GROWTH OF THE APPENDICULAR SKELETON OF THE MUSKRAT, *ONDATRA Z. ZIBETHICUS* (LINNAEUS)

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ABSTRACT.—Fusion and growth patterns of long bones of the muskrat in Illinois are described. Subadult and adult skeletons were separated into nine relative age groups by skull development and first upper molar extrusion. Means of the dimensions gathered for each age group were used to estimate relative growth rates. Distal elements of the limbs approach adult size earlier than the proximal elements and the possible use of these latter in age determination is indicated. The sequence of epiphyseal union closely parallels that of the albino rat and the guinea pig. Retarded fusion has a marked effect on growth and proportions of major long bones.

Although the appendicular skeleton of the muskrat has been described (Latimer and Riley, 1934; Müller, 1953; and Flaim, 1956), studies of postcranial development are lacking. This paper describes growth and fusion of long bones of the muskrat in Illinois.

MATERIALS AND METHODS

Specimens. The skulls and skeletons of 115 animals, trapped during November and December 1959 in McLean and Iroquois counties, Illinois and two immature specimens taken during the summers of 1960 and 1961 in Montgomery county were used in this study. Skeletons were prepared by macerating the bodies in water. They were stored in cardboard cartons at room temperature and are part of the collections of the Department of Biological Sciences, Illinois State University, Normal, Illinois. Nine known-age muskrat skulls from Iowa (Iowa State University catalogue numbers: 249a, 250a, 251a, 252a, 253a, 254a, 255a, 430a, and 638a) were used as reference in aging. These skulls were also studied by Galbreath (1954).

Age arrangement. Illinois muskrats breed from April to September (Hoffmeister and Mohr, 1957, p. 180); the sample therefore contained in addition to adults, subadults ranging in age from about three to eight months. Determining relative age in the subadults required development of a technique not previously used for aging muskrats. Skulls of the meadow vole (*Microtus pennsylvanicus*) were separated into nine age groups according to the development of certain skull characters by Snyder (1954). Similar changes in age occur in muskrats. Skulls of newly born muskrats have a smooth dorsal surface and lack postorbital processes (Hinton, 1926, plate II). With increasing age, postorbital processes enlarge, lambdoidal and interorbital crests develop, and small bony "horns" appear at the junction of the parietal and squamosal bones (Gould and Kreeger, 1948; Alexander, 1960). Undamaged skulls from 79 muskrat skeletons were examined; those with severely damaged crania were not aged. The postorbital processes on each skull were assigned a value of one, two, three, or four in order of increasing development. Similar values were assigned to a second character-complex, the development of the "horns" and the interorbital crest. The degree of first upper molar extrusion, a valuable age criterion, was assigned a value of two, three, or four; fluting end not visible, barely visible or visible respectively (see Olsen, 1959b). The sum of the three assigned values indicated the skull's relative age (Fig. 1). Nine sums represent nine relative age groups. A total or score of five represented the youngest of the animals trapped during the winter and a score of twelve the oldest. Four, the smallest possible total, fitted skulls of the two immatures collected in the summer.

Composition of each age group was: group four, 1 male, 1 female; group five, 5 males, 5 females; group six, 5 males, 7 females; group seven, 9 males, 4 females; group eight, 3 males, 7 females; group nine, 9 males, 8 females; group ten, 4 males; groups eleven and twelve, 6 males, 5 females.

Age groups eleven and twelve were considered adult because: (1) they alone had adult dentition as described by Gould and Kreeger (1948), Galbreath (1954), Sather (1954), and Olsen (1959b); (2) serious bone disease occurred more frenquently in the two groups; (3) the only specimens with completely fused sacral vertebrae were members of these groups; and (4) a known-age Iowa skull of 571 days was comparable to those of age group eleven. The other Iowa skulls, all subadults of 171 to 222 days, corresponded to age groups six and seven.

Morphological differences and, to a lesser degree, various dimensions of muskrat bacula may be valuable criteria for determining age (Elder and Shanks, 1962). Of 42 male skeletons aged, only 12 bacular shafts were recovered. Measurements were not significantly correlated with the age grouping, but there were definite size and morphological differences between bacula of subadults and adults. Another check on the age grouping was made. The degree of epiphyseal union in long bones, closely corre-

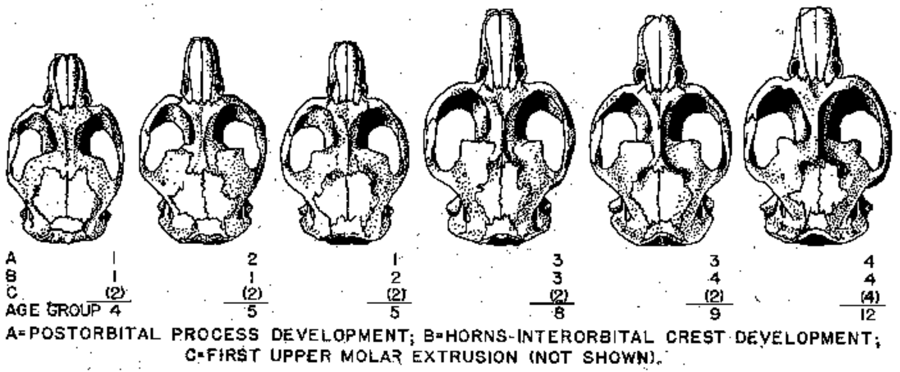

FIGURE 1. — Dorsal view of muskrat skulls and development of characters used in aging (about ½ natural size). From left to right, the age groups are: 4, 5, 5, 8, 9, and 12. Postorbital process development: 1, 2, 1, 3, 3, and 4; horns-interorbital crest development: 1, 1, 2, 3, 4, and 4; and first upper molar extrusion (not shown): 2, 2, 2, 2, 2, and 4.

lated with age, was determined for all skeletons. Only eight of the 79 skeletons aged did not fit their respective groups with regard to the numbers of epiphyses fused. Further study revealed that most of these skeletons also exhibited an irregular sequence of epiphyseal union (see discussion of sequence constancy under *Fusion* below). Whether the differences represent natural variations in the fusion patterns and characters used in aging, an overlapping of the age groups, or abnormal conditions, is unknown.

Measurements. A vernier caliper reading to one tenth of a millimeter was used. Bones were held so that the long axis was parallel with the caliper's back. Measures of left elements were recorded and if unobtainable, the corresponding right dimension substituted. Although Latimer and Riley (1934) stated that the long bones of *O. z. cinnamoninus* were asymmetrical, preliminary work revealed no measurable differences in those of Illinois muskrats.

The ilium was measured from its anterior end to the anterior lip of the acetabulum; the innominate bone, from the iliac crest to the posterior border of the pubis. Dimensions of the calcaneus and clavicle were maximum lengths. Skull measurements were taken in the manner described by Sather (1956): total skull length, from "anterior surface of the incisors to the condylions," and zygomatic width, "greatest distance between the outer surfaces of the zygomatic arches." Other long bone measurements (maximum lengths) were taken in the manner described by Olson and Miller (1958, p. 140-141). Grease content of bones varied considerably therefore weights were not taken.

Maceration destroys cartilage and occasionally detached epiphyses were held against diaphyses while measuring. To check the effect of missing epiphyseal cartilage, long bones from the carcass of a subadult male were defleshed and measured, and after thorough maceration and drying, remeasured. The differences, in millimeters, were: tibia, 0.7; femur, 0.5; humerus, 0.0; ulna, 0.3; and radius, 0.3. All differences were below one per cent of the lengths determined before maceration.

RESULTS AND DISCUSSION

Age, sex, and size. Sex differences in rates of body growth were reported by Errington (1939), Dorney and Rusch (1953) and Olsen (1959a). Differences in coefficients of variation of certain skull dimensions were reported by Sather (1956). No sexual dimorphism of skulls was observed when they were arranged by assigned age, sex, size, or the characters used in aging (such as rounded processes versus angular processes). This lack of sexual dimorphism of skulls was also observed by Gould and Kreeger (1948). Many authors have reported differences in absolute size of the animal, males being generally larger. Means and ranges of long bone dimensions of both male and female adults and subadults are given in Table 1. Little difference between sexes of the two ages was observed, but the sample is small. Skull and long bone dimensions increase with age. Skull dimensions are of value in separating subadults and adults (Alexander, 1951). Those of males, age groups five through twelve are shown in Figure 2.

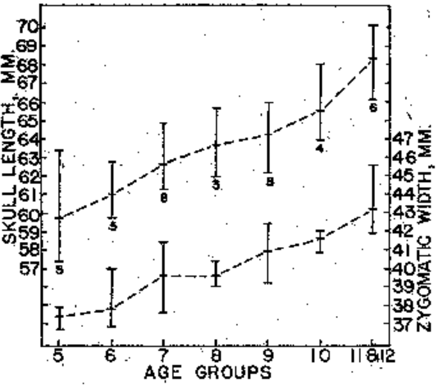

FIGURE 2.— Skull dimensions of male muskrats, age groups 5 to 12. Ranges shown by vertical lines; broken lines connect means; numbers of individuals measured are indicated.

Many techniques for aging muskrats involving measurements (such as upper incisor width, body weight, zygomatic width or breadth, testis length, and penis diameter) show an overlapping of age classes; with larger subadults falling within the adult range (Schofield, 1955). While my data are not sufficient for evaluating the use of long bones as age criteria, the more slowly growing elements may provide a more reliable scale for samples collected during the winter. Table 1 shows little or no overlap between dimensions of adult and subadult innominate bones.

Skeletal growth. Analyses of dimensions revealed similar growth trends in males and females. Trends for males, as revealed by a graphic method developed by Simpson (1941) and Snyder (1954), are shown in Figure 3. The calcanei, third metatarsal, and third metacarpal bones reach adult size earlier. The scapulae and innominate bones grow more slowly.

A growth gradient occurs in the limbs of muskrats. With increasing age, the distal elements (calcaneus, metatarsals, and metacarpals) decrease in the relative percentage they are of the total length of the limb, while the proximal elements (femur and humerus) increase. This is particularly evident in the specialized hind limb (Fig. 4). Muskrats with newly opened eyes and body lengths of not over five inches swim and dive (Johnson, 1925, p. 228; Errington, 1939; Sather, 1958). When they are first able to use the front feet in the diverse manipulations required for building lodges, digging tunnels, opening clams, etc. is not known; but much of the renewed building activity during the fall is credited to the young of the year (Johnson, 1925, p. 269; Smith, 1938). Young of even the slow-growing litters are self sustaining by the end of their first 30 days (Errington, 1939). A few workers, using hind foot lengths, have aged very young muskrats. It seems doubtful, because of this rapid maturation of the distal elements, whether older animals could be similarly aged.

Fusion. With increasing age, epiphyseal cartilage becomes reduced and epiphyses fit their diaphyses more closely. Classes of "closeness of fit" were apparent; fit was either loose and rocking of the epiphysis on its diaphysis evident, or firm with little or no rocking, indicating

Table 1.—Dimensions (in mm.) of long bones of muskrats, age groups five through twelve.

Bone		Subadults		Adults	
		Mean	Range	Mean	Range
Innominate	Male	73.9	64.5-82.0 (35)	83.4	82.0-86.0 (6)
	Female	74.1	62.7-81.4 (31)	83.9	82.7-86.8 (5)
Ilium	Male	36.9	32.4-41.2 (35)	42.0	39.4-43.0 (6)
	Female	37.1	31.0-40.7 (31)	41.9	40.7-44.3 (5)
Femur	Male	45.7	39.9-51.0 (35)	51.2	48.0-53.3 (6)
	Female	46.2	40.5-50.4 (31)	51.1	49.9-53.1 (5)
Tibia	Male	63.5	55.0-69.0 (35)	69.9	65.6-71.8 (6)
	Female	64.2	55.9-68.3 (31)	70.6	69.2-73.4 (5)
Calcaneus	Male	17.9	16.0-19.6 (35)	18.8	18.4-19.8 (6)
	Female	18.1	16.8-19.0 (31)	18.6	18.2-19.1 (5)
Metatarsal 3	Male	27.3	24.8-28.9 (34)	27.8	26.7-28.7 (6)
	Female	26.5	25.3-29.6 (30)	27.6	27.0-29.1 (5)
Clavicle	Male	26.5	23.7-29.6 (35)	29.1	27.6-30.9 (6)
	Female	26.8	22.9-28.9 (31)	30.7	30.2-31.7 (5)
Scapula	Male	42.6	36.7-46.8 (33)	46.8	45.8-48.0 (5)
	Female	42.2	35.0-45.9 (28)	47.9	47.0-49.5 (5)
Humorus	Male	37.3	32.8-40.3 (35)	40.8	38.6-42.4 (6)
	Female	37.5	32.9-40.7 (31)	41.4	40.4-42.8 (5)
Radius	Male	39.9	33.2-42.9 (35)	44.0	42.9-44.9 (6)
	Female	39.9	33.9-42.2 (30)	44.3	44.0-45.5 (5)
Ulna	Male	52.1	44.3-56.2 (35)	56.8	55.0-58.4 (6)
	Female	52.4	44.1-55.8 (29)	57.0	55.6-58.9 (5)
Metacarpal 3	Male	10.4	9.9-11.9 (35)	10.8	10.3-11.8 (6)
	Female	10.4	10.1-11.9 (28)	10.8	10.5-11.6 (5)

a more advanced development. The extent of the grooves or "epiphyseal lines" marking a point of fusion also indicate the recency of the fusion; late fusion being represented by deep or sharply defined lines. Epiphyses were ranked according to the number unfused in each age group and the appearance of the junction (epiphyseal lines and closeness of fit criteria). The arrangement closely parallels the sequence of fusion in the albino rat (Dawson, 1925) and the guinea pig (Zuck, 1938) as shown in Table 2. This method, although inadequate for determining an exact sequence, did reveal trends.

Eleven osteologically mature animals were examined and all lacked union in distal epiphyses of the radius, ulna and femur, and proximal epiphyses of the humerus and tibia. Fusion of the epiphyses in the albino

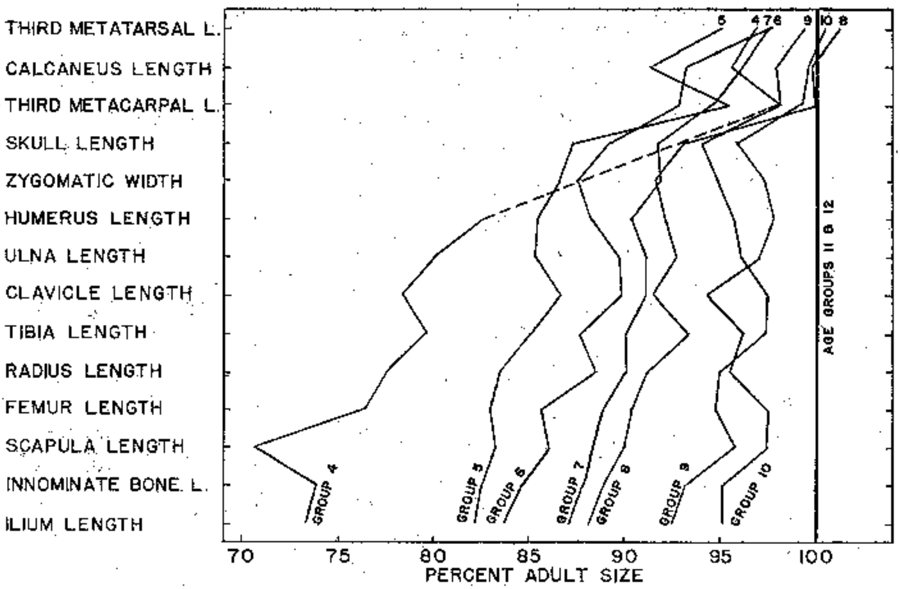

FIGURE 3.—Percentage of adult size reached by subadult male muskrats. The straight vertical line or 100 per cent coordinate represents mean values of adult dimensions. The points to either side represent mean values of subadult dimensions expressed as percentages of their corresponding adult mean values. Distance between a point and the 100 per cent line represents the percentage of adult size attained.

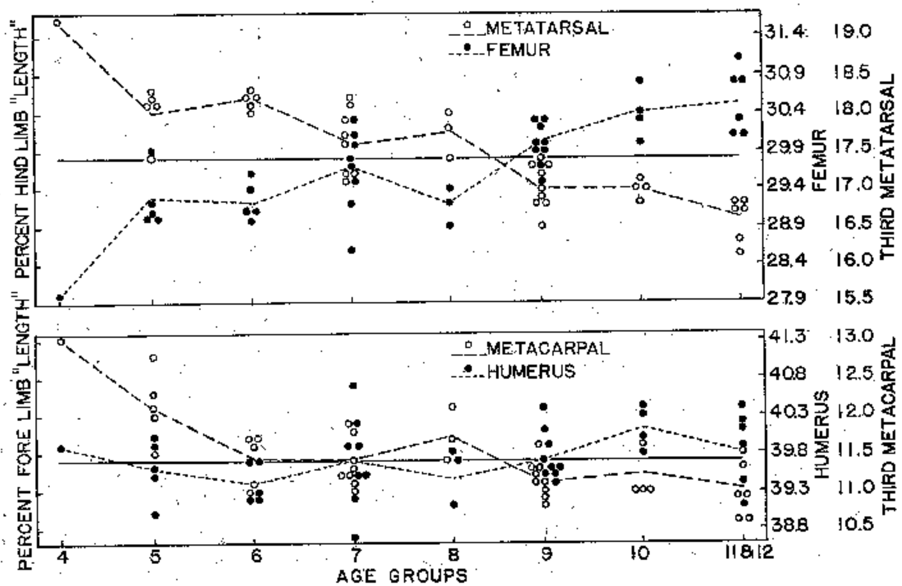

FIGURE 4.—Age changes in limb proportions of male muskrats. Horizontal scale represents age groups; vertical scale represents percentage that bone lengths are of their respective limb lengths. Broken lines connect means for each age group. Limb "lengths" are sums of bone lengths: femur, tibia, and metatarsal, the hind limb; humerus, radio-ulna average, and metacarpal, the fore limb.

TABLE 2.—Sequence of epiphyseal union in three rodents.

Albino Rat (after Dawson, 1925)	Guinea Pig (after Zuck, 1938)	Muskrat[1]
Dist. Humerus	Dist. Humerus	Dist. Humerus
Prox. Radius		Prox. Radius
	Pelvis, Primary Elements	Coracoid Proc.
		Lesser Trochanter
		Med. Epicondyle, Hum.
	Head, Femur	Metacarpal 3
Dist. Tibia	Dist. Tibia	Pelvis, Primary Elements
Dist. Fibula	Prox. Radius	Dist. Tibia
Med. Epicondyle, Hum.	Calcaneus	Acromion Proc.
Olecranon	Head, Humerus	Calcaneus[1]
Head, Femur	Metacarpal 3	Head, Femur[1]
Greater Trochanter	Metatarsal 3	Greater Trochanter
	Dist. Femur	Metatarsal 3
	Dist. Fibula	Dist. Fibula
	Olecranon	Olecranon
Dist. Femur		Dist. Femur
Prox. Tibia	Acromion Proc.	Prox. Tibia
Prox. Fibula	Prox. Tibia	Prox. Fibula
Dist. Radius	Dist. Radius	Dist. Radius[1]
Dist. Ulna	Dist. Ulna	Dist. Ulna[1]
Head, Humerus	Prox. Fibula	Head, Humerus

[1] A tentative sequence as explained in text. Sequence of adjacent epiphyses similarly marked could not be determined.

rat occurs during two age periods; from birth to the end of the fifth month, and from the thirtieth month to senility (Dawson, 1925). Since a similar state may exist in muskrats, a tentative order, utilizing closeness of fit data, was worked out. The distal epiphysis of the femur and proximal epiphysis of the tibia were weakly fused in one age group twelve skeleton. While diaphyseal surfaces of these epiphyses are different in contour and shape, 24% of the skeletons had loosely fitting femoral epiphyses and 69% had loosely fitting tibial epiphyses indicating an earlier fusion for the femur. The distal epiphyses of the radius and ulna fit their diaphyses closely in many specimens of several age groups. The head or proximal epiphysis of the humerus, the last to fuse in many mammals, fitted loosely in over 90% of the skeletons examined.

Rate of fusion may vary but the sequence of epiphyseal union is always the same in the human (Stevenson, 1924) and in the albino rat (Dawson, 1925). Correlated evidence suggests that the orderliness also characterizes normal muskrat fusion. But a few skeletons (the same skeletons which did not fit their respective age groups with regard to the number of epiphyses fused) exhibited a curiously irregular sequence. In addition to the epiphyses remaining unfused in all specimens, each of the following remained as the only unfused epiphysis: head of femur, acromion, greater trochanter, distal fibula, and olecranon.

Age limits for fusion of the distal epiphyses of radius and ulna in fox squirrels (*Sciurus niger*) raised in captivity are 54 weeks for males and 50 weeks for females (Carson, 1961). Sex differences in age at time of fusion for various muskrat epiphyses may also exist but no difference in order or sequence was observed.

Flaim (1956, p. 20) stated that the proximal end of the fibula articulates with the peroneal process of the tibia, but I found that the process actually originates on the proximal epiphysis of the fibula which may or may not fuse with the adjacent tibial epiphysis; being unfused in 29 animals of all age groups, fused in 10 animals of age groups eight, nine, eleven and twelve, and weakly fused in 40 animals of age groups five through twelve. Similarly, fusion between distal epiphyses of both bones may also occur, even before they are united with their respective diaphyses.

A cotyloid or acetabular bone was found in three immature skeletons (those of age group four and one of age group five). Fusion between the ramus of the pubis and the ramus of the ischium occurs after the fusion at the acetabulum. The innominate bone enlarges along the posterior borders of the ischium and the pubis as well as at the iliac crest long after union of most epiphyses. Similarly, prolonged growth occurs along the lateral crest or third trochanter of the femur and the deltoid tuberosity of the humerus. The scapula enlarges along the vertebral border.

Proportions. Proportions of various long bones change with increasing age. This was most notable in bones with areas of retarded fusion (Fig. 5). Huxley (1932, p. 40) referred to this lack of fusion in microtinae and the resultant slow growth through adult life. Because epiphyses fit diaphyses so closely in mature muskrats, cartilage, if at all present during life, must be diminutive. Data from known age specimens would be necessary for further analysis of adult growth patterns.

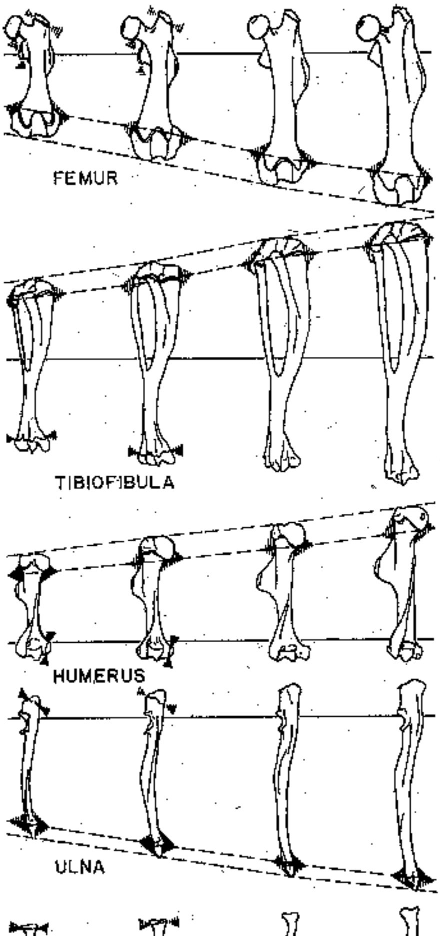

FIGURE 5.—Retarded fusion and related bone growth in bones of (from left to right) two group four immatures, a group seven subadult, and a group twelve adult. Hatching indicates unfused areas. Lateral aspect of ulna, medial aspect of tibia, and extensor surfaces of femur, humerus, and radius are shown (about ½ natural size).

SUMMARY

Seventy-nine muskrat skeletons were separated into nine relative age groups by skull development and first upper molar extrusion. Fourteen linear measurements were taken from major long bones of each skeleton. Means of the dimensions gathered for each age group were used in estimating growth trends. The more specialized distal elements of the limbs approach adult size earlier than the proximal elements. The possible use of dimensions of the innominate bone in age determination is worth more investigation.

The sequence of epiphyseal union in the muskrat closely parallels that of the albino rat and the guinea pig. A lack of union in otherwise osteologically mature skeletons was observed in certain epiphyses. This retarded fusion has a marked effect on growth and proportions of major long bones.

ACKNOWLEDGMENTS

I wish to extend sincere appreciation to Dr. Robert D. Weigel and Dr. Andreas A. Paloumpis for advice given during the course of this study; to Dr. Dale E. Birkenholz for reviewing this manuscript; and to Dr. Milton W. Weller and the late Dr. Paul L. Errington of the Iowa State University of Science and Technology for the loan of skulls of known age.

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Manuscript received January 21, 1964.