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Age criteria for American bison

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AGE CRITERIA FOR AMERICAN BISON

by

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INTRODUCTION

Understanding the structure of the population and of the kill of game animals is one of the most important tools of the wildlife biologist. Structure, in this sense, is the composition of the population according to age and sex classes. Knowledge of age ratios permits a determination of the proportion of breeding females, their young, the yearlings, and the older age classes. With a knowledge of herd composition the production and the survival of that production may be found, giving information important to an understanding of population dynamics (Taber, 1960).

Normally, big game animals are divided into four age groups; young, yearling, prime and aged. This grouping provides a good check on the production and survival of the young through maturity, especially in species which breed as yearlings, and on the effects of hunter kills of different intensities on herd composition (Leopold, Riney, McCain, and Tevis, 1951). If, however, members of the species breeds for the first time as two-year-olds, or even as three-year-olds, production can best be understood only if these age classes are distinguished in the herd. Ideally, methods accurate enough to age each individual to the year would be highly desirable for studies of many kinds.

The present study was set up to investigate aging techniques for bison. The objectives of the study were:

1. To develop a general aging technique for bison by tooth replacement and wear, using known-aged animals. The procedures were: (a) provide an eruption and replacement table for the permanent dentition, (b) note

visible characteristics in tooth wear of the older animals, and (c) measure the amount of wear on the molars of the older animals.

2. To develop more accurate methods of aging bison by sectioning the central incisor teeth and measuring the weight of the lens of the eye.

LITERATURE REVIEW

Many studies have been made either developing or using aging techniques for mammals. However, only the literature closely related to the present study will be reviewed here. This review will cover tooth development, tooth replacement and wear, incisor sectioning, and lens weight measurement.

I. TOOTH DEVELOPMENT

A tooth consists of two portions, the crown and the root. The crown is the portion above the gumline and is composed of dentine and a hard outer covering called enamel. The root is the portion below the gumline and is composed of dentine and a thin outer covering called cementum. The center of the tooth, the pulp cavity, is hollow and houses the nerves and blood vessels (Ham, 1953).

The incisor, canine, and premolar teeth develop in two sets—deciduous and permanent. No essential difference exists between the development of the two. As the deciduous teeth are being formed, the permanent tooth buds start their development. At regular intervals, the permanent teeth replace the deciduous incisors, canines and premolars. The three molars are not preceded by deciduous dentition (Ham, 1953).

In older big game animals, the teeth begin to wear down through the enamel, thus exposing the dentine. Exposure of the pulp cavity is precluded by a new dentine called secondary dentine being deposited around the inside of the pulp cavity; it eventually fills this cavity (Maximow and Bloom, 1957). In contrast, the cement begins to form

around the outside of the root before birth. New layers are continually deposited thereafter.

II. TOOTH REPLACEMENT AND WEAR

As has been stated above, two sets of teeth are developed; the deciduous and the permanent. Since the sequence of tooth eruption and replacement is rather regular, it, and relative tooth wear, have been used as a basis for age determination. The teeth of the lower jaw particularly have been used as criteria for age for most big game animals. However, it should be recognized that the schedule of eruption and replacement may deviate under severe conditions of disease or malnutrition and also during exceptionally good conditions for growth and development (Taber, 1960). After the animals get their adult dentition they may be aged by the amount of relative wear on the cheek-teeth. This is less accurate than use of tooth eruption and replacement, so the older animals can be aged only approximately (Severinghaus, 1949; Taber, 1960).

Several workers have made studies of tooth replacement and wear for aging big game. Severinghaus (1949), working with known-aged white-tail deer (Odocoileus virginianus), Banfield (1954), working with barren ground caribou (Rangifer arcticus), and Passmore, Peterson and Cringan (1955) working with Ontario moose (Alces alces), used an aging system described by Severinghaus (1949) based on sequence of eruption and relative wear of the molars. Measurements were made on the lingual (tongue) side of the tooth row from gumline to the highest point of the tooth crown. Robinette, Jones, Rogers, and Gashwiler (1957) working with known-aged mule deer (Odocoileus hemionus), used a similar

technique where measurements were taken on the seven occlusal surfaces of the buccal (cheek) side of the jaw, and on the height of the corresponding lingual crests. The sum of the occlusal measurements were divided by the sum of the height measurements; thus obtaining a ratio which increased with the animal's age. Quimby and Gaab (1957) aged elk by using specific characters which were present or absent. They listed five specific characters found in 3-year-old and five specific characters found in 4-year-old elk jaws. They concluded, however, that visual comparison with known-age jaws, if available, provided a more reliable basis for aging than the use of their specific age characters.

Deming (1952), working with Nelson bighorn sheep (*Ovis canadensis nelsoni*), and Brandborg (1955), working with the mountain goat (*Oreamnos americanus missoulae*), showed the sequence of tooth development, but did not use relative wear as a method of aging adult animals. Dow (1952) and Dow and Wright (1962), working with the pronghorn antelope (*Antilocapra americana*), found that this species possessed teeth of a type different from that found in the Bovidae and Cervidae. Therefore they used the number of infundibula (funnel shaped hollows) as a basis for age. Briefly, twelve infundibula are visible in the 2½ to 3½-year-old animals and these are lost by wear at the rate of about two per year. Fuller (1959), working with bison (*Bison bison*), developed a dichotomous key for aging. He did not attempt to recognize individual year classes for animals over four years. He grouped the older animals into classes of young adults, adults, and aged by the amount of wear on the molariform style. Hogben (no date) also aged bison by replacement and by wear on the molarian style.

III. INCISOR SECTIONING AND EYE LENS WEIGHT

Two other means of aging which have been gaining recognition are aging by use of growth layers in the dentine and cement of teeth and use of a lens-weight measurement. These two methods provide the most accurate available method for aging some mammals.

Incisor Sectioning

Laws (1953) developed a method of aging the elephant seal (*Mirounga leonina*) by preparing thin sections of the canine teeth and examining the regular sequence of growth layers in the dentine. This method has now been applied to a number of species of pinnipeds (Fisher, 1954; McLaren, 1958) and also to Odontocete whales (Nishiwaki, Hibiya, and Ohsumi, 1958). Scheffer (1950) using marked fur seals (*Callorhinus ursinus*) of known age showed that external ridges corresponded with growth layers in the dentine but were not useful for aging since they became obscured within a few years by deposition of overlying cement. Sergeant and Pimlott (1959) sectioned incisor teeth on moose and examined the structure of both dentine and cement. The cement showed regular layerings.

In Germany, von Marienfrid (1939) found annual dentinal layerings in the central incisor teeth of the red (*Cervus elaphus*), and fallow (*Cervus dama*) deer. The layerings were deposited starting with the third year of age. Each annual layer consisted of one light ring and one dark ring. The difference in rings probably represents seasonal changes in the feeding cycle (von Marienfrid, 1939) and possibly changes in endocrine rhythms (Sergeant and Pimlott, 1959).

Lens Measurement

The lens of the eye of man, rabbits, and probably most mammals grow continuously throughout life, thus providing a potential indicator of age (Lord, 1959). Lord (1959) presented a technique for determining the age of cottontail rabbits (*Sylvilagus floridanus*) based on the growth rate of the lens of the eye. The lenses were dried and weighed, and a weight-age curve was plotted. This proved to be reliable for estimating the age of rabbits. This same technique has been applied by Lord (1961) to the grey fox (*Urocyon cinereoargenteus floridanus*), by Sanderson (1961) to the raccoon (*Procyon lotor*), and by Kolenosky and Miller (1962) to the pronghorn antelope.

MATERIALS AND METHODS

The study material consisted of 108 bison lower jaws and seventy-three pair of bison lenses, all of known age, collected from the National Bison Range, Montana during the annual bison slaughter of 1959 and 1960.

The bison are branded as calves during the annual roundup in October. The first branding of calves occurred in 1940 and was undertaken to mark the animals that had been vaccinated for brucellosis. During the war years 1942, 1943, and 1944 no branding or vaccinating was accomplished due to shortage of personnel. In 1945 the branding and vaccinating were resumed and have been continued each year since. The calves are branded in the usual manner with a hot branding iron, using the last digit of the year that they are branded in; i.e. an "0" was used to denote the year 1940. Each ten years the branding is switched from the left to the right side, or vice-versa (C. J. Henry, pers. comm., 1962).

The surplus bison are selected for slaughter on the basis of physical characteristics and by the number of animals in each age class it is necessary to remove in order to maintain numbers in proper balance with the range. Ordinarily the bison selected for slaughter range from two and one-half to twelve to fifteen years, and include both sexes. These bison are kept in a corral by the slaughterhouse and are run, one at a time, into a squeeze chute and killed by a shot in the back of the head. A trap door opens on one side of the squeeze chute and the animal rolls into the slaughterhouse for butchering. Bison Range

personnel, assisted by temporary help, butcher the bison and take information on each individual. The information taken includes live and dressed weights, body length and height, sex and age, and status of pregnancy and lactation for cows. Also the bison's general condition is noted. The meat is sold to purchasers who are selected by a drawing and the hides are sold to the highest bidder, so the Bison Range is partially self-supporting (C. J. Henry, pers. comm., 1962).

The bison lower jaws and eye lenses are not normally saved but they were collected during 1959 and 1960 for this study. Aging techniques based on tooth replacement and eruption for the young, and tooth wear for the adults will be presented. Incisor sectioning results and a criterion based on a weight-age relationship of the lenses will also be presented. Statistical analysis is given for tooth wear by molar measurements and also for the eye lens weight data.

AGING BISON BY TOOTH REPLACEMENT AND WEAR

To develop a general aging technique for known-aged bison, lower jaws were collected during the 1959 and 1960 annual bison slaughter at the National Bison Range, Montana. A total of 108 lower jaws, ranging in age from two to seventeen years, were collected by the author and used in this study. They were examined for a sequence of replacement and eruption; visible characters were noted and molar measurements were taken. The points covered in this chapter are the procedures and results of tooth replacement, of tooth wear by visible characters, of tooth wear by molar measurements, and a discussion.

I. TOOTH REPLACEMENT

From the 108 lower jaws collected, eighty-one were used for aging by tooth replacement. These included animals from two and one-half to five and one-half years of age. Broken down into numbers per age class there were:

Age	Number
2.5	37
3.5	22
4.5	17
5.5	5

The bison teeth are of the selenodont, hypsodont type, which means the cusps assume a cresentic shape and the crown is long with a root that continues to develop months or years after the tooth erupts (Romer, 1956). The incisor teeth are the brachyodont type, meaning that

they have short crowns (Sisson and Grossmann, 1953). The dental formula is: I $\frac{0}{3}$, C $\frac{0}{1}$, P $\frac{3}{3}$, M $\frac{3}{3}$ 32 (Fuller, 1959). This formula is the same as that for the domestic cow.

Sisson and Grossmann (1953) in their work on domestic animals gave a sequence of replacement and eruption for the ox (Bus taurus), an animal in the same family (Bovidae) as the bison. Bison teeth are similar to those of the domestic cow, not only in shape and function, but also in time and manner of replacement. However, the cow has developed a full set of permanent teeth at three and one-half to four years, while the bison attains complete dentition at four and one-half to five years.

Progressing from the center of the lower jaw outward, in the bison, the first three pairs of teeth are the incisors; the fourth pair are the canines. The canines do not differ in shape or function from the incisors. The first premolar is absent, having been lost during the evolutionary process. The second premolar is rather simple in design, whereas premolars three and four are progressively more complex and molariform (Fuller, 1959). There is no replacement of the molar teeth; they erupt as permanent teeth. The lower jaws were examined for a sequence of replacement and eruption. The premolar replacement and the molar eruption were considered complete when slight wear was observed. The sequence of eruption will be described for the incisors first, for the premolars second, and the molars last.

Results

The replacement of the deciduous incisiform teeth begins when the animal is two years of age. During this second year the first deciduous

incisors are replaced by the permanent ones. In the third year the second incisors are replaced, and during the fourth year the third incisors and canines are replaced. The permanent incisiform teeth are thus all fully erupted by four and one-half or five years of age.

The premolars were mostly replaced during the third year. However, some deciduous second and third premolars were shed during the last half of the second year. On two occasions (out of twenty-two individuals) the fourth premolar was replaced before the second premolar.

The first molar starts erupting at approximately three months of age and is completely erupted by approximately one year of age. During the next year the second molar erupts and requires several months to complete eruption (Fuller, 1959). The first and second molars have two cusps each, but the third molar possesses an additional rudimentary third cusp. This third molar begins erupting during the second year and takes from one to two years to erupt fully. The complete molar dentition is obtained by the fourth or fifth year. Table 1 summarizes the schedule of replacement and eruption for the incisiform, premolar, and molar dentition.

The individual variations in replacement were noted for each age class. The total number of animals in each age class, and the number varying from the expected pattern, were noted. Table II shows the number of animals varying from the expected replacement and eruption. The variation in the schedule of replacement and eruption was further divided into sexes, and the numbers differing from the total were noted for each age class. Table III and IV show that there is probably little variation in tooth development between the male and female, except that the female seems to be slower in erupting fully the third molar.

Table I. Bison tooth replacement and eruption

Age in Years	Incisors 1	Incisors 2	Incisors 3	Canine 1	Premolars 2	Premolars 3	Premolars 4	Molars 1	Molars 2	Molars 3
1.5[a]	D[b]	D	D	D	D	D	D	P	(P) P	O
2.5	P	D P	D	D	D (P)	D (P)	D (P)	P	P	O (P)
3.5	P	P	D P	D (P)	(P) P	(P) P	D P	P	P	(P) P
4.5	P	P	D P	D P	P	P	P	P	P	(P) P
5.5	P	P	P	P	P	P	P	P	P	P

[a] age 1.5 is hypothetical as no jaws were collected for this age.

[b] D = deciduous tooth; P = permanent tooth; ( ) = tooth being erupted; O = tooth which has not erupted.

Table II. Variation of tooth replacement and eruption in bison

Age	Number of Animals	Expected Incisor Replacement				Variations in Incisor Replacement			
		1	2	3	4	1	2	3	4
2.5	37	P[a]	D	D	D		(P)-5[b] P -1		
3.5	22	P	P	D	D			(P)-3 P -1	
4.5	17	P	P	P	(P) P			D -1 (P)-2	D - 3 (P)- 5
5.5	5	P	P	P	P				

Age	Number of Animals	Expected Premolar Replacement			Variations in Premolar Replacement		
		2	3	4	2	3	4
2.5	37	D	D	D	(P)-8	(P)-11	
3.5	22	P	(P) P	(P) P	P -9	(P)- 7	D -4 P -3
4.5	17	P	P	P			

Age	Number of Animals	Expected Molar Eruption				Variation in Molar Eruption			
		1	2	3	M4[c]	1	2	3	M4
2.5	37	P	P	(P)	O			O - 1	
3.5	22	P	P	(P)	(P)			P - 1	O - 7 P - 1
4.5	17	P	P	(P) P	(P) P			(P)- 7	O - 1 (P)- 6
5.5	5	P	P	P	P				

[a] P = permanent; D = deciduous; ( ) = erupting tooth; O = tooth not erupted.

[b] number varying from expected.

[c] third cusp on third molar.

Table III. Variation of tooth replacement and eruption in male Bison

Age - Years	Number of Animals	Incisors 1	Incisors 2	Incisors 3	Canine 1	Premolars 2	Premolars 3	Premolars 4	Molars 1	Molars 2	Molars 3	Molars 4[a]
2.5	35	-- -- P-35	D[b]-30[c] (P)- 4 P - 1	D -35 -- --	D -35 -- --	D -27 (P)- 8 --	D -25 (P)-10 --	D -34 (P)- 1 --	-- -- P -35	-- -- P -35	0 - 1 (P)-34 --	0 -35 -- --
3.5	15	-- -- P-15	-- -- P -15	D -11 (P)- 3 P - 1	D -14 (P)- 1 --	-- (P)-10 P - 5	-- (P)- 6 P - 9	D - 3 (P)-10 P - 2	-- -- P -15	-- -- P -15	-- (P)-14 P - 1	0 - 5 (P)- 9 P - 1
4.5	10	-- -- P-10	-- -- P -10	-- (P)- 2 P - 8	D - 2 (P)- 2 P - 6	-- -- P -10	-- -- P -10	-- -- P -10	-- -- P -10	-- -- P -10	-- (P)- 3 P - 7	-- (P)- 3 P - 7

[a]third cusp on third molar.

[b]D = deciduous tooth; P = permanent tooth; ( ) = tooth being erupted; 0 = tooth which has not erupted.

[c]number of animals possessing that replacement. When the right and left side differed, the more developed replacement was noted.

Table IV. Variation of tooth replacement and eruption in female Bison

Age - Years	Number of Animals	Incisors 1	Incisors 2	Incisors 3	Canine 1	Premolars 2	Premolars 3	Premolars 4	Molars 1	Molars 2	Molars 3	Molars 4[a]
2.5	2	— — P -2	D[b] - 2[c] — —	D - 2 — —	D - 2 — —	D - 2 — —	D - 1 (P)- 1 —	D - 2 — —	— — P - 2	— — P - 2	— (P) - 2 —	0 - 2 — —
3.5	7	— — P -7	— — P - 7	D - 7 — —	D - 7 — —	— (P)- 3 P - 4	— (P)- 1 P - 6	D - 1 (P)- 5 P - 1	— — P - 7	— — P - 7	— (P) - 7 —	0 - 2 (P)- 5 —
4.5	7	— — P -7	— — P - 7	D - 1 — P - 6	D - 1 (P)- 3 P - 3	— — P - 7	— — P - 7	— — P - 7	— — P - 7	— — P - 7	— (P) - 4 P - 3	0 - 1 (P)- 3 P - 3
5.5	5	P -5	P - 5	P - 5	P - 5	P - 5	P - 5	P - 5	P - 5	P - 5	P - 5	P - 5

[a] third cusp on third molar.

[b] D = deciduous tooth; P = permanent tooth; ( ) = tooth being erupted; 0 - tooth which has not erupted.

[c] number of animals possessing that replacement. When the right and left side differed, the more developed replacement was noted.

II. TOOTH WEAR BY VISIBLE CHARACTERS

Studies of relative tooth wear were made on forty-eight bison jaws ranging from four and one-half to seventeen and one-half years of age. Broken down into numbers per age class there were:

Age	Number	Age	Number	Age	Number
$4\frac{1}{2}$	17	$8\frac{1}{2}$	4	$12\frac{1}{2}$	1
$5\frac{1}{2}$	5	$9\frac{1}{2}$	3	$15\frac{1}{2}$	1
$6\frac{1}{2}$	5	$10\frac{1}{2}$	4	$17\frac{1}{2}$	1
$7\frac{1}{2}$	6	$11\frac{1}{2}$	2		

As the bison are getting their full set of teeth, the teeth begin to wear, and certain characters become evident. As the wear continues these same characters change in shape or disappear and new characters appear, enabling age groupings to be described.

On each molar of the lower jaw there is a style which is found on the buccal side between the anterior and posterior cusps (Fuller, 1959). These are shown in Figure 1. At first only the tip of the style begins to wear, producing a circular enamel pattern on the occlusal surface. As wear continues the enamel pattern of the style becomes a loop (Fuller, 1959). Since hypsodont teeth grow up from the gums, continually, as fast as they are worn off at the crown, the molar styles do not show in the younger animals as the style is still beneath the gumline.

Results

By the time the bison is two and one-half years of age the style of the first molar (M1) is subjected to wear. The style of the second molar (M2) comes into wear at four and one-half, with the third molar

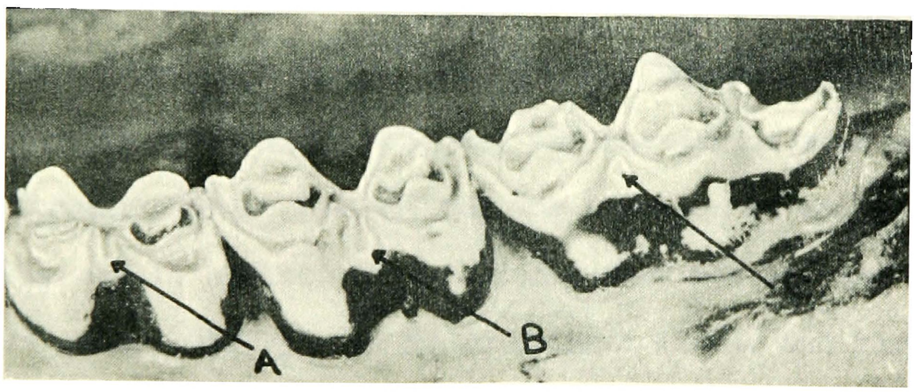

Figure 1. Twelve and one-half year old Bison showing molarian styles. A. Style on first molar; worn to a loop. B. Style on second molar; worn to a loop. C. Style on third molar; worn to a small circle.

(M3) style not wearing until approximately nine and one-half years.

Fuller (1959) considered three additional groupings beyond the full set of adult dentition which was attained by the fifth year. Working with unknown-aged bison he recognized "young adults", "adults", and "aged", by using the wear on the molarian styles supplemented by measuring the wear on the canine and defining these measurements arbitrarily. His "young adults" (he estimates these as five to six years) had the style on M3 worn to a circle with only slight wear on the canine—less than 2mm. The "adult" (7-12 or 15) group had M3 still in the circle stage with canine wear between 2mm and 4mm. The "aged" group had the M3 style worn to a loop and the canine wear exceeding 4mm.

My "young adults" ($5\frac{1}{2}$-$8\frac{1}{2}$) had the style on M3 showing but only occasionally was it a circle. The canine wear was between 2mm and 5mm. The "adult" group ($9\frac{1}{2}$-$17\frac{1}{2}$) had M3 as being a circle and rarely only showing. The wear on the canine was between 4mm and 8mm. The "aged" group cannot be described, due to lack of animals over seventeen years, but it probably has a loop on the style of M3. A difference probably exists in the amount of dust on the forage, in the range condition or the nutritive value of the food between Fuller's area and the National Bison Range; this could cause a difference in wear between the two studies.

Table V shows the individual variations of wear on the molarian styles within the age groupings, and Table VI shows the differences within each single age class.

Table V. Changes in molarian styles by age groupings

Age - Years	Number of Animals	M_1 Style[a] shows	M_1 circle	M_1 loop	M_2 Style does not show	M_2 shows	M_2 circle	M_2 loop	M_3 Style does not show	M_3 shows	M_3 circle
2.5 - 4.5	76	14[b]	46	16	28	42	6	--	71	5	--
5.5 - 8.5	20	--	--	20	--	1	10	9	8	10	2
9.5 - 17.5	12	--	--	12	--	--	3	9	--	2	10

[a]first molar style; second molar style; third molar style. Hypsodont teeth grow up from the gums, continually, as fast as they are worn off at the crown; so in young animals the style, sometimes, has not erupted and does not show. After the style appears, the tip begins to wear producing a circular enamel pattern. As wear continues the pattern becomes a loop.

[b]number of animals possessing that character. Some animals had different characters showing on the left and right sides, so the character indicating the most wear was noted.

Table VI. Changes in bison molarian styles by single age classes

Age - Years	Number of Animals	M_1 Style[a]			M_2 Style				M_3 Style		
		shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
2.5	37	13[b]	24	--	26	11	--	--	37	--	--
3.5	22	1	19	2	2	19	1	--	22	--	--
4.5	17	--	3	14	--	12	5	--	12	5	--
5.5	5	--	--	5	--	--	4	1	2	3	--
6.5	5	--	--	5	--	1	3	1	3	2	--
7.5	6	--	--	6	--	--	2	4	3	2	1
8.5	4	--	--	4	--	--	1	3	--	3	1
9.5	3	--	--	3	--	--	1	2	--	--	3
10.5	4	--	--	4	--	--	2	2	--	2	2
11.5	2	--	--	2	--	--	--	2	--	--	2
12.5 15.5 17.5	3	--	--	3	--	--	--	3	--	--	3

[a] first molar style; second molar style; third molar style. Hypsodont teeth grow up from the gums, continually, as fast as they are worn off at the crown; so in young animals the style, sometimes, has not erupted and does not show. After the style appears, the tip begins to wear producing a circular enamel pattern. As wear continues the pattern becomes a loop.

[b] number of animals possessing that character. Some animals had different characters showing on the left and right sides, so the character with the most wear was noted.

III. TOOTH WEAR BY MOLAR MEASUREMENTS

Molar measurements were made on thirty-five lower jaws ranging in age from four and one-half to seventeen and one-half years of age. Fewer jaws were used for molar measurements than for visible characters because some of the teeth became broken in handling and could not be measured accurately. Divided into numbers per age class there were:

Age	Number	Age	Number	Age	Number
4½	10	8½	4	12½	1
5½	2	9½	2	15½	1
6½	5	10½	2	17½	1
7½	5	11½	2		

Molar measurements of the seven occlusal surfaces were taken to the nearest tenth of a millimeter, with calipers, from the outer edge of the infundibulum across the widest part of each crown to the outer edge of the wearing surface (Figure 2). All measurements were taken from the left mandible.

Results

The data in Figure 3 suggested that a straight line relationship might exist between molar wear and age. Since the older ages had one animal each, only the age classes four and one-half through eleven and one-half years were analyzed. To establish whether a relationship did exist the correlation coefficient was determined by means of a linear regression analysis based on all individual bison molar measurements. This test indicated a value of 0.871 for the sum of the seven occlusal measurements indicating that a relationship did exist.

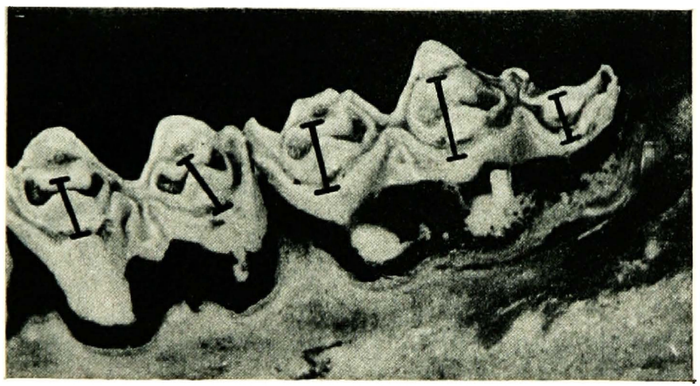

Figure 2. Method of taking occlusal measurements of Bison.

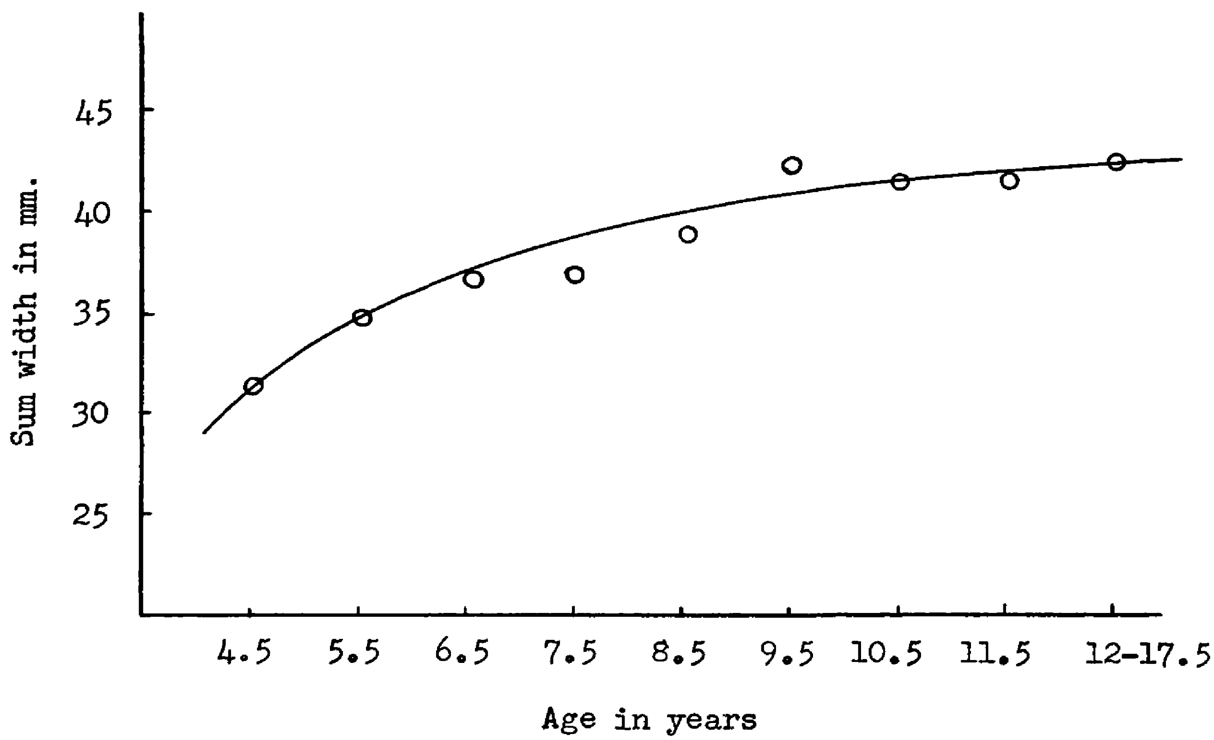

Figure 3. Relation of the sum of the occlusal surface measurements to age for Bison, based on the mean values for each age class.

The linear regression formula for the expected Y, $\hat{Y} = a + bX$, (Snedecor, 1956) was used to establish the degree of relationship between molar wear and age. The regression value for the occlusal measurements is $\hat{Y} = 26.82 + 1.4138X$. The standard error of the estimate is 3.67. Confidence limits for $\hat{Y}$ at the 95% probability level are shown in Figure 4 as curved lines on both sides of the regression line.

At the 95% confidence limits an overlap occurs between the age classes; as an example suppose the sum of the seven occlusal measurements was 40 millimeters, the estimated age would be about 9½ years, however, at the 95% confidence limits the actual age could be between 8½ years and 11½ years. In other words, an occlusal measurement of 40 millimeters would be between 8½ and 11½ years 95% of the time. The range of ages which a given occlusal measurement might indicate at the 95% level of accuracy is shown on Figure 4. Table VII shows the changes in bison occlusal measurements with age.

IV. DISCUSSION

The results of Fuller's (1959) study conducted at Wood Buffalo National Park, Northern Alberta, was quite similar to those of my study for both replacement and wear. One difference was noted; in Alberta incisor wear appeared less while molar wear appeared greater (see visible wear results).

A paper prepared by Hogben (no date) on bison jaw aging at the National Bison Range showed that the adult dentition was attained at six years instead of four and one-half or five as in my study. In Hogben's study known-aged animals were used for the one, two, and three

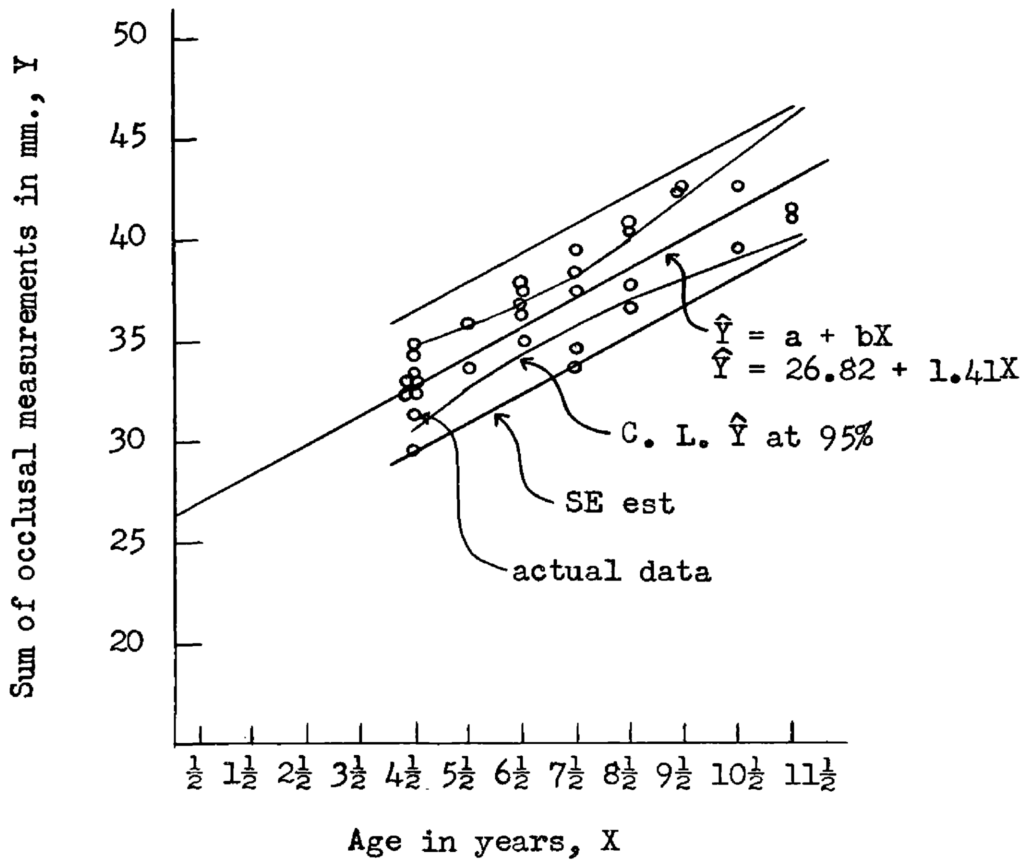

Figure 4. Regression and confidence limits of Bison occlusal measurements on age.

Table VII. Changes in Bison occlusal measurements (sum of seven occlusal surfaces) with age.

Age - Years	Mean	Range	Number of bison
4.5	31.5[a]	19.5--35.1	10
5.5	34.9	33.8--36.0	2
6.5	36.7	35.0--38.0	5
7.5	36.9	33.8--39.7	5
8.5	39.1	36.9--40.9	4
9.5	42.6	42.3--42.9	2
10.5	41.3	39.8--42.8	2
11.5	41.5	41.1--41.8	2
12.5--17.5	42.6	39.5--45.8	3

[a] Measurements in mm.

age classes, while ages four, five and six were hypothetical. The replacement and eruption differences noted between the two studies were:

	Hogben				Winchell			
Age	Incisor	Canine	Premolar	Molar	Incisor	Canine	Premolar	Molar
2½	—	—	P3-D	—	—	—	P3-D (P)	—
3½	I3-D	C1-D	P3-D (P)	—	I3-D P	C1-D (P)	P3-D P	—
4½	I3-P	C1-D	—	M3-P	I3-D P	C1-D P	—	M3(P) P
5½	—	C1-(P)	—	—	—	C1-P	—	—
6½	—	C1-P	—	—	—	—	—	—

The techniques for aging animals by tooth wear can be used only with limited accuracy; this accuracy decreases with age. Other authors (Severinghaus, 1949; Robinette, et al, 1957; Quimby and Gaab, 1957) have tried using wear as a means of aging deer and elk and arrived at this same conclusion. Quimby and Gaab (1957) recommended the following aging techniques, "in the order of their apparent accuracy: (1) direct comparison with known-aged jaws, (2) comparison with assigned age jaws, and (3) comparison with good drawings or photographs of known-age jaws."

Known-aged jaws have been photographed and are shown in Figure 5. By using the photos in conjunction with Appendices A through D a limited accuracy in aging can be attained.

Three Wildlife graduate students aged a set of twenty-two jaws, ranging in age from 2½ to 17½ years, using the guide sheet shown in Appendix D and the photos shown in Figure 5. The students aged each

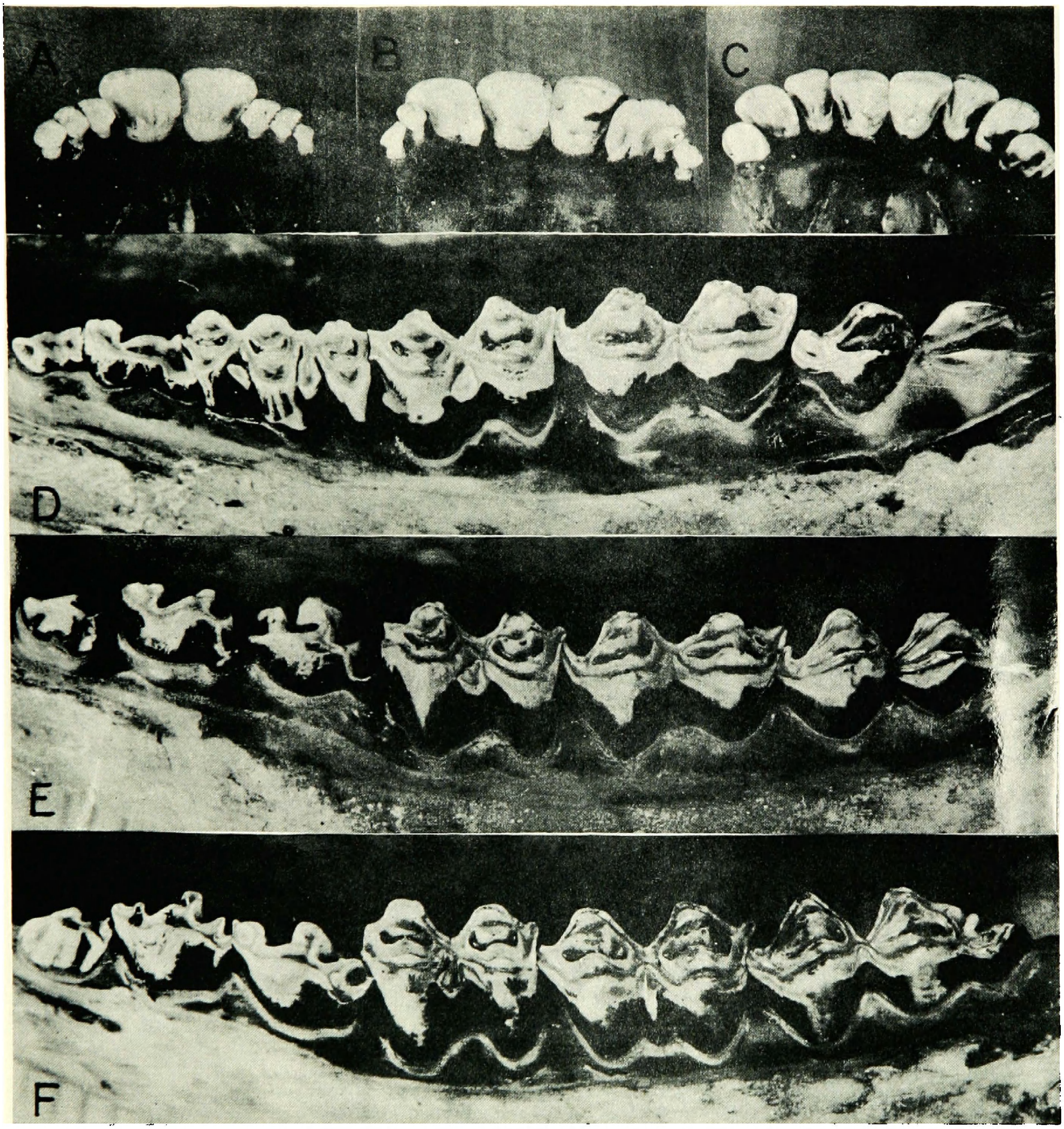

Figure 5. Progressive tooth replacement and wear of Bison lower jaws from age 2½ to age 17½. A. Incisiform teeth of typical 2½-year old showing permanent first or central incisors. B. Incisiform teeth of typical 3½-year old showing permanent first and second incisors. C. Incisiform teeth of 4½-year old showing a full set of permanent incisors. D. Jaw of 2½-year old showing deciduous second, third and fourth premolars. Third molar starting to erupt. Style on first molar, M1, is worn to a circle. Style on second molar, M2 barely shows; usually does not show. E. Jaw of 3½-year old. Premolars are erupting. Third molar still erupting. Style on M1 worn to a circle. Style on M2 barely shows. F. Jaw of 4½-year old. Permanent premolars erupted. Third cusp on third molar still erupting. M1 style worn to a loop. M2 style shows.

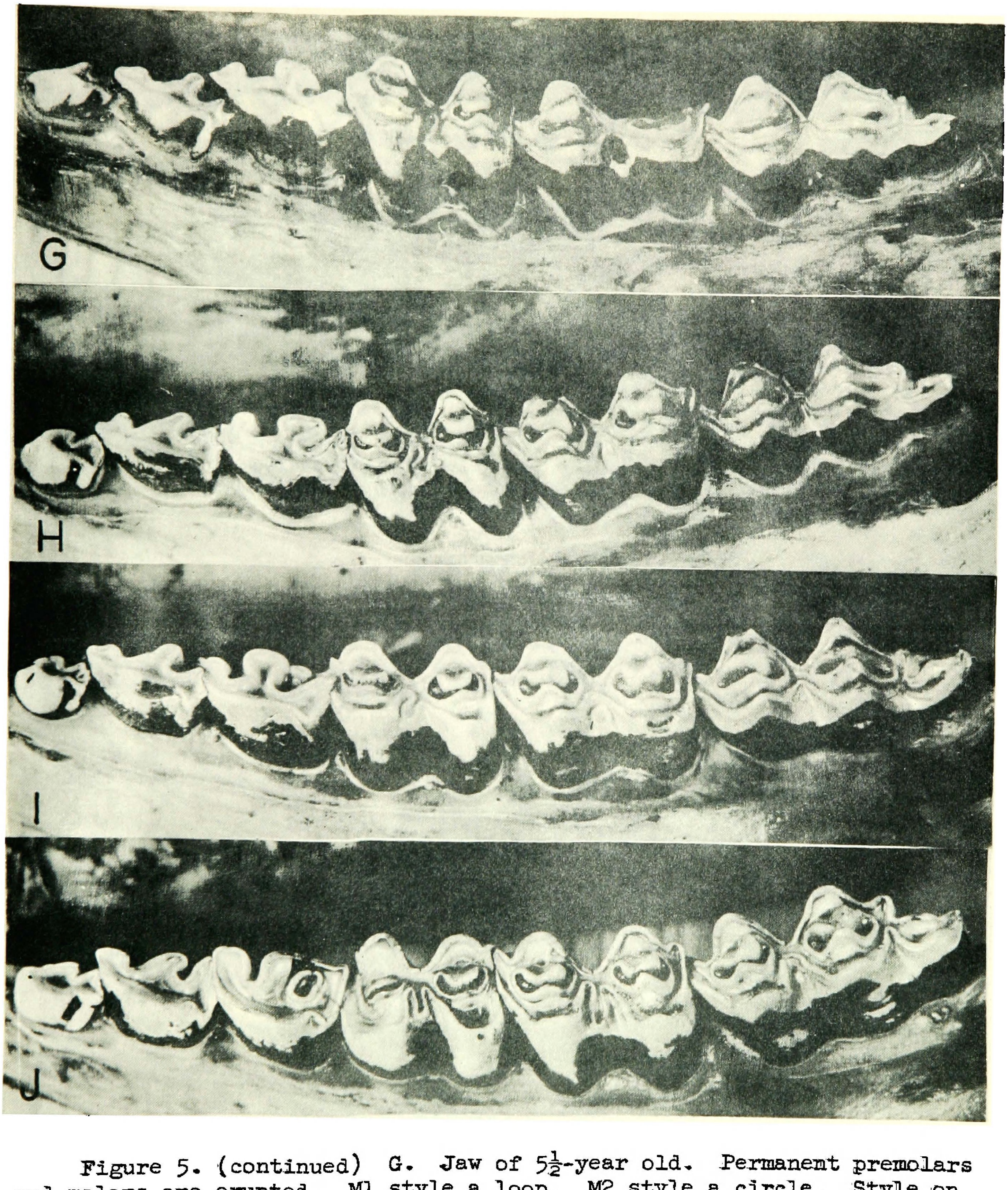

Figure 5. (continued) G. Jaw of $5\frac{1}{2}$-year old. Permanent premolars and molars are erupted. M1 style a loop. M2 style a circle. Style on third molar, M3, barely shows. H. Jaw of $6\frac{1}{2}$-year old. M1 style a loop. M2 style a small circle. M3 style does not show. I. Jaw of $7\frac{1}{2}$-year old. M1 style a loop. M2 style a circle. M3 style barely shows. J. Jaw of $8\frac{1}{2}$-year old. M1 style a loop. M2 style a loop. M3 style shows.

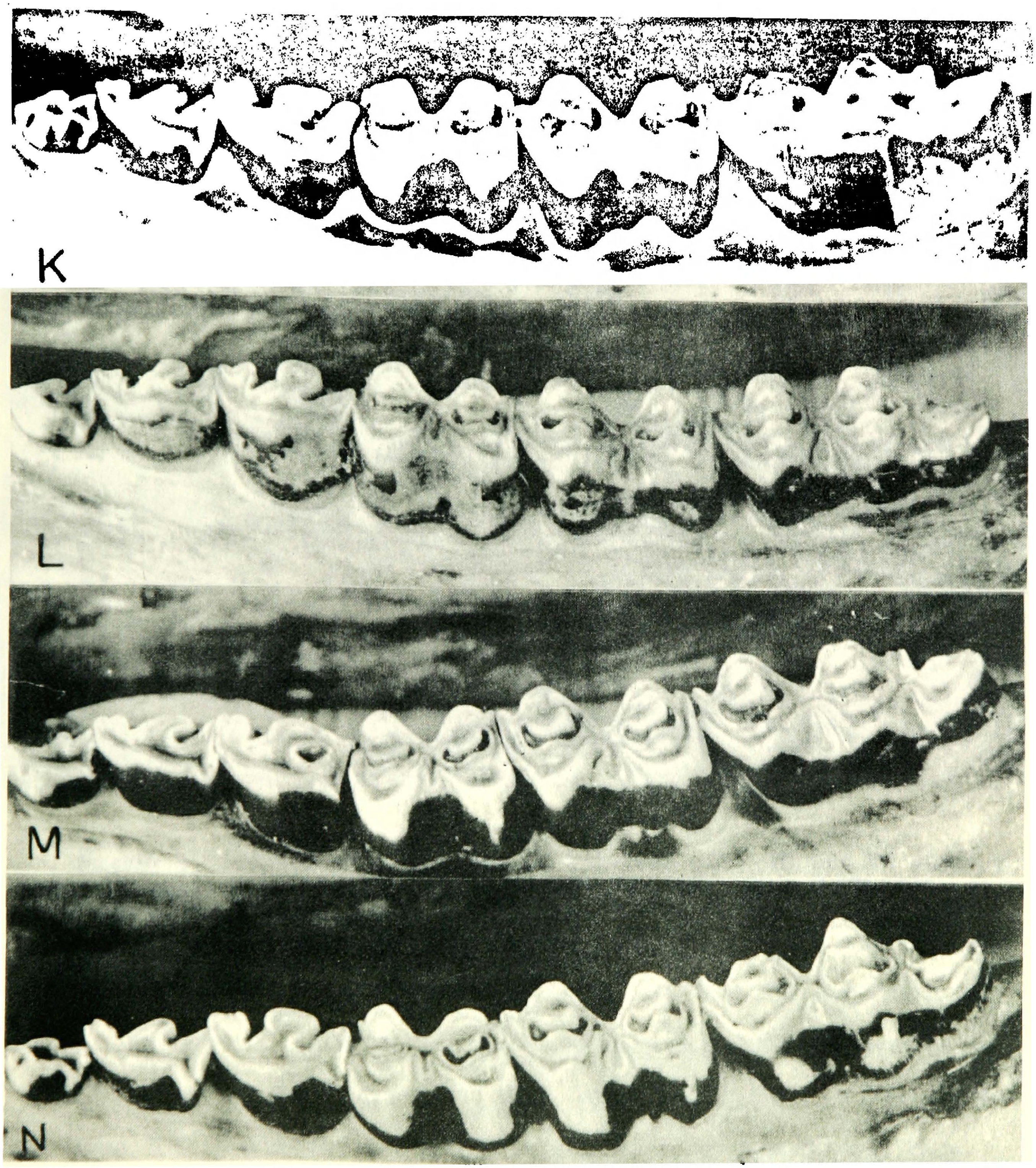

Figure 5. (continued). K. Jaw of $9\frac{1}{2}$-year old. M1 style a loop. M2 style a large circle. M3 style a small circle. L. Jaw of $10\frac{1}{2}$-year old. M1 and M2 style a loop. M3 style a circle. M. Jaw of $11\frac{1}{2}$-year old. M1 and M2 style a loop. M3 style a circle. N. Jaw of $12\frac{1}{2}$-year old. M1 and M2 style a loop. M3 style a circle.

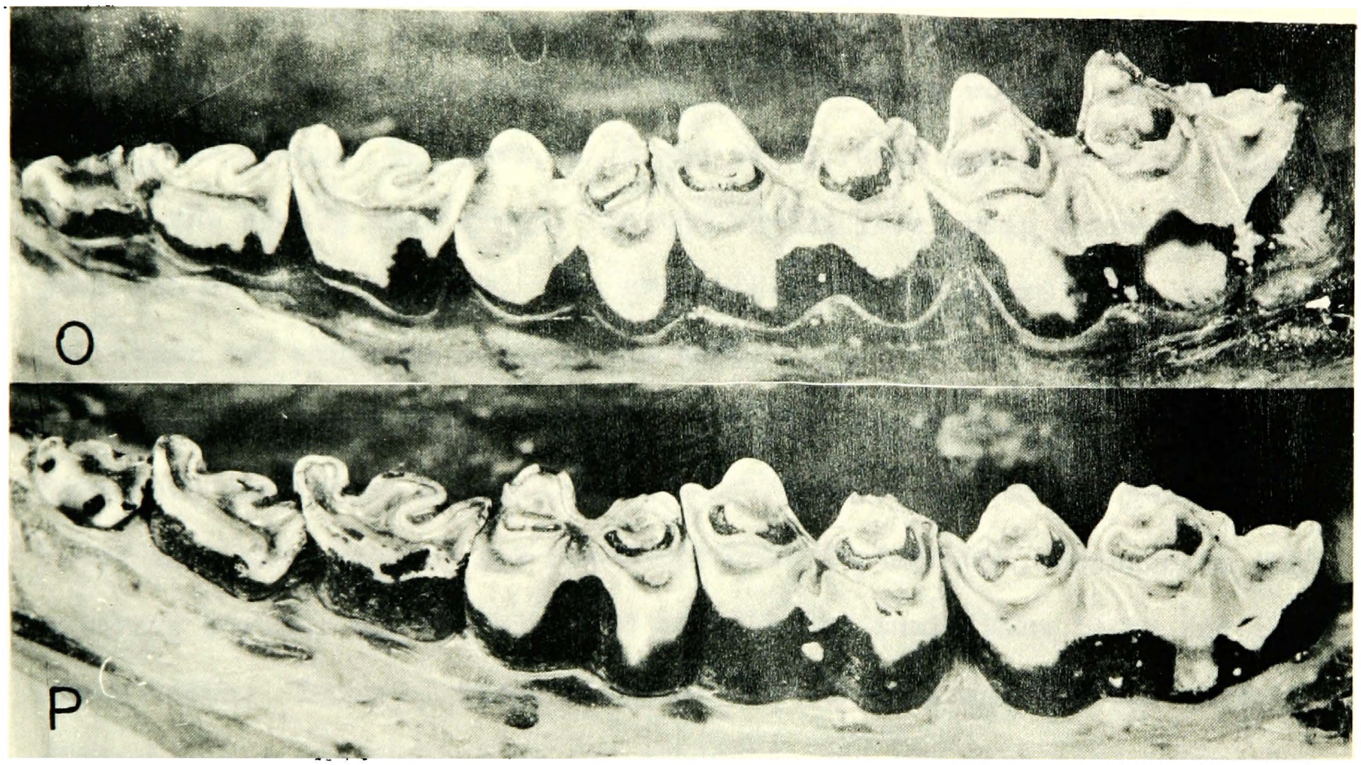

Figure 5. (continued). O. Jaw of 15½-year old. M1 and M2 style a loop. M3 style a circle. P. Jaw of 17½-year old. M1 and M2 style a loop. M3 style a circle.

jaw individually rather than laying them all out for comparison. Fewer errors might have been made if all the jaws were compared with each other. The data will be analyzed by age groupings. Broken down into three groups of jaws there were: seven $2\frac{1}{2}$-$4\frac{1}{2}$, eight $5\frac{1}{2}$-$8\frac{1}{2}$, and seven $9\frac{1}{2}$-$17\frac{1}{2}$. No errors were made in aging the seven jaws in the $2\frac{1}{2}$-$4\frac{1}{2}$ year group. Six errors were made by each graduate student in the $5\frac{1}{2}$-$8\frac{1}{2}$ year group. Two jaws, a $7\frac{1}{2}$ and an $8\frac{1}{2}$, were aged, by each student, within the $9\frac{1}{2}$-$17\frac{1}{2}$ year group. In the $9\frac{1}{2}$-$17\frac{1}{2}$ year group there were four jaws out of seven misaged. One graduate student misaged three jaws and the other two students misaged two each.

Of the twenty-two jaws aged, six were considered atypical. The jaws were considered atypical when they appeared either younger or older than the expected age based on tooth replacement, changes in the molarian styles, and visible wear on both the incisiform teeth and the cheek teeth. Three of these atypical jaws were misaged by all three students, one was misaged by two students, and two were aged correctly. The students' results are shown in Table VIII. The small letter a behind the assigned number represents the atypical jaws.

The graduate students' correct percentage for aging the jaws into individual years (not into groups) were 60%, 64% and 64% respectively, with an average of 63% correct. The percentages correct for errors not over one year off were 68%, 82% and 68% respectively with an average of 71% correct. For errors not over two years off the percentages were 82%, 86% and 91% respectively with an average of 86% correct.

Table VIII. Bison jaw aging results by graduate students

Specimen Number	Specimen Age	Student A Age	Student B Age	Student C Age
115	2½	2½	2½	2½
137	2½	2½	2½	2½
133	2½	2½	2½	2½
146[a]	3½	3½	3½	3½
144	3½	3½	3½	3½
145	4½	4½	4½	4½
116[a]	4½	4½	4½	4½
114	5½	5½	5½	5½
120[a]	6½	5½[b]	6½	5½[b]
113[a]	6½	7½[b]	7½[b]	8½[b]
149	7½	5½[b]	5½[b]	5½[b]
122[a]	7½	10½[b]	10½[b]	10½[b]
143	7½	7½	8½[b]	7½
119[a]	8½	11½[b]	11½[b]	10½[b]
141	8½	5½[b]	5½[b]	5½[b]
129	9½	9½	9½	9½
124	9½	9½	9½	9½
263	10½	10½	11½[b]	10½
123	11½	9½[b]	10½[b]	9½[b]
162	12½	10½[b]	12½	12½
139	15½	15½	15½	15½
159	17½	11½[b]	17½	15½[b]

[a] represents atypical jaws.
[b] indicates jaws which were misaged by students.

The number of animals misaged by students were:

Student	Number Misaged	Number Over-Aged	Number Under-Aged
A	9	6	3
B	8	3	5
C	8	5	3

If an animal was misaged by more than one student, it was always misaged in the same direction. More jaws were under-aged than over-aged; however, the errors tended to compensate each other up to $11\frac{1}{2}$ years. All errors made in jaws older than $11\frac{1}{2}$ years were under-aged.

Statistical analysis of the molar measurements show that the equation appears to be a fair fit of the data; however, the confidence limits, Figure 4, show an overlap between the age classes.

INCISOR SECTIONING AND LENS WEIGHT

Bison central incisors were sectioned and examined for layerings in the secondary dentine and cement, and the eye lenses were weighed to find if their increase in weight could be correlated with increase in age. The procedures and results of the incisor sectioning and of the eye lens weight are presented in the following section.

I. INCISOR SECTIONING

Known-aged bison incisor teeth were sectioned and examined for layerings in the secondary dentine and cement.

Procedure

The bison incisors were extracted with pliers. The plier jaws were covered with cloth to keep from chipping the tooth. A downward pressure was applied to the pliers; this cracked the alveolar bone and allowed the tooth to come free. The extracted teeth were put in individual plastic bottles containing alcohol to keep them from drying out and cracking.

Different methods were tried for sectioning. Some incisors were embedded in plaster of paris, then sectioned with a circular saw and polished by hand. Some were cut and ground without embedding. Some were cut in half and some were ground thin, approximately 300 microns. Most of these last incisors cracked and broke at the crown; in addition the root cracked and broke in the younger animals.

A molding plastic was used for embedding the remaining incisors. This plastic hardened at room temperature, usually in three days. The plastic prevented the teeth from breaking and chipping while being

sectioned. Some still cracked at the crown but the plastic held them together.

The incisor root, embedded in plastic, was cut in half transversally with a circular saw and polished on a grinding machine, Figure 6, made by J. R. Winchell, Nyssa, Oregon. The incisor crown was cut longitudinally off center, ground to the halfway mark, and polished. Some were ground to approximately 300 microns. Some were stained with iron hematoxylin and others were polished to a high gloss with jeweler's rouge.

Results

No positive results were obtained. Indications of layering in both the secondary dentine and cement were observed. The layerings were indistinct and could not be correlated with age. More work is needed for developing a useable technique.

II. LENS WEIGHT

From the seventy-three pair of lenses collected during 1959 and 1960, fifty-one were used for lens weight measurements. Broken into pairs per age class there were:

Age	Number	Age	Number	Age	Number
$2\frac{1}{2}$	13	$6\frac{1}{2}$	4	$11\frac{1}{2}$	3
$3\frac{1}{2}$	5	$7\frac{1}{2}$	7	$12\frac{1}{2}$	1
$4\frac{1}{2}$	7	$8\frac{1}{2}$	4	$15\frac{1}{2}$	1
$5\frac{1}{2}$	2	$9\frac{1}{2}$	3	$17\frac{1}{2}$	1

Procedures

The twenty-two pairs of lenses collected during 1959 were each removed from the eye and placed in 10% formalin for hardening. This was

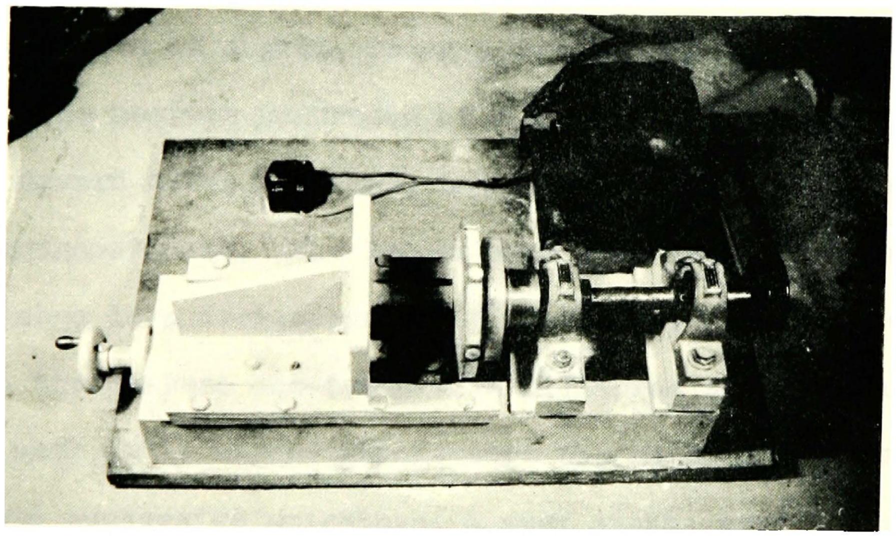

Figure 6. Grinding machine used for incisor grinding and polishing.

a poor method of lens removal, because the lenses were cut during removal and portions peeled off while they were being placed in formalin. These lenses were not used in the study. In the 1960 collections each eye was removed whole, tagged, and placed in a jar with 10% formalin for two weeks of hardening. The hardened lenses were then removed from the eye and placed in individual plastic bottles containing formalin.

A wet measurement was taken by weighing the lenses to the nearest one-tenth of a gram, using a Mettler electric balance that weighed to the nearest hundredth of a gram. A scatter diagram showed a general upward curve with age, indicating that the lenses gained weight throughout life. The lenses were then placed in numbered Stender dishes in a desiccator at 85° C. to dry. The lenses were weighed to the nearest one-tenth of a milligram each day for a week, then each week until two weighings were the same. They were assumed dry when two successive weighings, a week apart, were the same. Because the lenses are hygroscopic (Lord, 1959), they were weighed immediately after removal from the desiccator. This was a slow process as only a few could be removed at a time in order to keep the temperature constant. The lenses took five weeks to dry, probably because the desiccator was being used for other purposes at the same time. A Roller-Smith precision balance was used for weighing the lenses. This balance provided the necessary speed that was needed for accuracy.

Results

Figure 7 shows the relation of dry weight of paired lenses to

age, based on mean values of each age class. Figure 8 contains the graphic presentation of the relationship of lens weight to age. Lens weight is expressed as the square of the actual weight in order to help take the curve out of the data and permit statistical analysis by means of linear analysis. The regression formula for the expected Y^2, $\hat{Y}^2 = a + bX$ (Snedecor, 1956) was used. The regression value of age on lens weight is $\hat{Y}^2 = 645{,}988 + 49916.27X$. The standard error of estimate of $\hat{Y}^2$ is 99,440. The confidence limits of $\hat{Y}^2$ at the 95% probability level shows an overlap between age classes. The coefficient of correlation (r) is .8761. The equation appears to be a fair fit of the data; however, it appears that a more suitable equation is needed for removing the curvilinearity.

III. DISCUSSION

The change of weight in eye lens with advancing age has been used previously on cottontail rabbits (Lord, 1959), grey fox (Lord, 1961), and pronghorn antelope (Kolenosky and Miller, 1962). Lord (1959, 1961) presented a growth-rate curve of the lens of the eye. Kolenosky and Miller (1962) gave both a growth-rate curve and a linear regression of eye lens weight. The data given in the present paper for bison shows a similar growth-rate curve as that obtained by Lord (1959, 1961) and Kolenosky and Miller (1962), and a linear regression similar to that of Kolenosky and Miller. However, the correlation coefficient of 0.995 as derived by Kolenosky and Miller (1962) provides a highly significant value while

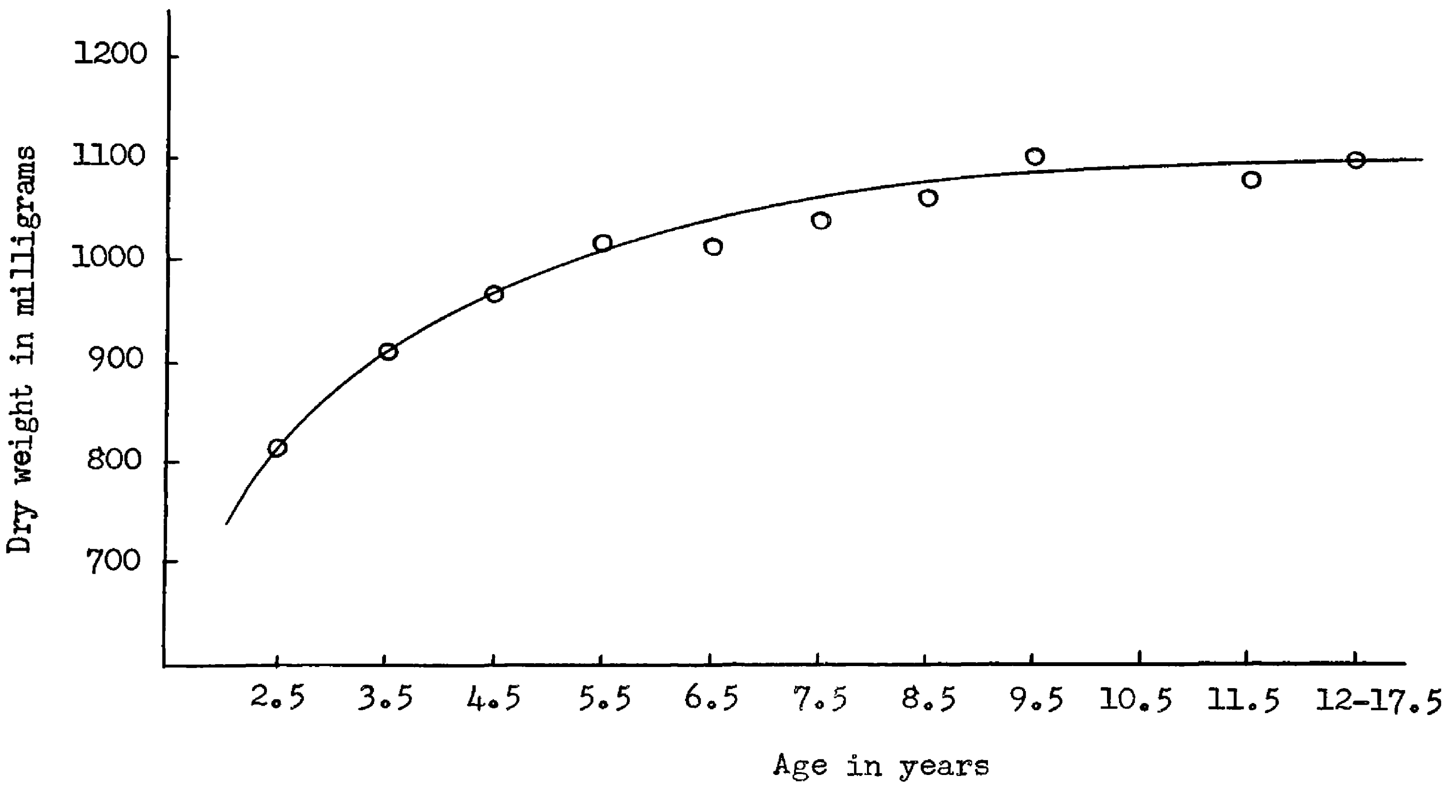

Figure 7. Relation of dry weight of paired lenses to age for Bison, based on mean values for each age class.

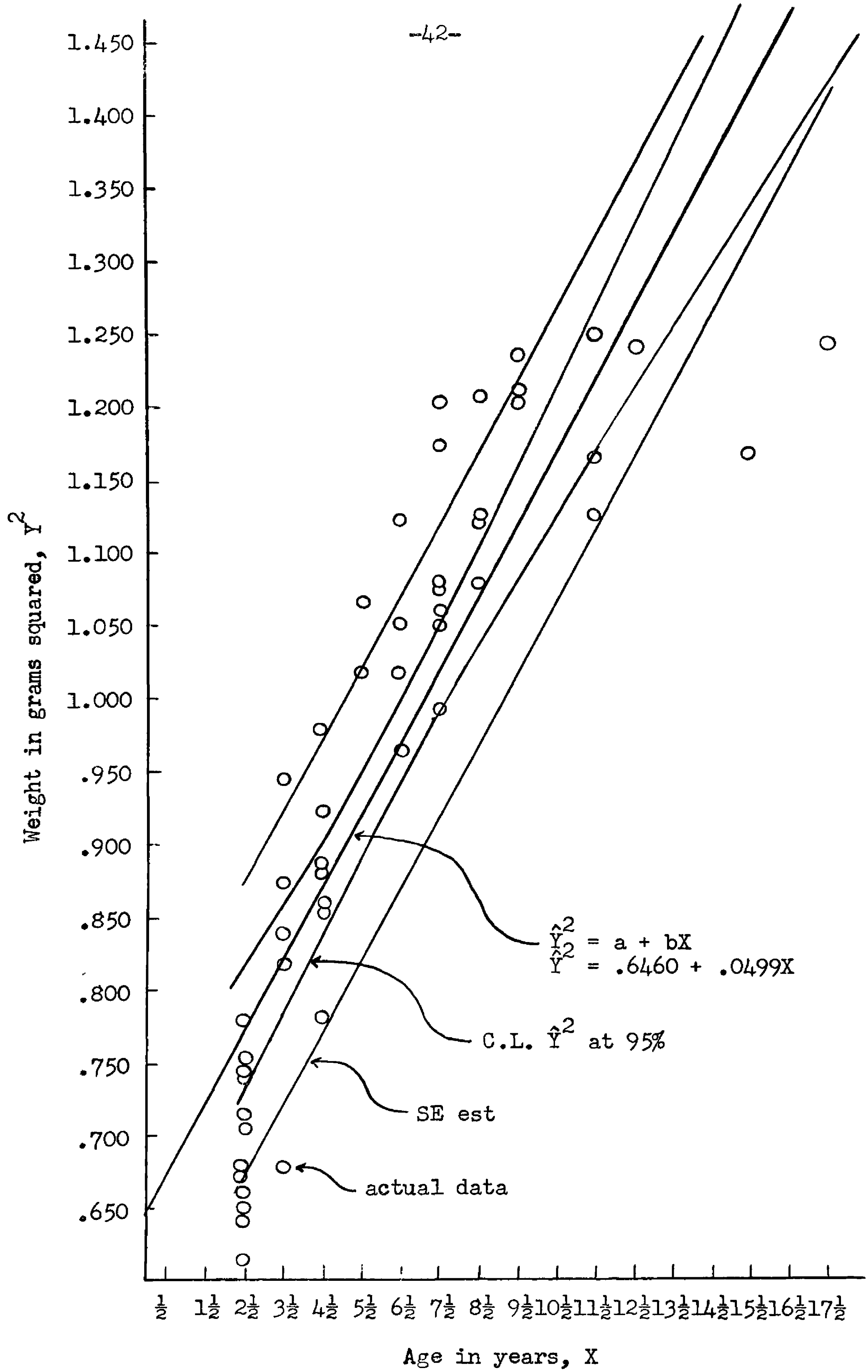

Figure 8. Regression and confidence limits of ns weight on age.

the correlation coefficient of 0.8761 for the present bison study indicated only a significant value.

The extent of the relationship between eye lens weight and age is difficult to establish since the prerequisite for such an analysis is that the samples have to be obtained from known-age animals (i.e. the results obtained by using unknown-age animals would give only an assumed relationship). Though Lord (1959) worked with known-aged rabbits and Kolenosky and Miller (1962) could divide their antelope into assigned age groups, neither of these workers tested their data against confidence limits as was done in the present bison study.

Twelve lenses were a little light or a little heavy for their particular age class; however, when the specimen number of the lenses were compared to the specimen number for tooth replacement and wear, all but two were normal. Specimen number 130, a three and one-half year old, appeared as a two and one-half by the eye lens weight and also by the tooth replacement data. Specimen number 139, a fifteen and one-half year old, could be aged as much as three years younger by the lens weight but the tooth wear was similar to that of the seventeen and one-half year old. One specimen, a four and one-half year old, number 153, was not used for the lens weight technique as its lenses weighed less than the two and one-half year olds; its tooth replacement was normal.

At the 95% confidence limits an overlap in lens weight occurs between the age classes; as an example, suppose a lens's squared weight was 1,200,000 milligrams (1.2 grams), the estimated age would be about 11 years; however, at the 95% confidence limits the actual age could be between 10.2 years and 12.1 years. So 95% of the time a lens's squared

weight of 1,200,000 milligrams (1.2 grams) would be between 10.2 and 12.1 years of age. The range of ages which a given lens weight might indicate at the 95% level of accuracy is shown on Figure 8. Table IX shows the changes in bison lenses weight with age.

Table IX. Changes in Bison lenses with age

Age - Years	Mean	Range	Number of bison
2.5	813.8[a]	641.1-- 867.6	13
3.5	910.3	822.0-- 973.0	5
4.5	937.5	885.3-- 988.1	7
5.5	1021.2	1009.9--1032.6	2
6.5	1019.6	982.0--1060.6	4
7.5	1043.9	996.3--1097.7	7
8.5	1064.1	1039.2--1099.3	4
9.5	1103.6	1098.2--1112.3	3
11.5	1086.7	1060.8--1119.0	3
12.5--17.5	1104.2	1081.4--1115.9	3

[a] weight in milligrams.

SUMMARY

Eighty-one lower jaws were used for studies of tooth replacement and eruption. A full set of permanent dentition is achieved when the bison is four and one-half or five years of age. The first permanent incisor is normally replaced during the second year, the second incisor during the third year, the third incisor and canine during the fourth year. The premolars are generally replaced during the third year. The first molar completes eruption by approximately one year of age, the second molar by approximately two years of age and the third molar by either the fourth or fifth year. The only sex difference noted in development was that the female was slightly slower than the male in eruption of the third molar.

Forty-eight lower jaws were used for comparing visible characters. On each molar a style is found on the buccal side between the anterior and posterior cusps. At first only the tip of the style begins to wear, producing a circular enamel pattern on the occlusal surface. As wear continues the enamel pattern of the style becomes a loop. Two groupings were made, a "young adult" ($5\frac{1}{2}$-$8\frac{1}{2}$) and an "adult" ($9\frac{1}{2}$-$17\frac{1}{2}$), on the basis of wear on the molarian style.

Molar measurements were taken on the seven occlusal surfaces of the lower jaw. A linear regression analysis with confidence limits established at the 95% level showed that overlap occured between the age classes.

No positive results were found by observing sectioned central incisor teeth. Indications of layering were observed in both the

cement and secondary dentine, but the layerings were indistinct and could not be correlated with age.

Bison lenses were dried, weighed and a Y^2 regression analysis with confidence limits was established. Results showed a fair fit of the data; however, a more suitable equation is needed for coping with the curvilinearity of the data. Confidence limits at the 95% level show overlap with the present method of analysis. Overlap varies from 1 to over 3½ years, depending on age. The least overlap occurs at age 6½ with the overlap gradually increasing with advance or decrease in age.

At present, it would appear that bison can be aged to the year by tooth eruption up to the fifth year. Thereafter, the most accurate age determination can probably be made by use of lens weight, assuming the present equation is suitable. With a little experience reliable aging can be made on the basis of wear by comparing visible characters with known-age jaws or photos.

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A P P E N D I C E S

LIST OF APPENDICES

APPENDIX PAGE

Appendix A. Tooth replacement and eruption for known-age Bison used in this study. Specimens are 2½-5½ years.

			Tooth Replacement and Eruption										
	Specimen		Incisors			Canine	Premolars			Molars			
Age	Number	Sex	1	2	3	1	2	3	4	1	2	3	M4
2½	131	F	P[a]	D	D	D	D	D L[b] (P)R	D	P	P	(P)	O
2½	115	F	P	D	D	D	D	D	D	P	P	(P)	O
2½	--	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	36	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	9	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	137	M	P	(P)	D	D	(P)	(P)	D	P	P	(P)	O
2½	154	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	138	M	P	P	D	D	D R (P)L	D	D	P	P	(P)	O
2½	142	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	152	M	P	D	D	D	D	D R (P)L	D	P	P	(P)	O
2½	150	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	118	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	151	M	P	D	D	D	D	D	D	P	P	O	O
2½	133	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	160	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	155	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	126	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	156	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	31	M	P	D L (P)R	D	D	D	D	D	P	P	(P)	O

Appendix A. (continued)

			Tooth Replacement and Eruption										
	Specimen		Incisors			Canine	Premolars			Molars			
Age	Number	Sex	1	2	3	1	2	3	4	1	2	3	M4
2½	44	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	35	M	P	D	D	D	(P)	(P)	D	P	P	(P)	O
2½	16	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	3	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	14	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	48	M	P	(P)	D	D	(P)	(P)	D	P	P	(P)	O
2½	51	M	P	P	D	D	(P)	(P)	(P)	P	P	(P)	O
2½	21	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	24	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	37	M	P	(P)	D	D	(P)	(P)	D	P	P	(P)	O
2½	50	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	43	M	P	D	D	D	(P)	(P)	D	P	P	(P)	O
2½	34	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	10	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	5	M	P	(P)	D	D	(P)	(P)	D	P	P	(P)	O
2½	22	M	P	D	D	D	D	D L (P)R	D	P	P	(P)	O
2½	15	M	P	D	D	D	D	D	D	P	P	(P)	O
2½	39	M	P	D	D	D	D	(P)	D	P	P	(P)	O
3½	27	F	P	P	D	D	P	P	(P)	P	P	(P)	(P)
3½	---	F	P	P	D	D	P	P	(P)	P	P	(P)	(P)
3½	59	F	P	P	D	D	P	P	(P)	P	P	(P)	(P)
3½	58	F	P	P	D	D	P	P	(P)	P	P	(P)	O

Appendix A. (continued)

Age	Specimen Number	Sex	Tooth Replacement and Eruption										
			Incisors			Canine	Premolars			Molars			
			1	2	3	1	2	3	4	1	2	3	M4
3½	53	F	P	P	D	D	(P)	P	P	P	P	(P)	O
3½	23	F	P	P	D	D	(P)	P	(P)	P	P	(P)	(P)
3½	26	F	P	P	D	D	(P)	(P)	D	P	P	(P)	(P)
3½	49	M	P	P	D	D	P	P	(P)	P	P	(P)	(P)
3½	19	M	P	P	D	D	(P)	(P)	D	P	P	(P)	O
3½	—	M	P	P	D	D	(P)	P	(P)	P	P	(P)	O
3½	38	M	P	P	(P)	D	(P)	P	P	P	P	(P)	(P)
3½	37	M	P	P	D	D	(P)	(P)	D L (P)R	P	P	(P)	O
3½	130	M	P	D	D	D	(P)	(P)	D	P	P	(P)	O
3½	136	M	P	P	D	D	D L (P)R	(P)	(P)	P	P	(P)	(P)
3½	144	M	P	P	D	D	(P)	P	(P)	P	P	(P)	(P)
3½	146	M	P	P	(P)	D	P	P	(P)	P	P	(P)	(P)
3½	132	M	P	P	D L (P)R	D	P	P	(P)	P	P	(P)	(P)
3½	52	M	P	P	P	(P)	P	P	P	P	P	P	P
3½	35	M	P	P	D	D	P	P	(P)	P	P	(P)	O R (P)L
3½	2	M	P	P	D	D	(P)	(P)	(P)	P	P	(P)	(P)
3½	49	M	P	P	D	D	(P)	P	(P)	P	P	(P)	(P)
3½	47	M	P	P	D	D	(P)	(P)	D	P	P	(P)	O
4½	33	F	P	P	P	(P)	P	P	P	P	P	P	P
4½	—	F	P	P	D	D	P	P	P	P	P	P	P

Appendix A. (continued)

			Tooth Replacement and Eruption										
	Specimen		Incisors			Canine	Premolars			Molars			
Age	Number	Sex	1	2	3	1	2	3	4	1	2	3	M4
4½	153	F	P	P	P	(P)	P	P	P	P	P	(P)	O
4½	145	M	P	P	P	(P)	P	P	P	P	P	P	P
4½	134	M	P	P	P	P	P	P	P	P	P	P	P
4½	136A	M	P	P	P	P	P	P	P	P	P	P	P
4½	4	M	P	P	D R (P)L	D	P	P	P	P	P	(P)	(P)
4½	125	M	P	P	P	P	P	P	P	P	P	(P)	(P)
4½	135	M	P	P	P	P	P	P	P	P	P	(P)	(P)
4½	116	M	P	P	P	P	P	P	P	P	P	P	P
4½	32	F	P	P	P	P	P	P	P	P	P	(P)	(P)
4½	11	F	P	P	P	P	P	P	P	P	P	(P)	(P)
4½	27	F	P	P	P	(P)	P	P	P	P	P	(P)	(P)
4½	42	F	P	P	P	P	P	P	P	P	P	P	P
4½	4	M	P	P	D R (P)L	D	P	P	P	P	P	P	P
4½	30	M	P	P	P	P	P	P	P	P	P	P	P
4½	13	M	P	P	P	(P)	P	P	P	P	P	P	P
5½	57	F	P	P	P	P	P	P	P	P	P	P	P
5½	24	F	P	P	P	P	P	P	P	P	P	P	P
5½	55	F	P	P	P	P	P	P	P	P	P	P	P
5½	33	F	P	P	P	P	P	P	P	P	P	P	P
5½	114	F	P	P	P	P	P	P	P	P	P	P	P

[a]P = adult tooth; ( ) = tooth being replaced; D = deciduous tooth

[b]R = right side; L = left side

Appendix B. Tooth wear changes in the molarian style for known-aged Bison used in this study, $2\frac{1}{2}$-$17\frac{1}{2}$ years.

			Changes in Molarian Style									
			First Molar			Second Molar				Third Molar		
Age	Specimen Number	Sex	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
$2\frac{1}{2}$	131	F		X[a]			X			X		
$2\frac{1}{2}$	115	F		X		X				X		
$2\frac{1}{2}$	--	M		X			X			X		
$2\frac{1}{2}$	36	M	XR	XL		X				X		
$2\frac{1}{2}$	9	M		X		X				X		
$2\frac{1}{2}$	137	M		X			X			X		
$2\frac{1}{2}$	154	M	X			XL	XR			X		
$2\frac{1}{2}$	138	M	X			X				X		
$2\frac{1}{2}$	142	M	X			X				X		
$2\frac{1}{2}$	152	M		X		X				X		
$2\frac{1}{2}$	150	M		X		X				X		
$2\frac{1}{2}$	118	M		X		X				X		
$2\frac{1}{2}$	151	M		X		X				X		
$2\frac{1}{2}$	133	M	X			X				X		
$2\frac{1}{2}$	160	M	X			X				X		
$2\frac{1}{2}$	155	M		X			X			X		
$2\frac{1}{2}$	126	M	X			X				X		
$2\frac{1}{2}$	156	M		X		XR	XL			X		
$2\frac{1}{2}$	44	M		X		X				X		
$2\frac{1}{2}$	31	M		X		X				X		
$2\frac{1}{2}$	35	M		X		X				X		

Appendix B. (continued)

			Changes in Molarian Style									
			First Molar			Second Molar				Third Molar		
Age	Specimen Number	Sex	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
$2\frac{1}{2}$	16	M	X			X				X		
$2\frac{1}{2}$	3	M	X			X				X		
$2\frac{1}{2}$	14	M	X			X				X		
$2\frac{1}{2}$	48	M		X		X				X		
$2\frac{1}{2}$	51	M		X			X			X		
$2\frac{1}{2}$	21	M	X			X				X		
$2\frac{1}{2}$	24	M	XR	XL		X				X		
$2\frac{1}{2}$	37	M	X				X			X		
$2\frac{1}{2}$	50	M	X			X				X		
$2\frac{1}{2}$	43	M		X			X			X		
$2\frac{1}{2}$	34	M		X		X				X		
$2\frac{1}{2}$	10	M		X			X			X		
$2\frac{1}{2}$	5	M	X			X				X		
$2\frac{1}{2}$	22	M		X		X				X		
$2\frac{1}{2}$	15	M		X			X			X		
$2\frac{1}{2}$	39	M		X		X				X		
$3\frac{1}{2}$	27	F		X			X			X		
$3\frac{1}{2}$	--	F		X			X			X		
$3\frac{1}{2}$	59	F		X			X			X		
$3\frac{1}{2}$	58	F		X			X			X		
$3\frac{1}{2}$	53	F		X			X			X		

Appendix B. (continued)

			Changes in Molarian Style										
			First Molar			Second Molar				Third Molar			
Age	Specimen Number	Sex	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
3½	23	F		X		XR	XL			X		
3½	26	F		X			X			X		
3½	—	M		X			X			X		
3½	19	M		X		X				X		
3½	49	M		X			X			X		
3½	130	M	XL	XR			X			X		
3½	37	M		X			X			X		
3½	38	M		X			X			X		
3½	146	M	XR	XL			X			X		
3½	144	M	X				X			X		
3½	136	M		X			X			X		
3½	132	M		X			X			X		
3½	52	M			X			X		X		
3½	35	M		X			X			X		
3½	2	M		XR	XL		X			X		
3½	49	M		X			X			X		
3½	47	M	XR	XL		X				X		
4½	33	F		X			X			X		
4½	--	F		X			XR	XL		X		
4½	153	F			X		X			X		
4½	145	M			X		XR	XL			X	

Appendix B. (continued)

			Changes in Molarian Style									
			First Molar			Second Molar				Third Molar		
Age	Specimen Number	sex	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
4½	134	M			X		X			X		
4½	136A	M			X			X			X	
4½	4	M			X		X			X		
4½	125	M			X		X			X		
4½	135	M			X		X				X	
4½	116	M		XR	XL		X			X		
4½	32	F			X		X			X		
4½	11	F			X			X		XL	XR	
4½	27	F			X		X			X		
4½	42	F			X		X			X		
4½	4	M		X			X			X		
4½	30	M			X			X			X	
4½	13	M			X		X			X		
5½	57	F			X			XR	XL	XR	XL	
5½	24	F			X			X		X		
5½	55	F			X			X		XR	XL	
5½	33	F			X			X		X		
5½	114	F			X			X			X	
6½	21	F			X		XR	XL		XL	XR	
6½	140	F			X			X			X	

Appendix B. (continued)

			Changes in Molarian Style									
			First Molar			Second Molar				Third Molar		
Age	Specimen Number	Sex	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
6½	148	F			X		X			X		
6½	113	F			X				X	X		
6½	120	F			X			X		X		
7½	149	F			X			X			X	
7½	—	F			X			X		X		
7½	122	F			X				X			X
7½	147	F			X				X	X		
7½	143	F			X			XL	XR		X	
7½	157	F			X			X		X		
8½	117	F			X			XR	XL		X	
8½	141	F			X			X			X	
8½	119	F			X				X			X
8½	161	F			X			XR	XL		X	
9½	124	F			X			X			XR	XL
9½	39	F			X			XR	XL			X
9½	129	F			X			XR	XL			X
10½	14	M			X				X			X
10½	22	F			X			X			X	
10½	7	F			X				X			X
10½	263	F			X				X			X

Appendix B. (continued)

			Changes in Molarian Style									
			First Molar			Second Molar				Third Molar		
Age	Specimen Number	Sex	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
11½	123	F			X				X			X
11½	128	F			X				X			X
12½	162	F			X				X			X
15½	139	F			X				X			X
17½	159	F			X				X			X

[a]Hypsodont teeth grow up from the gums, continually, as fast as they are worn off at the crown; so in young animals the style, sometimes, has not erupted and does not show. After the style appears, the tip begins to wear producing a circular enamel pattern. As wear continues the pattern becomes a loop.

Appendix C. Occlusal surface measurements for known-aged Bison used in this study, 4½-17½ years.

			Molar Wear Measurements						
			First Molar		Second Molar		Third Molar		
Age	Specimen Number	Sex	1st. cusp	2nd. cusp	1st. cusp	2nd. cusp	1st. cusp	2nd cusp	3rd. cusp
4½	116	F	5.5[a]	5.6	5.0	6.0	5.0	5.0	1.5
4½	153	F	4.5	5.1	4.9	5.0	0.0	0.0	0.0
4½	33	F	5.0	5.5	5.0	5.5	5.0	5.0	2.0
4½	—	F	5.0	5.0	4.5	5.5	5.0	5.0	1.5
4½	4	M	5.0	6.0	5.0	6.5	6.0	4.0	0.0
4½	134	M	5.5	6.0	5.2	6.0	5.5	5.0	1.5
4½	135	M	5.5	6.0	5.1	5.0	5.0	6.0	0.0
4½	136A	M	5.0	5.5	5.0	5.2	5.0	5.0	2.4
4½	125	M	4.5	5.8	5.0	5.0	5.0	4.0	0.0
4½	145	M	5.0	6.2	4.4	6.5	6.5	5.5	1.0
5½	24	F	5.0	5.0	5.5	5.8	5.0	5.0	2.5
5½	114	F	5.0	6.0	5.0	6.0	6.0	7.0	1.0
6½	21	F	5.0	6.5	6.0	6.5	5.5	5.0	2.0
6½	140	F	5.0	6.5	6.0	6.0	6.0	5.5	2.5
6½	148	F	5.0	5.5	6.0	6.0	5.0	5.0	2.5
6½	120	F	6.0	7.0	5.6	6.0	6.0	4.5	1.5
6½	113	F	5.5	6.0	6.0	6.0	5.0	6.0	3.5
7½	143	F	5.0	5.5	6.0	6.0	5.9	6.0	3.0
7½	157	F	5.0	6.0	6.0	6.1	6.0	5.5	4.0
7½	122	F	5.9	6.5	5.9	6.5	5.0	6.0	3.9
7½	147	F	4.1	5.5	4.9	6.0	5.0	5.1	3.2
7½	149	F	4.9	5.6	5.6	5.8	5.1	5.0	2.9

Appendix C. (continued)

			Molar Wear Measurements						
			First Molar		Second Molar		Third Molar		
Age	Specimen Number	Sex	1st. cusp	2nd. cusp	1st. cusp	2nd. cusp	1st. cusp	2nd. cusp	3rd. cusp
8½	119	F	5.1	6.9	5.0	4.9	5.1	5.9	4.0
8½	161	F	6.1	7.5	5.9	5.9	5.8	5.9	3.8
8½	141	F	5.1	6.9	6.9	6.8	6.0	6.0	2.9
8½	117	F	4.9	5.9	6.0	6.0	6.0	6.0	3.1
9½	129	F	5.5	7.0	6.5	7.6	6.0	6.0	3.7
9½	124	F	6.5	7.3	5.9	7.5	5.5	6.2	4.0
10½	263	F	5.0	7.0	6.0	6.4	5.1	6.0	4.3
10½	7	M	b	7.5	7.0	7.9	6.5	7.0	6.9
11½	123	F	5.6	6.0	6.0	6.4	7.1	6.0	4.0
11½	128	F	6.0	6.7	5.9	6.1	6.0	6.1	5.0
12½	162	F	5.5	6.0	6.0	6.2	6.8	6.9	4.5
15½	139	F	b	7.0	6.0	7.0	6.5	7.0	6.0
17½	159	F	6.0	6.2	6.5	7.2	7.2	7.2	5.5

[a]occlusal surface measurement in mm.

[b]excessive wear. Infundibulum worn away.

Appendix D. Guide sheet used in graduate student aging of bison

INSTRUCTIONS

1. Age each jaw individually or, preferably, use Table 1 to put jaws into three age groupings.

   (a) put all animals with circle or less on M1 into one group (2.5-4.5).

   (b) put all animals with circle on M3 into another group (9.5-17.5).

   (c) rest of animals are mostly in age group 5.5-8.5.

2. Use Tables 3 and 4 to put jaws into the first four or five individual ages.

3. Use Table 2 for older individual aging.

4. Use photos along with Tables 1-4 for final check on ages.

The incisors, canine and premolars have deciduous teeth which are replaced with permanent ones. The third deciduous premolar has three cusps; the permanent has only two. The molar teeth erupt as permanent teeth. The third molar has three cusps; the last cusp usually begins to show wear at five to six years of age.

The amount of wear on the styles can help determine the older animals from the younger ones within each of the three age groupings in Table 1. A small circle indicates less wear while a large circle indicates more wear; same with the loops. Also the wear on the incisors and canines will help with the final aging.

Appendix D. (continued)

TABLE 1. Changes in molarian styles by age groupings

Age - Years	M_1 Style			M_2 Style				M_3 Style		
	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
2.5 - 4.5	XX*	XXX	XX	XX	XXX	X	—	XXX	X	—
5.5 - 8.5	—	—	XXX	—	X	XXX	XXX	XXX	XXX	X
9.5 - 17.5	—	—	XXX	—	—	X	XXX	—	X	XXX

* X = occasional; XX = frequent; XXX = majority

TABLE 2. Changes in molarian style by single age classes

Age - Years	M_1 Style			M_2 Style				M_3 Style		
	shows	circle	loop	does not show	shows	circle	loop	does not show	shows	circle
2.5	XX*	XXX	—	XXX	XX	—	—	XXX	—	—
3.5	X	XXX	X	X	XXX	X	—	XXX	—	—
4.5	—	X	XXX	—	XXX	XX	—	XXX	X	—
5.5	—	—	XXX	—	X	XXX	XX	XXX	XXX	—
6.5	—	—	XXX	—	X	XXX	X	XXX	XXX	—
7.5	—	—	XXX	—	—	XX	XXX	XXX	XXX	X
8.5	—	—	XXX	—	—	X	XXX	—	XXX	X
9.5	—	—	XXX	—	—	X	XXX	—	X	XXX
10.5	—	—	XXX	—	—	X	XXX	—	X	XXX
11.5	—	—	XXX	—	—	—	XXX	—	—	XXX
12.5 15.5 17.5	—	—	XXX	—	—	—	XXX	—	—	XXX

* X = occasional; XX = frequent; XXX = majority.

Appendix D. (continued)

TABLE 3. Bison tooth replacement and eruption

Age	Incisors			Canine	Premolars			Molars		
Years	1	2	3	1	2	3	4	1	2	3
2.5	P*	D	D	D	D (P)	D (P)	D (P)	P	P	O (P)
3.5	P	P	D P	D (P)	(P) P	(P) P	D P	P	P	(P) P
4.5	P	P	D P	D P	P	P	P	P	P	(P) P
5.5	P	P	P	P	P	P	P	P	P	P

* P = permanent; (P) = tooth being erupted; D = deciduous tooth; O = tooth which has not erupted.

TABLE 4. Expected bison tooth replacement and eruption

Age	Incisors			Canine	Premolars			Molars			
Years	1	2	3	1	2	3	4	1	2	3	M4**
2.5	P*	D	D	D	D (P)	D (P)	D	P	P	(P)	O
3.5	P	P	D	D	P	(P) P	(P) P	P	P	(P)	O (P)
4.5	P	P	P	(P) P	P	P	P	P	P	(P) P	(P) P
5.5	P	P	P	P	P	P	P	P	P	P	P

* P = permanent; (P) = tooth being erupted; D = deciduous tooth; O = tooth which has not erupted.

** M4 = third cusp on third molar.

Appendix E. Eye lens weight for known-aged Bison used in this study, $2\frac{1}{2}$-$17\frac{1}{2}$ years.

Age	Specimen Number	Sex	Eye Lens Weight	
			Wet Weight	Dry Weight
$2\frac{1}{2}$	115	F	1830[a] 1830	838.2 840.0
$2\frac{1}{2}$	131	F	1960 1930	849.0 841.5
$2\frac{1}{2}$	137	M	2162 2174	866.6 868.6
$2\frac{1}{2}$	152	M	2030 2070	799.0 801.2
$2\frac{1}{2}$	142	M	2056 1920	794.8 773.3
$2\frac{1}{2}$	156	M	1918 1922	640.6 641.6
$2\frac{1}{2}$	138	M	2112 2140	859.7 867.7
$2\frac{1}{2}$	154	M	2298 2300	859.7 861.5
$2\frac{1}{2}$	151	M	2102 2108	809.5 816.0
$2\frac{1}{2}$	126	M	1810 1840	824.0 824.7
$2\frac{1}{2}$	118	M	1796 1782	809.3 800.8
$2\frac{1}{2}$	133	M	2000 2010	824.0 813.5
$2\frac{1}{2}$	155	M	2138 2132	819.6 815.0
$3\frac{1}{2}$	130	M	1864 1890	817.0 828.2

Appendix E. (continued)

Age	Specimen Number	Sex	Eye Lens Weight: Wet Weight	Eye Lens Weight: Dry Weight
3½	132	M	2154 2142	909.8 900.2
3½	144	M	2310 2330	931.6 937.8
3½	146	M	2428 2420	967.4 978.6
3½	136	M	2270 2288	911.1 921.2
4½	163	M	2080 2088	921.3 927.0
4½	125	M	2156 2118	940.6 937.1
4½	134	M	2242 2248	932.2 947.7
4½	135	M	blind 2158	blind 885.3
4½	136A	M	2480 2568	980.4 995.8
4½	145	M	2810 2286	928.2 922.6
4½	116	F	2098 2098	963.8 957.4
4½	153[b]	F	1732 1538	654.2 597.1
5½	114	F	2296 2278	1046.5 1018.6
5½	127	M	2298 2292	1012.8 1007.0

Appendix E. (continued)

Age	Specimen Number	Sex	Eye Lens Weight	
			Wet Weight	Dry Weight
6½	113	F	2270 2300	1059.6 1061.6
6½	120	F	2278 2192	999.5 1020.0
6½	140	F	2480 2388	985.7 978.2
6½	148	F	2578 2604	1024.0 1028.3
7½	111	M	2240 2284	1034.6 1024.7
7½	121	M	2440 2492	1099.4 1096.0
7½	143	F	2508 2678	1033.9 1040.6
7½	147	F	2594 2570	1028.1 1019.6
7½	122	F	2494 2514	1081.4 1086.0
7½	149	F	2650 2620	1036.6 1040.5
7½	157	F	2518 2582	1005.6 987.0
8½	117	F	2264 2294	1057.5 1062.2
8½	119	F	2210 2230	1038.8 1039.5
8½	141	F	2748 2838	1097.2 1101.4

Appendix E. (continued)

Age	Specimen Number	Sex	Eye Lens Weight	
			Wet Weight	Dry Weight
8½	161	F	2642 2650	1058.8 1057.6
9½	112	M	2382 2358	1098.2 1100.2
9½	124	F	2442 2370	1100.7 1099.8
9½	129	F	2538 2520	1110.2 1114.4
11½	110	M	2352 2400	1117.7 1120.2
11½	123	F	2490 2460	1071.4 1050.2
11½	128	F	2464 2500	1069.4 1091.0
12½	162	F	2880 2900	1117.0 1113.6
15½	139	F	2578 2590	1083.4 1079.5
17½	159	F	2896 2842	1116.8 1115.0

[a] weight in milligrams.

[b] this animal was not used in the study.