative to each other. Round brackets enclose teeth which erupt simultaneously.
** Sequence of eruption derived from domestic forms.

Aging by Increments in the Dental Cementum

Cementum is an interstitial bone substance which is deposited over the root of the tooth by the cementoblast cells of the periodontal membrane which surrounds the tooth. The layer of cementum increases in thickness with age, especially near the end of the root (Bloom and Fawcett, 1962).

In Dall sheep cementum deposition begins at approximately the same time as the tooth emerges from the alveolus. An ultraviolet fluorescing light-colored zone of rapid deposition is added during the summer and a narrow non-fluorescing dark zone is added during the winter. The timing of these events corresponds to the formation of annual segments and annual rings in the horns. Growth of the dark zone begins in the fall, before the rut, and ceases the following spring,
during the lambing period. A count of the dark zones proved most satisfactory for determination of age, since they are analogous to annual rings of the horns. One year must be added to the age obtained from the teeth since $I_1$ does not erupt until the animal is approximately 13 months old. To compensate for this the dentino-cemental interface was chosen to represent the first year increment. Therefore by counting each dark zone, including the dentino-cemental interface, the age in years can be determined and if the date of death is known age can be estimated to the nearest month.

Figure 14, a tooth section from an animal 52 months old, illustrates growth zones during successive years. The first summer is represented by Zone A and subsequent summers by Zones B-D. The dentino-cemental interface is labeled 1, and Zones 2-4 represent winter growth. The narrow white layer surrounding the tooth is the periodontal membrane. The area inside the dentino-cemental interface is dentine (X). In this specimen Zone 5 is just beginning to form and is represented by the thin dark line just inside the periodontal membrane. If the date of death were not known its age would be estimated at between 4 1/2 and 5 years.

Occasionally lamellae may be seen within the light zones (Fig. 15), but the difference between the lamellae and the dark
Figure 14—Internal anatomy of the first incisor and fine structure of the dental cementum. Bold diagonals represent enamel, the narrow diagonals dentine, the stippled area cementum, and the clear area pulp cavity. Photo shows cementum layer. Zones A-D represent summer growth and Zones 2-4 represent winter growth. Zone 1 is the dentino-cemental interface. The dentine is indicated by X.
zones is readily apparent and does not complicate age determination. Nishiwaki et al. (1958), Low and Cowan (1963), Gilbert (1966), and McCutchen (1966) described similar lamellae for the sperm whale, mule deer, white-tailed deer, and pronghorn antelope, respectively.

One specimen was found which showed one less annual increment than revealed by a count of the annual rings of the horns. Bloom and Fawcett (1962) reported that if the periodontal membrane is damaged or destroyed the cementum readily undergoes necrosis and may be reabsorbed. A pathological condition of this type may have resulted in the loss of one annual increment from the above specimen.

The amount of cementum which is deposited annually in Dall sheep tends to decrease with age, but the dark and light zones, using the fluorescence technique, are always well differentiated (Fig. 15). Novakowski (1965), using a technique requiring partial decalcification, had some difficulty when counting the cementum increments in the teeth of old bison. This was due to the annual increments becoming progressively thinner with advancing age. McCutchen (1966) found that annual increments in the cementum of pronghorn antelope appear to become thicker with age.

Various workers have encountered some difficulty when attempting to count the annual rings in the horns of wild sheep.
Murie (1944) reported that growth rings of old ewes fall very close together and in some specimens it is difficult to get an accurate age determination. Chernyavskii (1962a) found it impossible to determine the age of snow sheep ewes from the horns. Cowan (1940) found that in bighorn sheep of both sexes it is often impossible to distinguish the annual rings after the age of 8-10 years. The present study has also revealed that in some old Dall sheep, horn rings may be difficult or impossible to count and in some cases the horns of females may be broken to within a few inches of the base making it impossible to count the annual rings. However, I found that annual increments of the cementum are well defined and can be accurately counted in animals to at least 17 years, which is close to the ultimate age in wild sheep. Counts of the annual increments of the cementum are therefore much more reliable than counts of annual rings of the horns.

There has been considerable speculation as to the cause of differential growth in the teeth of artiodactyls. Wood et al. (1962) found that deer restrict their food intake during fall and winter, even when food is plentiful. Low and Cowan (1963) suggest that this may be due to cyclic hormonal changes or other related photoperiodic responses. Thus, these and other workers (Sergeant and Pimlott, 1959; Novakowski, 1965) have
Figure 15--Fluorescence photomicrographs showing cementum increments of 7 year-old (upper photo) and 10 year-old (lower photo) Dall sheep. Lamellae are evident in the upper photo.
suggested a relationship between deposition of opaque and translucent cemental increments and seasonal variations in feeding conditions.

This hypothesis is supported by the present findings. Since the ability of a substance to fluoresce depends on the presence of specific molecular structures, it is assumed that if no dietary chemical deficiencies occurred during the annual cycle, the chemical composition and structure of the cementum should remain the same and its fluorescing potential should remain constant even though the rate of deposition of this material may change. In other words if the chemical composition of the cementum remained constant throughout the year the entire cementum layer should fluoresce. It was found that only cementum material deposited during the summer fluoresced, suggesting a seasonal change in structure or chemical composition. Sampson (1952) reported that, in most grasses and forbs, there is a continuous decline in the percentages of crude protein, silica-free ash, phosphorus, and potassium from early growth to maturity. If the chemical composition of forage plants changes markedly during the annual cycle it seems probable that deficiencies may result in animals which utilize these plants and as a result the chemical composition of the material deposited by the cementoblast cells may be altered. Dixon (1938) reported that Dall sheep in Mount McKinley National Park use mineral "licks" in the spring and suggests that this activity helps to restore required minerals
which are lacking in winter food. An analysis of a sample of rock from one of these "licks" revealed the presence of soluble calcium and iron phosphate and certain insoluble substances, chiefly magnesia and silicates. He found that "licks" were seldom visited after the first part of June. As a result I suggest that the apparent change in chemical composition of the cementum layer between summer and winter may be due to seasonal changes in the chemical composition of forage plants which are ingested by the animal.

Differences in the rate of growth of the cementum may be due to other factors. Taylor (1962) reported that the weight of the thyroid gland in bighorn sheep increases rapidly in March, reaches maximum size in May and then gradually decreases in size until December. He also emphasized that the thyroid gland is large when the testes are small and vice versa. These data lend support to the hypothesis of Low and Cowan (1963), but further investigation is required.

Longevity

The incisiform teeth of Dall sheep are normally spatulate in shape, tapering uniformly to the base. The teeth of sheep continue to erupt throughout the life of the individual. If one assumes a constant rate of eruption and abrasion from material in the diet, one could expect to find a constant rate of tooth
wear and therefore be able to determine the life span of the teeth. Cowan (1940) reported that longevity of the individual is limited largely by the progressive wear and subsequent loss of the teeth. By measuring the maximum width of the first incisor from 78 specimens it was found that the rate of wear in the sample is relatively constant (Fig. 16). However, there is a great deal of individual variation within each year class. Fuller (1959) separated older bison into broad age groups based on wear of the incisiform teeth, but since broad age groups do not lend themselves to precise studies of population dynamics, incisor width was not used to define age groups in this study. However, the rate of wear indicates that the first incisor in Dall sheep could be completely worn away at the age of 15-17 years, if not earlier.

In a sample of 129 Dall sheep, aged by counting annual rings in the horns or annual increments in the cementum of \( I_1 \), only three animals exceeded the age of 15 years. All were females, one 15 years 4 months and two 17 years 5 months. The oldest male was slightly over 14 years old. At 15 years \( I_1 \) has erupted to a point where it no longer is contained within the alveolus and the root stub, which remains, is held in place by the gingiva.

Other workers have found a similar situation. Murie (1944)
Figure 16—Changes in the width of the first incisor due to wear.
examined a series of 829 skulls of Dall sheep and found only three animals, all males, which achieved an age of 14 years. Cowan (1940) found only two males 15-17 years old in a sample of 761 bighorn sheep. Taylor (1962) reported a female bighorn which he estimated to be at least 17 years old. Chernyavskii (1962a), on the basis of the study of 46 skulls of snow sheep, assumed the age limit for snow sheep to be 14-15 years. It appears that each of these species, under natural conditions, has the same longevity and that longevity is limited by the loss of functional teeth. Seton (1929) reported a captive bighorn ram in the Washington Zoo which achieved an age of 20 years. Presumably captive individuals under ideal conditions should be able to live longer than wild individuals.

SUMMARY

A sample of 129 skulls or horns and mandibles were used to develop age criteria for Dall sheep. The use of annual rings of the horns to determine age is a completely reliable field technique for the trained biologist, but in most cases the horns from hunter-killed sheep are not available. To rely on hunter-made counts of annual rings of the horns would undoubtedly introduce a great source of error and instead techniques utilizing incisor replacement and growth are
advocated. The timing of tooth replacement was found to be sufficiently precise to indicate the age of Dall sheep in their first 4 years of life. The mandibular dentition of animals ranging in age from 5 days to 4 years is described. However, only the incisiform tooth row is needed to determine the age of immature animals. The age of adult Dall sheep can be precisely determined in the laboratory by counting annual increments in the cementum of the first incisor. A new technique utilizing fluorescence microscopy is described for counting cementum annuli. The differences between the light and dark cementum increments appears to be related to a seasonal decline in the nutritive value of forage. Evidence in support of this hypothesis is presented.

The relationship of age to degree of horn-curl in rams is described.

From the evidence presented it appears that wild Dall sheep are limited to a life span of approximately 15 years. Under natural conditions longevity appears to be limited largely by the loss of functional teeth.

In the subgenus Pachyceros it was found that Ovis dalli and O. nivicola have identical sequences of permanent tooth eruption, but O. canadensis has a slightly different sequence of replacement.
LITERATURE CITED


Fuller, W.A. 1959. The horns and teeth as indicators of age in bison. J. Wildl. Mgmt. 23:342-344.


