RELATIONSHIP OF MANDIBULAR TOOTH WEAR TO GENDER, AGE AND PERIODONTAL DISEASE OF ISLE ROYALE MOOSE

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ABSTRACT: We reviewed the literature for current age determination techniques, and for differences in foraging habits that may affect tooth wear and periodontal disease. We analyzed the relationship between wear-class and age determined by cementum annuli in over one thousand moose older than one year which died in Isle Royale National Park, MI. In our large sample, we found that age determination by wear-class correlated well with cementum annuli counts, however, variance in age increased as wear-class increased. We compared the distribution of age and wear-class by gender to determine if dimorphism existed in rates of wear on occlusal surfaces. In the higher wear-classes, the mean age of bulls was significantly younger than the mean age of cows, indicating that males experienced greater wear on their teeth at an earlier age. We also found high correlations between age, periodontal disease, and mandibular tooth wear suggesting that mandibular and periodontal dynamics are important physiological processes that influence longevity in moose.

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Accurate determination of the age at death of animals is of great importance in determining population structure, survival rates, the condition of the population, and in making management decisions for the future. Teeth provide the most imperishable record of the history of a variety of factors that have affected the growth and life of an individual, and therefore are useful in faunal analyses.

Characteristics of mandibular teeth, including tooth eruption, replacement, and wear, are commonly used to estimate age. The biological nature of teeth is the basis for their usefulness in age determination. Teeth are composed of an organic inner pulp cavity with blood vessels and a nerve, surrounded by mineralized dentine and an outer root wall of cement, topped by an enamel-covered crown. Enamel and dentine experience the direct pressure of mastication, while cement anchors the root in the socket (Gordon 1982).

The wear class technique of Passmore, Peterson, and Cringan (1955) was one of the first systematic methods of determining age in moose and is still a useful scale. It was based on the examination of the occlusal surfaces of over 400 lower jaws arranged in order of degree of wear, resulting in nine classes of similarly worn specimens. Broad wearing surfaces develop concavity, described as "scooping", or "troughing" in the case of the long narrow crests. The patterns of wear are largely determined by the differential wear of the enamel of the tooth, which is much harder than the dentine, and the light dentine, which is slightly harder than the dark dentine. In addition to progressive mandibular and incisor tooth wear, the movement and forces applied to the teeth influence remodelling of the alveolar bone which supports the teeth to such an extent that loss of teeth and periodontal disease may lead to excessive resorption of the alveolar bone with age (Atkinson *et al.* 1982).

Incremental growth structures are found in all three types of mineralized dental tissue: enamel, dentine and cementum. Cementum is a bone-like tissue that is deposited around mammalian teeth below the gum line, anchoring them to the periodontal ligament; it consists of collagen and calcium phosphate (hydroxyapatite) that is formed at the roots of the teeth by cementoblasts (similar to osteoblasts, the cells that form bone). As the tooth undergoes mechanical pressure, more cementum is formed. It accumulates throughout the life of the tooth and once calcified is rarely remodelled or resorbed, in contrast to bone which is continuously remodelled and resorbed. Once the pulp cavity is filled, dentine is no longer deposited; and once a tooth is fully formed, enamel ceases to be created (Lieberman and Meadow 1992).

When teeth are cut or sectioned and examined microscopically, a single year's growth appears in bands associated with seasonal growth periods. Annual increments appear as alternating translucent and opaque bands under reflected light (their alternation reverses under transmitted light). The cementum layers surrounding the dentine of the root form dark bands which accumulate in the winter when little or no growth occurs, while the lighter and wider bands form in the late spring, summer and early autumn during the most nutritionally active times (Gordon 1982).

Although based on the same principle of comparing differential mineral structures in teeth as age determination by wear class, annuli counts are superior in accuracy and precision for determining age (Fancy 1980). Variations of this technique have been reported for many species, including: cementum annuli from sectioned incisors in moose (Sergeant and Pimlott 1959), incisor cementum annulations using histological techniques in mule deer (*Odocoileus hemionus*) (Low and Cowan 1963), dental cementum of M_1 in white-tailed deer (*Odocoileus virginianus*) (Ransom 1966), cementum annuli of incisor roots embedded in resin blocks in mule deer (Erickson and Seliger 1969), a comparison of cementum annuli of incisors to tooth eruption and wear in elk (*Cervus canadensis*) (Keiss 1969), cementum annuli of stained and etched incisors of pronghorns (*Antilocapra americana*) (McCutchen 1969), a comparison of methods using cementum increments in the incisiform canine, P_4, and M_1 in greater kudu (*Tragelaphus strepsiceros*) (Simpson and Elder 1969), cementum annuli of molariform teeth of moose as an alternative when incisors are not recovered (Wolfe 1969), cementum annuli of incisors and molars using histological techniques in white-tailed deer (Lockard 1972), secondary dentine annuli in young and middle-aged moose incisors (Haagenrud 1976), cementum annuli in the first permanent incisor in North American sheep (*Ovis* spp.) (Turner 1977), a comparison of stains and sectioning methods in the canines of gray wolves (*Canis lupus*) (Goodwin and Ballard 1985), and a cementum annuli technique of encapsulating teeth from archeological sites in epoxy to protect them (Bourque and Morris 1978).

When relating age to population dynamics, growth, or reproduction, an accurate age estimate is especially important. The accuracy of age determinations of moose using incisor cementum layers was studied by Gasaway *et al.* (1978). Their data indicated that an over-estimate of age is the most frequent error, with a mean error of 0.5 years (minimum -1, maximum +3), which generates underestimates of the rate of growth of a population and loss of cohort identity. They suggested that the most common sources of errors were in the first wide opaque layer, which calves do not develop until they have lived through one winter (in their seventh to tenth month), and in the last increment for moose dying in late winter, because the formation of the last opaque layer is variable.

In current management practice, many methods of determining age are being used. A survey of the status of moose aging technology in North America (Dalton and Francis 1988) revealed that out of 21 units, 3 did not have age determination programs, 2 used wear-class only, 16 used cementum annuli of incisors (5 by sawing or grinding the tooth face, 7 with sawn thin sections, 4 by histologically prepared sections), and 4 used both cementum annuli and wear-classes. Cumming and Evans (1978) showed that even within one jurisdiction using a standard method, substantial variation was possible. Because all methods are subject to errors in counting and interpretation of the sequence of deposition, as well as inadequate verification of quality control, they suggested that more jurisdictions should take advantage of the maximum technology available by using histological sectioning and staining, and that image enhancement techniques hold the greatest potential for the future.

A method using computer image enhancement and analysis was developed by Lieberman *et al.* (1990) for estimating age and season of death from cementum increments in mammalian teeth from archeological sites. Once the best image was obtained from thin sections, it was transferred to a video digitizer. Because the opaque increments have relatively high luminance and translucent increments have low luminance, graphing the luminance of a section across the increments provides a quantitative display of the number and magnitude of increments, ensuring greater visualization and objectivity. This method also provides a convenient way of storing images of thin sections that were previously reproduced as photographs. The next logical step in this process would be the development of quantitative analysis software packages specific to particular taxa for interpretation of age and season of death.

Another high technology application has been the use of scanning electron microscopy (SEM) for analysis of wear and microwear on teeth. Young and Marty (1986) analyzed incisors from a population of moose in Manitoba, Canada, with excessive wear by measuring crown heights, percent tooth tissue loss, and tooth wear with age. They concluded that abrasion by particulate matter harder than the dentine or enamel destroyed the incisal edges and resulted in reduced cropping efficiency and damage to the periodontium. Similarly, Peterson *et al.* (1982) found striking differences in incisiform tooth wear between Kenai Peninsula, AK, and Isle Royale moose. Incisors of Kenai moose were consistently worn to rounded or irregular stubs, most pronounced at the base of the teeth, and often markedly different among the teeth, while Isle Royale moose incisors were more regularly worn with sharp, flat edges. They suggested that the differences may be attributed to the degree of feeding on ground vegetation with its associated soil and debris producing rapid incisor wear. High incidence of incisiform tooth breakage was found in moose from the Seward Peninsula, AK, and Smith (1992) speculated that this could be an early symptom of density related problems.

There is lack of consensus in the literature regarding the effect of sexual dimorphism on foraging habits, and resulting tooth wear differences in males and females. Bartosiewicz (1987) found sexual dimorphism in the cranial development of moose, specifically that greater growth of the premolar tooth row occurs in males. Mandibular length grows over a longer time in bulls, and it is a better predictor of body weight in males. Van Soest (1982) proposed that because females have higher energy requirements during pregnancy and lactation, higher intake is needed to meet their metabolic requirements. Consumption of lower quality diets will produce faster passage rates and reduced retention times. Moreover, the gut capacity of herbivores increases linearly with body weight and the ratio of metabolic requirements to gut capacity decreases with increasing body size (Demment and VanSoest 1985). Consequently, differences in nutritional requirements may affect the degree of tooth wear.

Franzmann *et al.* (1978) stated that moose require large quantities of high quality early-successional woody vegetation, and that their seasonal weight changes were remarkable. At Alaska's Kenai Moose Research Center, females experienced their minimum annual weight in June with an average of 278 kg., and their maximum in December, 393.5 kg, a 42% increase. Males averaged 381.7 kg in June and experienced their maximum in September at 469.5 kg, a 47% increase. Bulls were

19% heavier than cows. Schwartz *et al.* (1984) found that males lose large amounts of body fat during the rut, but that females continue to gain body fat until early winter.

Geist and Bayer (1988) proposed that sexual dimorphism in cervids is a function of the openness of cover: the denser the cover, the more females converge towards males. This concept may explain the vastly contrary findings of Staines *et al.* (1982) in regard to differences in the quality of winter food eaten by male and female red deer (*Cervus elaphus*) living on open-hill ground in Scotland. Hinds occupied more fertile soils with better quality grasslands, and ate more grasses and fine-leafed species, selecting for quality. Stags had more rumen contents per unit body weight, had larger proportions of larger food particles, and opted for a greater amount of poorer quality food. They hypothesized that stags were obliged to eat poorer foods with higher available biomass because they were unable to get sufficient digestible material from grasslands to satisfy their requirements. Risenhoover (1987) also considered quality versus quantity in the value of ingested forage related to its digestible energy and digestible protein. He determined that for Isle Royale moose, the highest protein and energy ingested was in deciduous-aspen habitat types and was the result of higher intake rates rather than diet quality.

Ultimately, the quality and amount of forage processed by each individual moose will determine the extent of tooth wear. Geist (1982) discussed the difference in foraging strategies between male and female elk. Because a cow's main objective is to maximize security for calves, she will compromise forage quality and abundance for safety but will enter the winter with greater stores from summer and autumn feeding. Bulls compromise security in favor of better forage in the summer. Being larger, they can feed on more fibrous forage, resulting in greater wear on teeth. A bull's tooth mass is only slightly greater than a cow's, but because of increased nutritional requirements for their size, males experience about 15% greater tooth wear per year than the females (Geist 1982).

Thus, the cumulative effects of foraging habits throughout a lifetime are recorded in the mandibles at the time of death. Tooth wear-classes correspond reasonably well with age-classes, especially at the younger end of the scale, which is important in many field situations where the hunter harvest is normally composed of younger moose. Tooth wear differences between male and female moose have not been widely studied. In addition, no relationship between periodontal disease (jaw necrosis) and tooth wear has been reported.

Because the skeletal archives of Isle Royale moose provide access to a large sample size, we studied the relationships between wear class and age by gender and with the occurrence of periodontal disease. The purposes of this study were: to analyze the relationship between wear-class and age determined by cementum annuli in moose > 1 year-old which died in Isle Royale National Park, MI; to compare the distribution of age and wear-classes by gender to determine if there were differences in the rates of wear; and to compare wear-classes with the occurrence of periodontal disease (jaw necrosis). We hypothesized that age and wear-class are correlated but that as age increases, wear-classes becomes more variable; that males exhibit faster wear of occlusal surfaces; and that high wear-class and presence of periodontal disease are related. These analyses will enhance the current knowledge of mandibular tooth and bone dynamics, and its usefulness in evaluating the structure and fitness of moose populations.

STUDY AREA AND METHODS

Isle Royale National Park, Michigan (48°N, 89°W) is an archipelago in Lake Superior approximately 24km (15mi) from the

Canadian north shore. The main island is 544 km^2 and sufficiently far from the mainland to isolate it from colonization by many terrestrial species. Moose skeletal remains have been collected on Isle Royale since 1958 during an on-going long term study of wolf-moose dynamics (Peterson 1977). Moose carcasses, mostly wolf-kills, were located in winter by aerial search throughout the island and in summer during extensive coverage of the island on foot. Recovery rate of skeletal remains from the total number of dead moose is estimated at about 1/3 (Peterson *et al.* 1982). An autopsy record file was started in 1958; > 2400 individual moose skeletal remains have been examined, although in many cases only partial skeletons were available for inspection. Throughout the collection period, lower mandibles, metatarsal bones, and any bones exhibiting pathology or abnormality were retrieved. Since 1979, all skulls have been collected.

Sex of the moose was determined by the presence or absence of antlers or antler pedicels on the skull. Age was estimated from counts of cementum annuli in incisors, if available, or in molars if the incisors were not recovered (Sergeant and Pimlott 1959, Wolfe 1969). The mandibles were evaluated for tooth wear and assigned a wear-class between I and IX following the methods of Passmore et al. (1955). Skeletal remains were examined for osteoarthritis, osteoporosis, periodontal disease, and other bone abnormalities. Each skeletal pathology was quantitatively graded as: 1=absent, 2=slight, 3=moderate and 4=severe (Peterson 1977). The autopsy record file is maintained on QuattroPro Database Management System and was imported into SAS (SAS Institute Inc. 1989) for analysis of statistical relationships among parameters. To analyze the relationship between the presence or absence of periodontal disease (jaw necrosis) and wear-class, we used logistic regression, with periodontal disease as the dependent variable and wear-class as the independent variable.

Only moose greater than one year old were considered in our analyses since the age of most calves is determined by tooth eruption and replacement patterns. In Isle Royale moose, Peterson et al. (1983) found that the deciduous I_1 is lost in December or early January and the permanent I_1 is functional by late January. Full emergence of M_2 does not occur until late March or April and may be delayed even longer when nutritional stress is experienced. They suggested that eruption patterns of teeth indicate developmental age as well as genetic and nutritional influences.

RESULTS AND DISCUSSION

In moose older than one year, wear-class and age determined by cementum annuli were highly correlated (Pearson correlation coefficient = 0.78554, P = 0.0001). There was low variation in the lower wear-classes, but increasing variability as wear-class increased up to class VIII (Table 1). The mean age and modal age differed only slightly; both had an asymptote at 12 to 13 years in wear-classes VIII and IX.

Number of moose by age were tabulated by wear-class to illustrate age distribution (Table 2). Similar to a correlation matrix, the diagonals represent agreement and the off-diagonals indicate variation. Because mortality in Isle Royale moose is from wolf-kills and other natural causes, the large sample size better represents the higher wear-classes and older moose than most samples from previous studies using hunted moose. Univariate statistics of the frequencies of each wear-class indicated that the range of ages increased with increasing wear-class.

Age distributions by gender suggested that the average age of females was higher than that of males in the upper five wear-classes (Table 3). There was no differences in age distributions between males and females within each wear-class through the first seven wear-classes (P > 0.074), but there were sig-

Table 1. Wear-classes compared with ages determined by cementum annuli in Isle Royale moose skeletal remains collected from 1958-1992.

Wear-Class	N	Mean Age	S.D.	Min. Age	Max. Age	Modal Age
I	54	1.17	0.42	1	3	1
II	39	1.61	0.58	1	3	2
III	48	2.56	1.50	1	7	3
IV	83	4.42	1.91	1	13	3-4
V	138	7.49	2.61	3	18	6
VI	226	9.88	2.84	5	18	9
VII	204	11.87	3.12	5	20	12
VIII	201	12.86	3.06	7	20	12
IX	80	12.64	2.65	6	21	12-13

Table 2. Age distribution by wear-class for Isle Royale moose from skeletal remains collected from 1958-1992.

	AGE																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
I	46	7	1																		
II	17	21	1																		
III	11	10	13	6	6	1															
IV	2	7	19	19	13	11	7	3	1				1								
V			1	14	12	26	24	19	12	10	9	7	1	2				1			
VI					5	16	21	31	37	26	24	22	17	8	7	8	3	1			
VII					2	4	6	17	17	25	23	29	11	24	20	10	9	4	2	1	
VIII							2	10	13	21	25	31	19	21	16	14	16	5	5	3	
IX						1	1	1	7	4	10	16	16	7	7	5	1	2	1		1

nificant differences for wear-classes VIII and IX (P = 0.022 and P = 0.029 respectively). In higher wear-classes, mean age of bulls was 1-2 years younger than that of cows, indicating that bulls experience greater tooth wear at an earlier age. Moreover, the number of males and females in each wear class was similar despite differences in mean age, suggesting that later tooth wear may contribute to longer life-span in cows. The location and variability of the age distributions for each gender indicate variability increases as age and wear class increase (Fig. 1). Considering that gender differences in wear were found in Isle Royale moose, where relatively small but significant dimorphism exists (Peterson *et al.* 1982), we suggest that the gender differential in tooth wear will be greater in populations that exhibit a higher degree of sexual dimorphism.

Finally, wear-class and periodontal disease were significantly correlated (P=0.0001). However, when both age and wear-class were included as predictors of periodontal disease, age was more highly correlated (P=0.0001) than wear-class (P=0.1083). The model in-

Table 3. Comparison of the distributions of ages of male and female moose by wear-classes from skeletal remains collected on Isle Royale from 1958-1992.

	MALE				FEMALE				
	N	Mean	SD	SE	N	Mean	SD	SE	T-Test
I	30	1.67	.379	.069	15	1.27	.594	.153	.495
II	20	1.50	.607	.136	12	1.75	.452	.130	.227
III	22	3.09	1.72	.366	18	2.33	1.188	.280	.121
IV	39	4.62	2.147	.344	36	4.33	1.772	.295	.539
V	59	7.42	2.634	.343	68	7.56	2.662	.323	.775
VI	109	9.66	2.799	.268	100	10.36	2.837	.284	.074
VII	92	11.63	2.858	.298	95	13.37	3.318	.333	.136
VIII	93	12.33	2.879	.298	95	13.37	3.262	.335	.022
IX	36	12.03	1.978	.329	38	13.37	3.088	.501	.029

cluding gender, and the interaction between gender and age and gender and wear-class, indicated that these parameters were insignificant as predictors of periodontal disease (P > 0.4543). A contingency table of presence or absence of periodontal disease by wear-class illustrated that the frequency of occurrence was very low in the first four wear-classes but progressively increased in the higher classes. The point at which presence of the disease exceeded its absence was at wear-class VII (logistic model prediction, 6.68). Prevalence of periodontal disease progressively increased from 6% in wear-class I to 73% in wear-class IX (Fig. 2).

Our data support the concept that increasing tooth wear may influence remodelling of the alveolar bone that supports the teeth, and that periodontal disease and loss of teeth may lead to excessive resorption of the alveolar bone (Atkinson *et al.* 1982). Radiographs of representative moose mandibles from each of the nine wear-classes displayed reduction in the size of pulp cavities, increase in the space

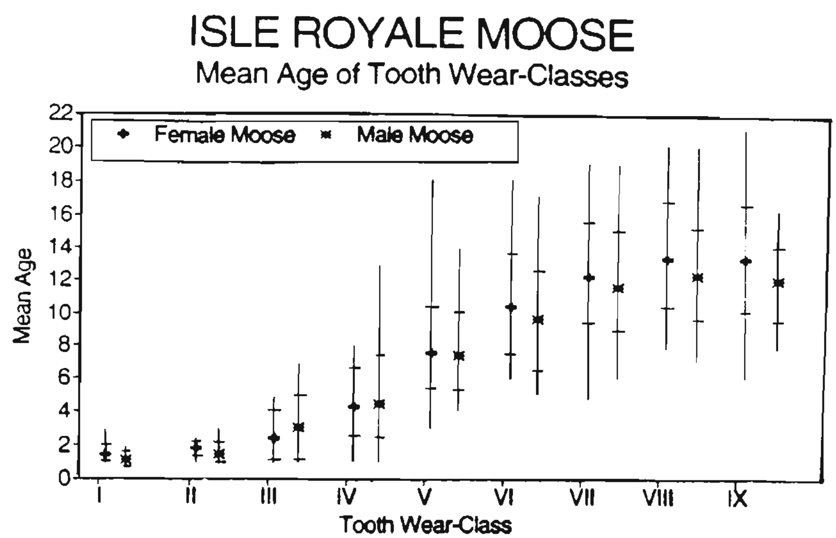

Fig. 1. Mean age of 1084 male and female moose within each wear-class determined from skeletal remains collected on Isle Royale since 1958. Quartiles indicated by vertical lines, minimum age and maximum age indicated by horizontal bars.

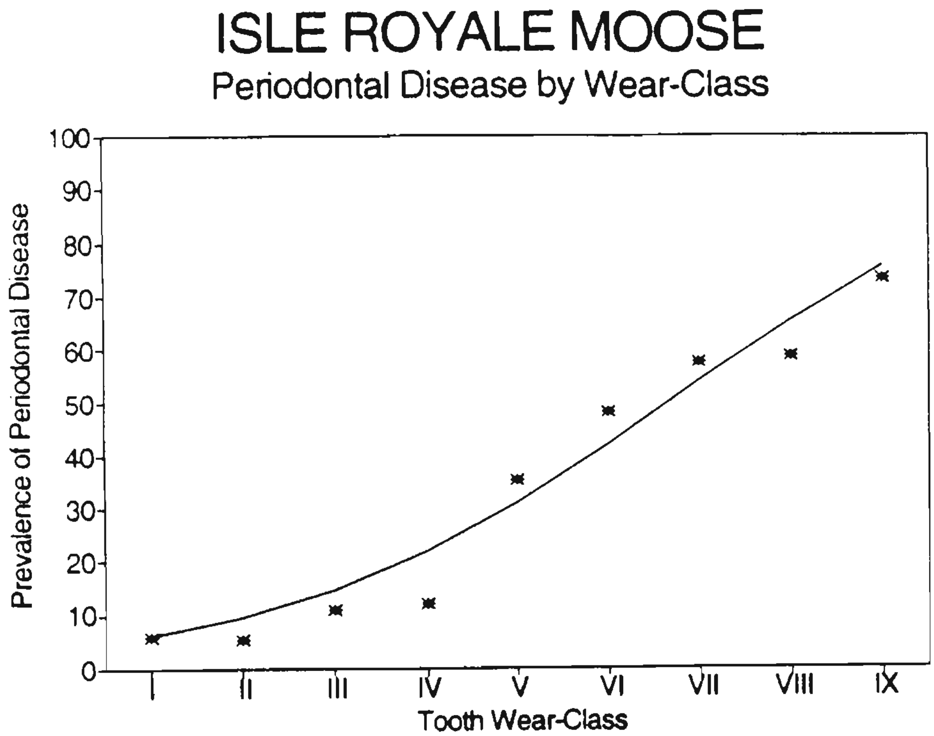

Fig. 2. Prevalence of periodontal disease by wear-class in moose skeletal remains collected from Isle Royale between 1958 and 1992. (Logistic regression $PD = 100 \times [e^{-0.4769WC+3.1866}]/[1+e^{-0.4769WC+3.1866}]$, P=0.0001).

between the roots of the teeth, and greater porosity of the alveolar bone supporting the teeth as wear-class increased (Fig. 3). The mandible in wear-class IX exhibited destruction of the periodontium and resorption of the alveolar bone underlying the heavily worn M_1.

CONCLUSIONS

The two most commonly used techniques for determining age in moose (wear and cementum annuli) were found to give compatible results. The large sample size in all wear-classes was particularly helpful in this study in evaluating the reliability of moose age determination techniques used in assessing population structure, survival rates, and the condition of the population. With the understanding that living populations are made up of individuals and generations of various levels of fitness (Bubenik and Pond 1992), the degree of tooth wear and the presence or absence of periodontal disease are valid indicators of the vitality of individuals and populations. We suggest that the fittest animals employ foraging strategies that not only optimize nutrition but also result in minimal tooth wear. This could be an important physiological process that influences the life-span in moose.

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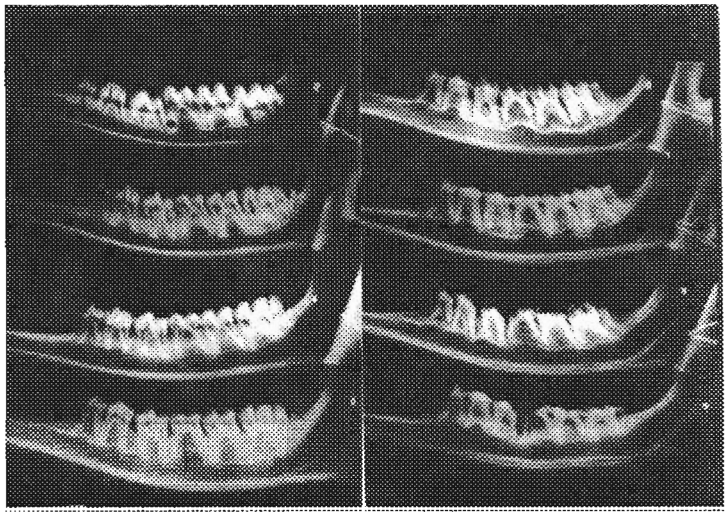

Fig. 3. Radiographs of Isle Royale moose mandibles representing wear-classes II - IX, from upper left to lower right. Note reduction in size of the pulp cavities, increase in space between the roots of the teeth, and increase in porosity of the alveolar bone supporting the teeth as wear-class increases. The mandible in wear-class IX exhibits destruction of the periodontium and resorption of the alveolar bone underlying the heavily worn M_1.

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