5

Geology

6

16

FIELDIANA · GEOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 16 March 27, 1970 No. 16

Population Dynamics of *Leptomeryx*

JOHN CLARK
FIELD MUSEUM OF NATURAL HISTORY
AND
THOMAS E. GUENSBURG
ROCKFORD NATURAL HISTORY MUSEUM

The large, carefully-documented collections of middle Oligocene fossils made in connection with the paleogeographic studies of Clark *et al.* (1967) offer unusual opportunities for interpretation of population dynamics. Unlike several other collections which have been used for this purpose (Shotwell, 1958; Van Valen, 1964; Voorhies, 1969), these collections have been demonstrated to constitute perthotaxes[1] accumulated over a period of time and buried essentially without transportation. The enormous biases of selective transportation have not operated upon them.

Eight lines of evidence demonstrate that these collections are true perthotaxes:

1. Individuals in every stage of disintegration, from entire skeletons to separate chips, have been found (see Field Museum specimens B147, B159, B163, also *Hypertragulus* skeletons at the South Dakota School of Mines).
2. Coprolites are abundant.
3. None of the bones show water abrasion.
4. Some partially disintegrated specimens have their broken chips dispersed around them uniformly in all directions (see FM specimens B150 and B160).
5. Complete skeletons have been found in death poses (see South Dakota School of Mines *Hypertragulus* herd).

---

[1] Perthotaxis: "A death assemblage with the animal corpses in various stages of destruction by the set of processes normally operative under the environment concerned."—Clark *et al.*, 1967, p. 155.

Library of Congress Catalog Number: 70-115192

6. The entombing sediments are heterogeneous mudstones, which can be demonstrated to have engulfed bone without transporting it appreciable distances.
7. *Celtis* seeds and bones of very small animals occur scattered throughout, never accumulated as they would be along a strand line, or washed against an obstacle.
8. Bones and skeletons of all sizes occur indiscriminately throughout. (Field Museum B150, a shattered *Metamynodon* skull and jaws, occurred a few feet from various scattered rodent and small artiodactyl bones).

These lines of evidence cumulatively indicate that the fossils represent death assemblages, essentially untransported. Specimen B159, a group of *Hypertragulus* skeletons somewhat dissociated by perthotaxy before burial, occurred as a convex layer on a front 18 inches high. This could only represent one roll of a rapidly-congealing mudflow; the bones, although dissociated before burial, had not been scattered by the agency of deposition and therefore could not have been transported more than a few inches. The thickness of this single-herd deposit indicates an incrementation of at least 18 inches in one episode.

Leptomeryx was selected as the subject for study because it is monospecific within the Scenic Member of South Dakota, occurs in the collections in greater abundance than any other genus except *Paleolagus*, and has measurable, relatively brachyodont molars with closed roots. It has the added advantage of a close enough anatomical analogy with *Tragulus* and the cervids to make limited developmental and ecological analogy reasonable.

We chose for study the two FMNH collections from South Dakota having the largest numbers of *Leptomeryx*. The preliminary results were so surprising that we included for comparison an excellent collection of *Leptomeryx* from Sioux County, Nebraska. This latter collection was made for the Walker Museum, many years ago, with excellence of specimens rather than totality of sample as the purpose. Correspondence of this collection with those made as part of a statistical study is at least as amazing as any other result of this study (Fig. 1).

Data on individual collections

1. Collection 26. Lower Nodular zone, Scenic Member, Brule Formation, SW-¼ of SW-¼, sec. 15, T. 2S., R. 15E., Pennington

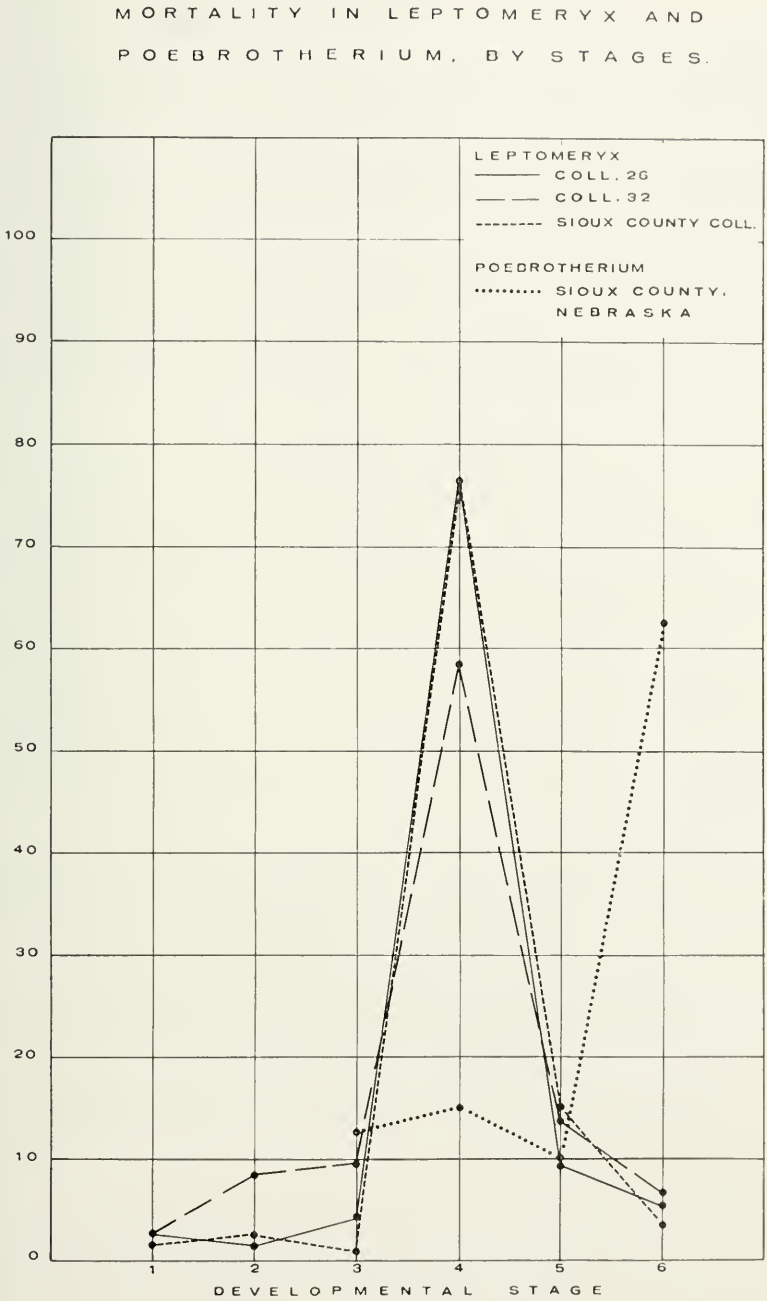

FIG. 1. Mortality in *Leptomeryx* and *Poebrotherium*, by stages.

County, South Dakota. Collected by J. Clark and K. K. Kietzke, 1965. This collection comes almost entirely from the stratum including and immediately overlying a pond limestone ± 4 feet below the top of the Lower Nodular zone. Essentially, it represents the perthotaxic assemblage buried by one episode of deposition.[1] The local environment was a swamp on a grassy or savannah plain. This collection came from an area of not over 30 acres, along the east and south sides of a draw, roughly one quarter mile from the site of Collection 32. It comprises 163 specimens of *Leptomeryx,* of which 73 are suitable for the present study. The remainder consist either of upper teeth, of lower premolars, or of specimens too fragmentary for use.

2. Collection 32. Lower Nodular zone, Scenic Member, Brule Formation, SE–¼ of SE–¼, sec. 16, T.2S., R.15E., Pennington County, South Dakota. Collected by J. Clark, O. L. Gilpin, and J. Granath, 1966. This collection comes principally, but not entirely, from a highly fossiliferous stratum ± 4 feet below the top of the Lower Nodular zone, which is continuous with the fossiliferous level of Collection 26. At least three-fourths of this collection, therefore, represent one perthotaxic assemblage buried during one episode of deposition; the remainder was buried a few years to tens of years earlier or later (Clark *et al.*, 1967, pp. 99–102). The local environment was a savannah plain. The collection comprises 281 specimens, of which 114 are suitable for the present study.

3. Sioux County, Nebraska. Collection made during the decades preceding 1940, chiefly by Paul Miller, for the Walker Museum, University of Chicago. Various specimens are recorded as coming from various tributaries of Hat Creek. All are stratigraphically located as coming from "Lower Nodular zone, Brule," but no effort was made to establish positions within this zone. The collection includes 115 specimens suitable for this study. Many consist of complete skulls and jaws; most include all three lower molars; in completeness of specimens the collection far exceeds the two better-documented ones from South Dakota.

Derivation of data

Preliminary study led to the conclusion that the lower molars show more consistent development of wear patterns, coincident with decreasing crown height, than do the upper molars or the premolars.

---

[1] Clark *et al.*, 1967, p. 83.

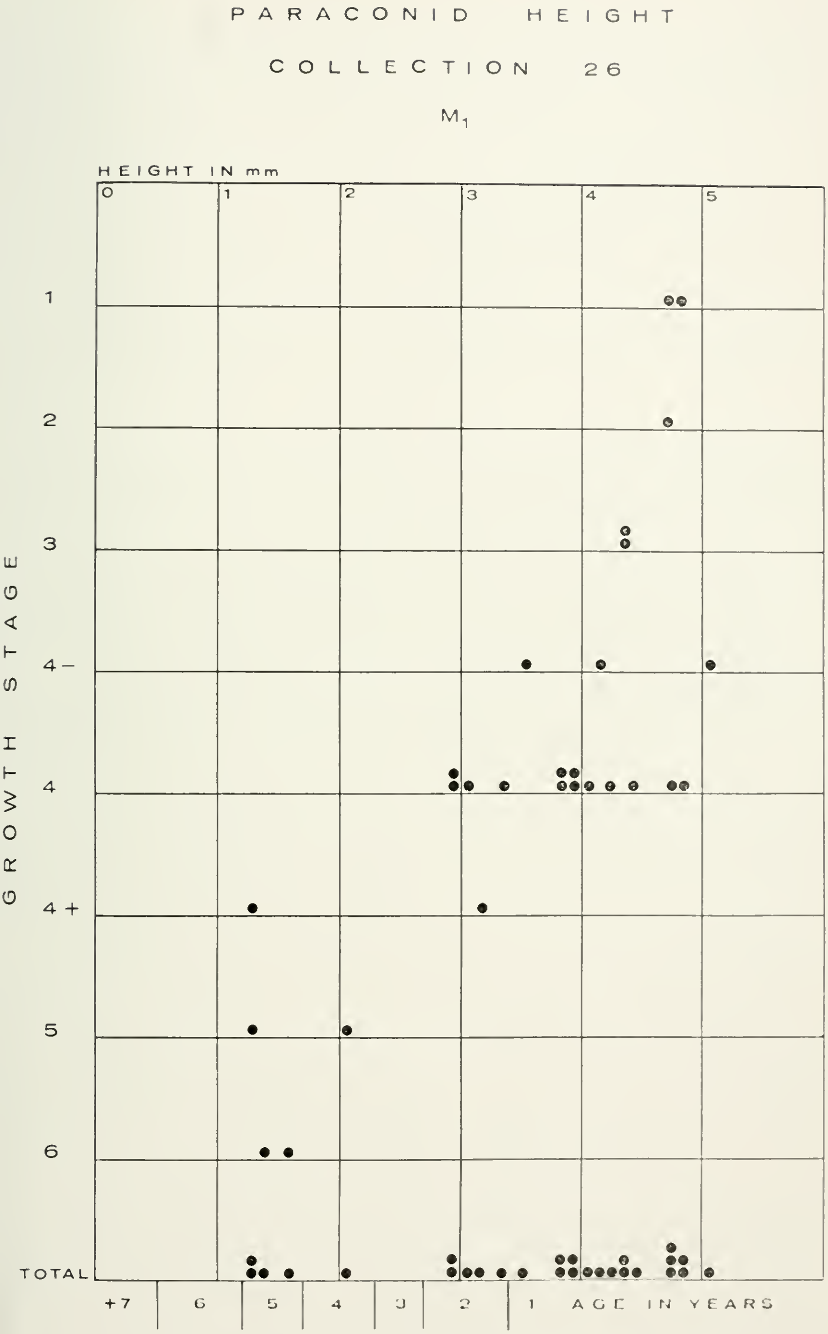

FIG. 2. Collection 26: paraconid height, M_1.

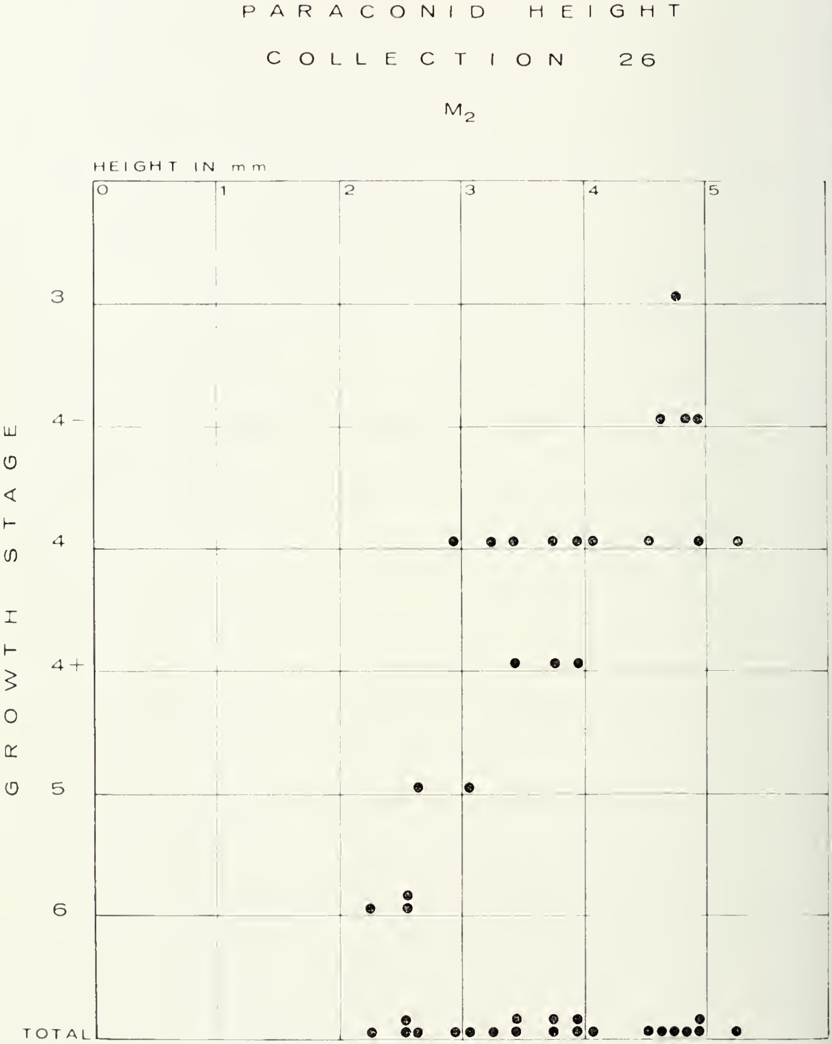

Fig. 3. Collection 26: paraconid height, M_2.

The lower molars also show a more consistent progression of wear, from the third through the first, than do the uppers (see figs. 3, 4, 6, 7, 9, 10). Presumably these differences are due either to slight differences in height of crowns relative to lakes, or to differential wear caused by more complexity in upper-molar pattern. In any case, we decided to use the lower molars as our basis for age determination.

We then set six arbitrary but objectively determinable age stages, as follows:

	Stage	*Terminated by*
1.	Infancy	Beginning of wear on M_1
2.	Juvenility	Beginning of wear on M_2
3.	Adolescence	Beginning of wear on M_3
4.	Young Adulthood	Elimination of anterior lake of M_1
5.	Middle Age	Elimination of posterior lake of M_1
6.	Senility	Death

The specification "beginning of wear" was found preferable to "complete emergence" because in some individuals M_3 seems to have been actively in use for some time before growth of the jaw permitted complete emergence of the posterior lobe of the tooth.

These stages are definite and objective. As a further refinement, minus and plus signs were recorded for those individuals respectively ust entered into their age group or almost passing from it. This required subjective decisions, which we minimized but could not eliminate completely by ranking the specimens independently and conferring on the few borderline cases in which our ranking differed.

Observations on wear of teeth in Oligocene *Poebrotherium* and *Protoceras*, plus observations on the large cervid collection in Field Museum, demonstrate that these wear stages approximately repreent their corresponding age stages. If anything, "senility" includes ome middle-aged animals. This is further discussed on page 426.

Comparison with the wear patterns of those specimens possessing omplete molar batteries made it possible to assign individual molars o stages. We experimented by assigning to a stage individual teeth of a series without observing the whole series, then checking against he other teeth of the series. Since the error demonstrated by the xperiments is insignificant, we have included evaluations of single eeth. Tables 1, 2, and 3 list the teeth present in each specimen, makng the data susceptible to critical re-examination in detail.

In the hope of arriving at actual measurements rather than ranks, eeth in various stages of wear were studied closely. It was at once pparent that measurements of the external crescents would give uneliable results, due to the interaction of variations in the slope of the rescent at different elevations from its base and to considerable ariations in occlusal pattern. Of the internal crescents the para-

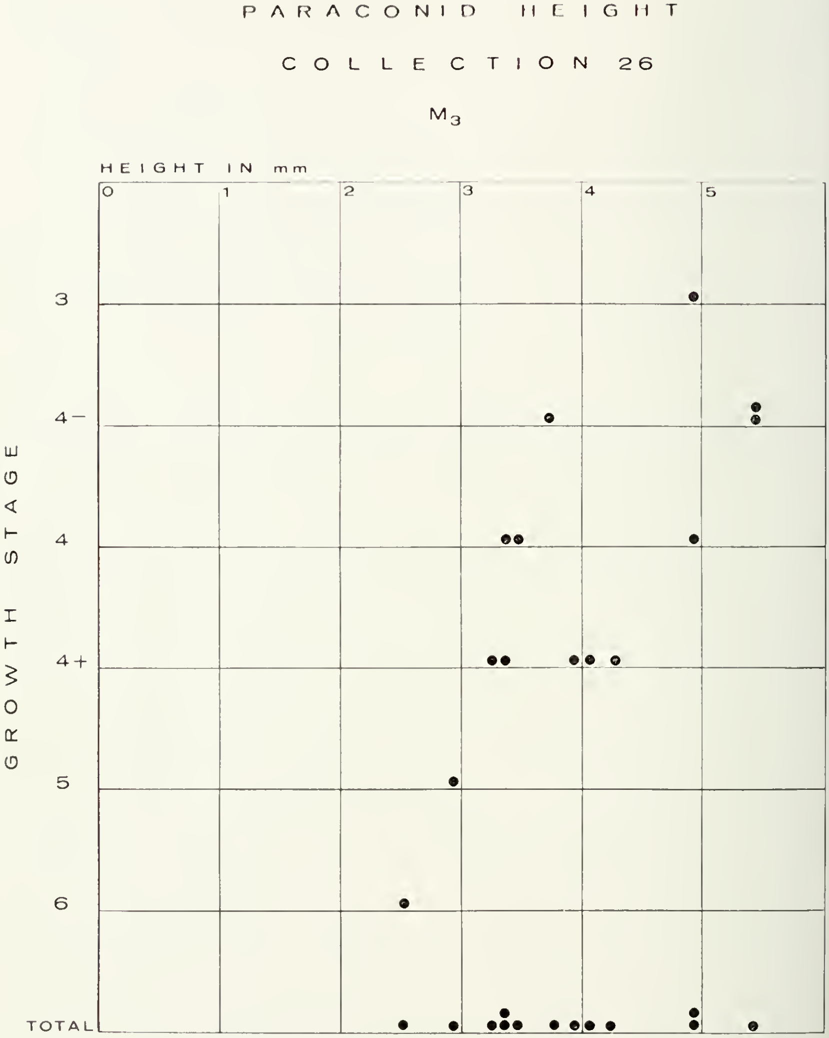

FIG. 4. Collection 26: paraconid height, M_3.

conid seemed the more satisfactory since it received wear earliest and gave a uniform basis for measurement of all three molars. Measurements were made from the enamel border upward along the outermost ridge of the cusp, which is usually inclined at a slight angle forward of normal to the antero-posterior axis of the tooth. In unworn teeth, this measurement invariably gives a maximum dimension, running to the apex of the cusp.

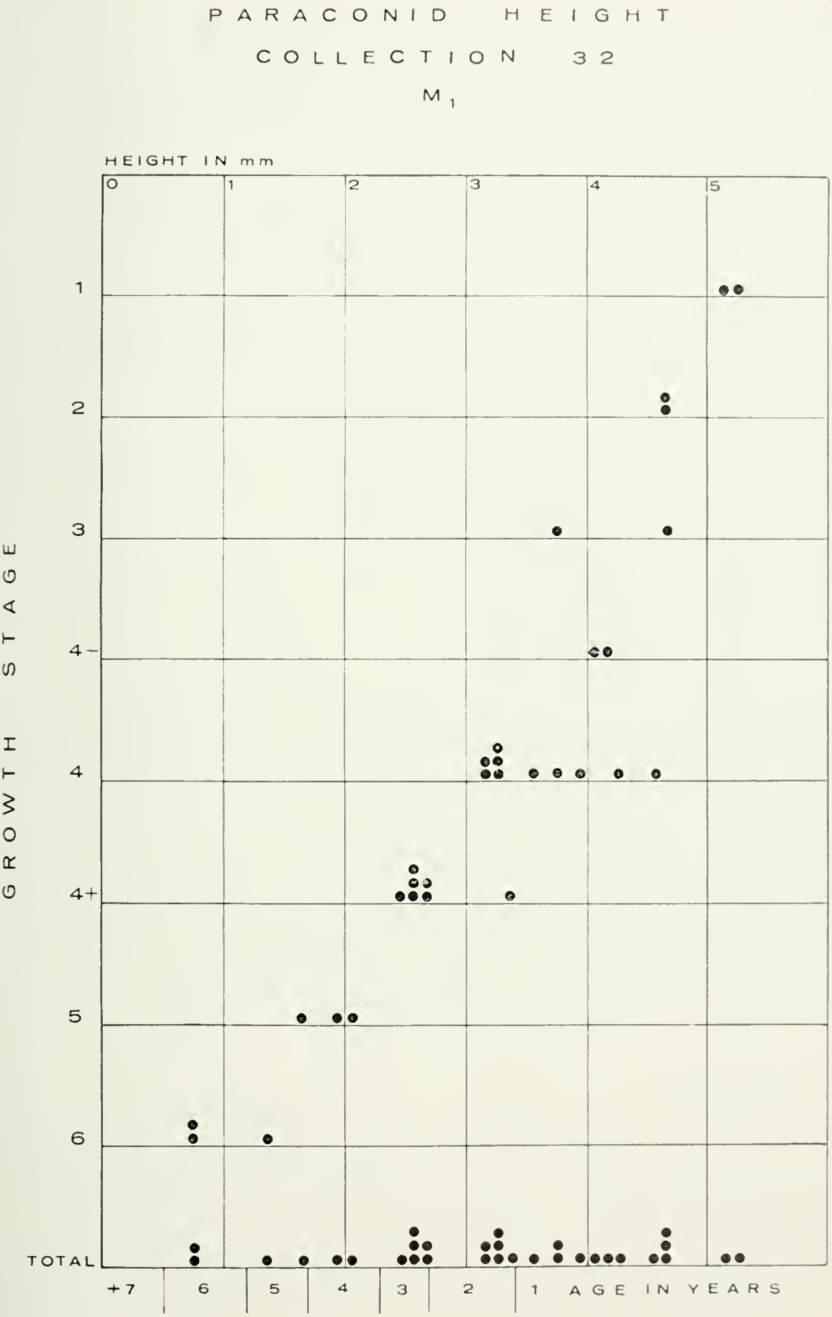

FIG. 5. Collection 32: paraconid height, M_1.

However, three unavoidable sources of variation enter into these measurements. First, the enamel border is not at all uniform in outline. Figure 11 illustrates the three commonest configurations. A fourth consists of a gradual downward thinning of enamel, effecting a gradation rather than a sharp border. These variations can produce more than 0.1 mm. difference in measurement of teeth in equivalent stages of wear.

The second source of variation is difference in occlusal wear. All conceivable permutations of the three patterns illustrated in Figure 11 have been observed. They can produce variations of at least 0.2 mm. in teeth of equivalent wear stages.

Finally, differences in overall size of teeth can certainly influence measurements of paraconid height. Attempts to arrive at a meaningful ratio of paraconid height to tooth length were defeated by interdental wear, which changes the tooth length considerably with increasing age. Measurements of tooth width proved to be not comparable from specimen to specimen, due to variations in curvature and position of the cusp perimeters.

Visual inspection of the specimens revealed no such relation between size and hypsodonty as occurs in *Mesohippus*. A large individual is not proportionally more hypsodont than a small one. Therefore, the wear stages are equally valid in large and small specimens, and are probably more valid than measurements of paraconid height.

Measurements of total size of teeth failed to reveal a significant dichotomy which could be referred to sexual dimorphism. This might be due to the considerable size range within the species, to an absence of dimorphism in tooth size, or to the blurring effect of other sources of variance. We are, therefore, compelled to make estimates of sex ratios based upon comparisons with tragulids, cervids, and antelopes of roughly similar size and habits.

Analysis of Data

The graph by stages reveals a highly anomalous situation: 60 per cent of the individuals in Collection 32, and 76 per cent of those from Sioux County and from the better documented collection 26, died in early maturity. The small number of infants and juveniles usual to fossil collections is balanced by an equally small number of individuals dying in middle age to old age. The mortality graph is almost perfectly inverse to what a mortality graph in a stable, natural population should be. Since these specimens were not subject to transportation before burial, they represent perthotaxic assemblages

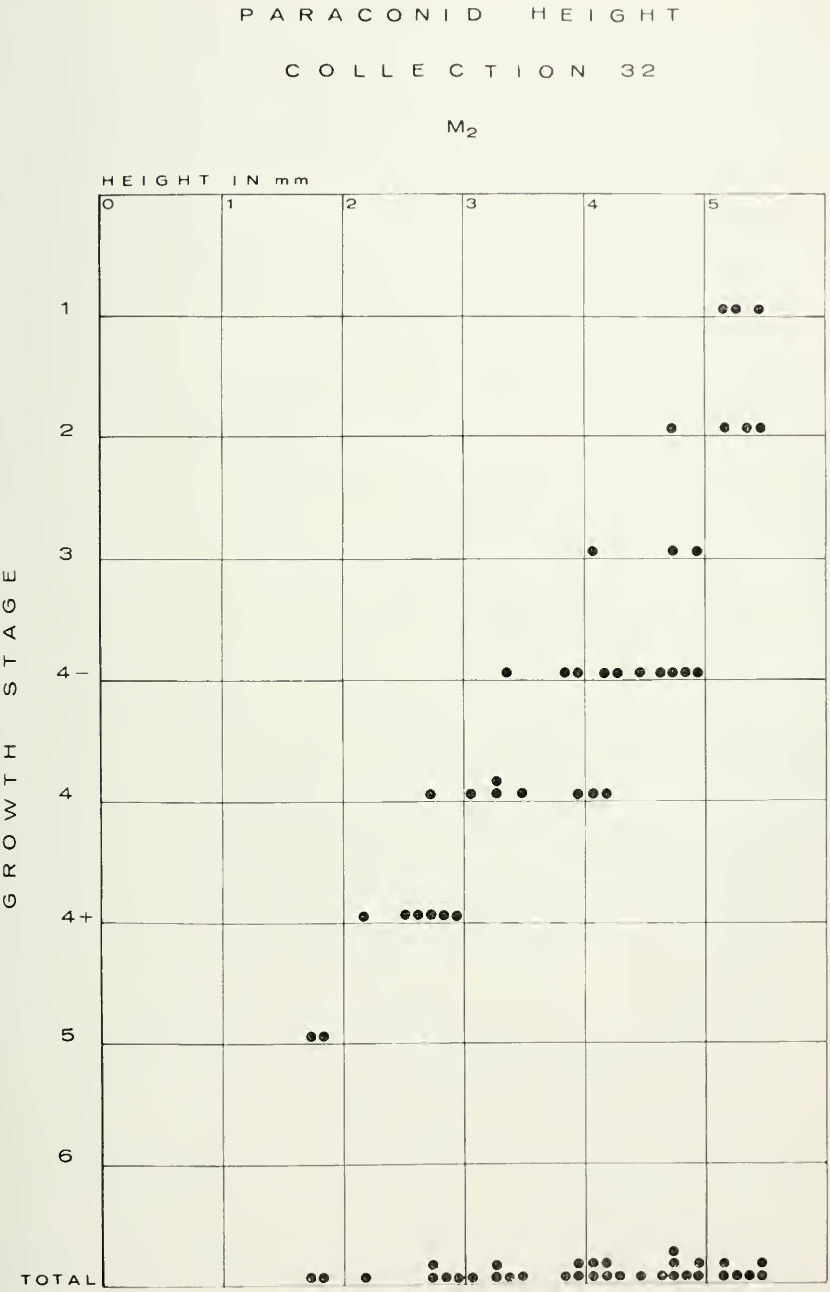

FIG. 6. Collection 32: paraconid height M_2.

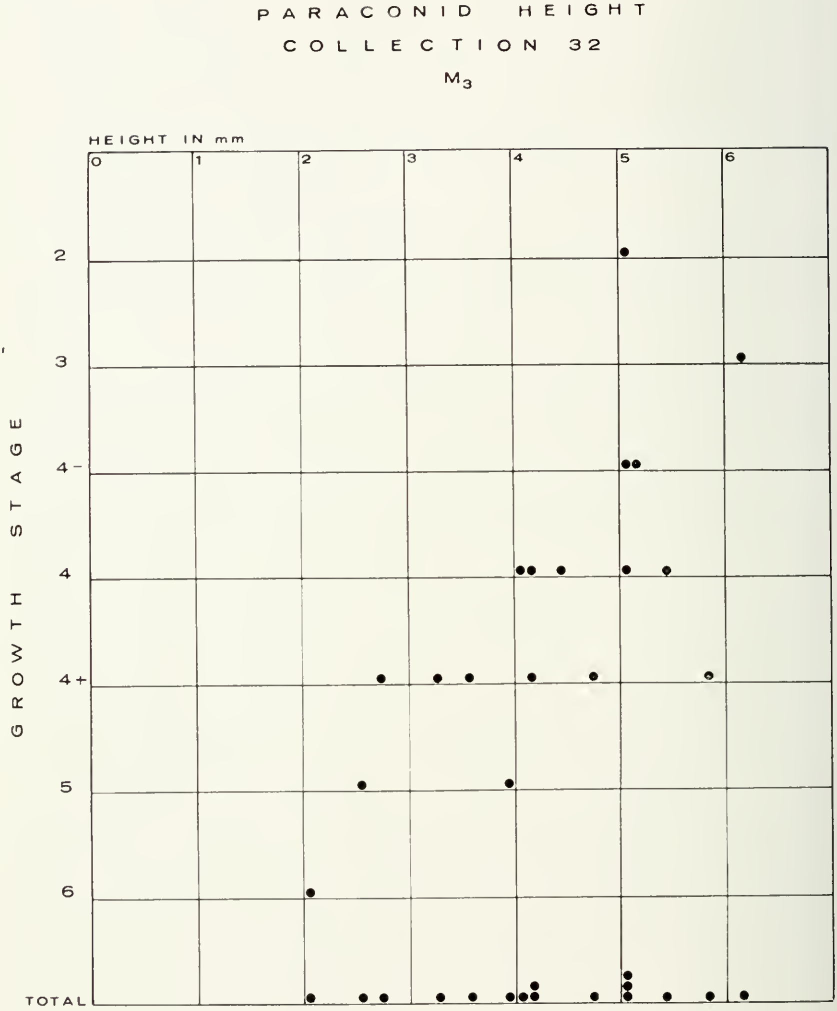

FIG. 7. Collection 32: paraconid height, M_3.

(Clark *et al.*, 1967, pp. 117–118). The factors influencing these populations, therefore, must be biotic, thanatic, or perthotaxic, or some interaction of the three.

Figures 8 and 13 demonstrate that even simple measurements of tooth height support the conclusion of high young-adult mortality. Since the height of unworn M_1 paraconids is ± 5.0 mm. and wear to 0.0 is demonstrable, 2.5 mm. constitutes the purely arithmetic midpoint of wear, or approximately of the animal's life. Fifty-five specimens of the Nebraska collection have paraconids more than 2.5 mm. long, and 23 have shorter, for a 71.8 per cent young-adult mortality. In the two South Dakota collections combined the figures are 43 of 58, for a 74.1 per cent young-adult mortality.

Whether one uses as a standard wear stage, or overall height of tooth, or interpretation of age in years, the results are the same; between two-thirds and three-quarters of these animals died before middle age.

These specimens comprise perthotaxic assemblages at three places, one more than 100 miles from the other two. The two neighboring ones therefore represent all individuals who died within a two to three month period scattered over a 30-acre swampy area and a 20-acre grassy savannah, respectively. The Nebraska collection represents individuals who died on a grassy to forested savannah over an area of several square miles. It is, therefore, reasonable to presume that these are fair samples of the death assemblages of their respective districts for the times of year represented, not merely a single mass mortality at a particular place. The close correspondence of the three collections increases the probability that they represent a general situation rather than a local one.

Let us consider what inferences may be drawn regarding the life history of *Leptomeryx* relative to thanatic and perthotaxic factors. First, *Leptomeryx* probably attained full adult size, represented by stage 4 in the graph, within six to eight months of birth. Davis (1965) recorded that in *Tragulus javanicus* breeding maturity is attained at 4½ months and adult size at five months. In the much larger *Moschus*, "This deer attains puberty before it is 1 year old. Rut takes place in January and the young are born in June after a gestation of 160 days" (Asdell, 1964, p. 558). In *Rhynchotragus* "The females reach puberty at about six months" (Asdell, 1964, p. 616). The general growth pattern of small tragulines, cervids, and antelope seems to be attainment of adult size and of breeding maturity in about six to eight months.

Second, the period of gestation in *Leptomeryx* was probably 120–160 days. Davis (1965) gives 152–155 days as normal for *Tragulus; Rhynchotragus* is recorded at 170–174 days, and *Moschus* at 160 (Asdell, 1964, p. 558).

Third, *Leptomeryx* almost certainly had a definite annual life cycle, including a rutting season and a fawning or birth season. Davis records a most amazing life cycle for *Tragulus javanicus*, with copu-

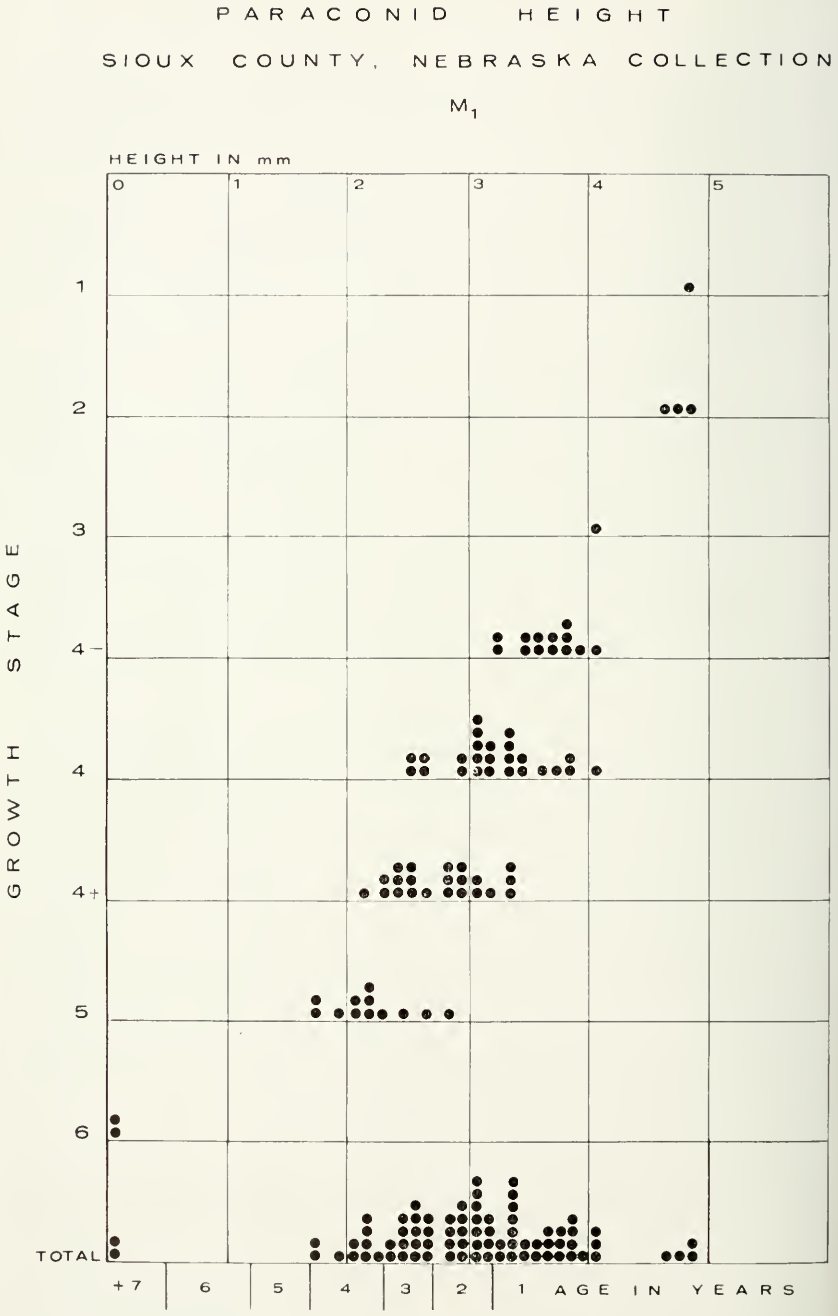

FIG. 8. Sioux County: paraconid height, M_1.

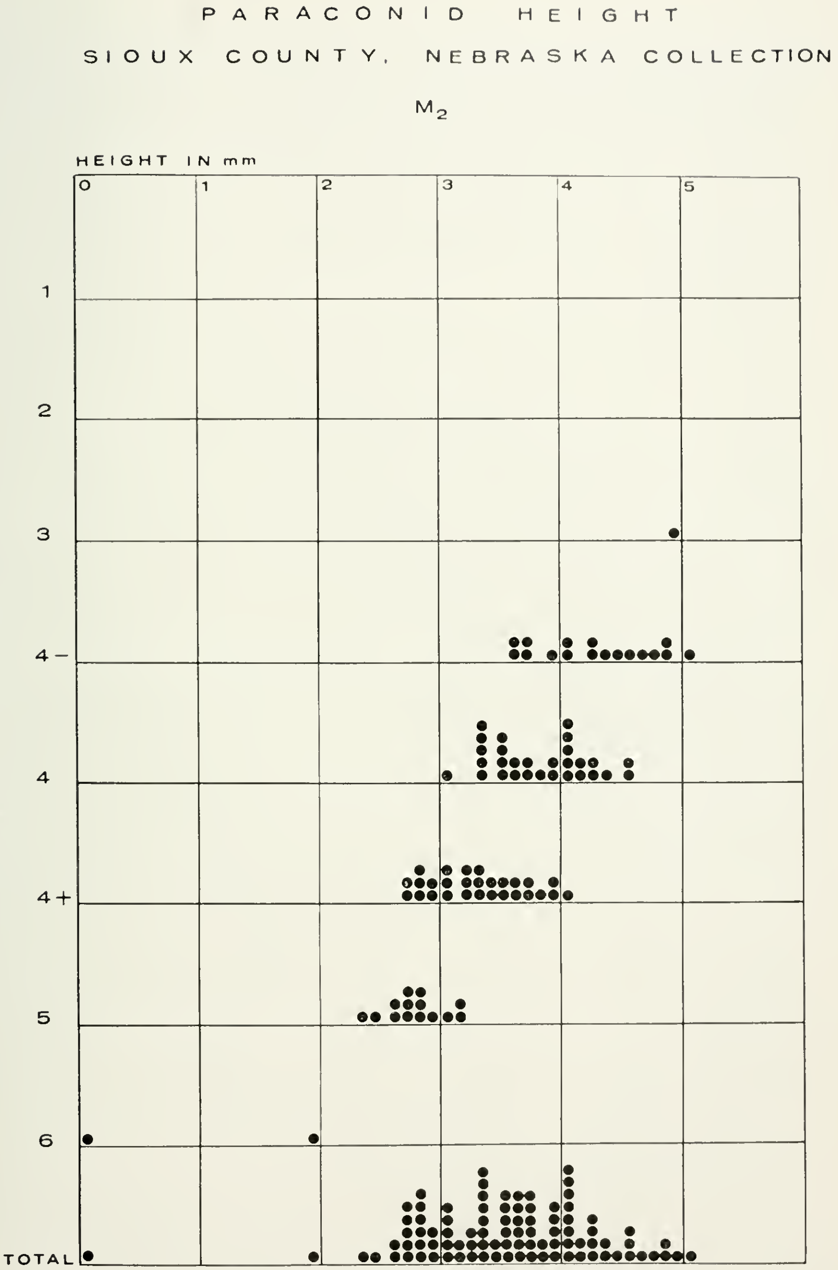

FIG. 9. Sioux County: paraconid height, M_2.

lation taking place within 48 hours of parturition. With a gestation period of 153 days and a growth period of $4\frac{1}{2}$–6 months, births of successive generations would be out of phase and might occur at any season. However, *Tragulus* is a tropical animal inhabiting regions of very low seasonal pressures upon its life. Cervids and antelopes in general have life cycles highly attuned to seasonal fluctuations in temperature or rainfall (Asdell, 1964, pp. 557–581; 607–619). The range of species without definite breeding seasons extends very little beyond the tropics.

Fourth, the probability is high that one young was produced at a birth, with only occasional twins. Davis found this true of *Tragulus javanicus*. Blanford (1891, p. 556) mentions that Tickell (p. 420) reported that the young of *T. meminna* are two in number. However, Phillips (1935, p. 346) says, "It has been stated that the female has two young at a birth, but I have never found more than one." All other references available to us make general statements, none of them suggesting definite experience on the author's part. Phillips' statement of actual observation seems the most valid; until further evidence is adduced, we regard *T. meminna* as also producing but one young at a birth. One young is also characteristic of *Moschus, Muntiacus, Blastocerus, Cephalophus, Sylvicapra,* and *Rhynchotragus,* plus many of the larger cervids and antelopes. It must be admitted that *Capreolus, Hydropotes,* and *Mazama,* among the smaller deer, customarily have twins or multiple births, but the heavier weight of evidence favors single births. The three last-named genera all consist of considerably larger animals than *Leptomeryx* and *Tragulus.*

Fifth, the life span in *Leptomeryx* was probably not over eight years. It is difficult to find estimates of the average life span of cervids not subject to hunting or other human modification, but Child and Wilson (1964) suggest that wear on M_1 of duikers with milk teeth not yet replaced indicates that the teeth are worn down rapidly in an area of sandy soils. Taber and Dasmann's (1957) survivorship curves show life spans of about 10 years for the much larger black-tailed deer, and 7 to 9 for the roe deer, but both of these are influenced by hunting and migration.

Internal evidence of the life span of *Leptomeryx* is not lacking, but depends upon interpretation of the rate of growth. Figures 3, 7, and 11 show that unworn M_1 paraconids (Stage 1) have a height of 4.8–5.1 mm. By the time M_3 has erupted and begun to wear, in stage 4-, the M_1 paraconid height averages about 3.7 mm. If, as postulated above, growth to adult size required not over six to eight months, then the difference in time represented by first use of M_1 and M_3 could not have been over six months. Projection of a wear of 1.1–1.2 mm. per six months would give a life span of about 2.5–three years until M_1 was worn absolutely to the roots. However, this is improbable: first, *Tragulus* is known to have a breeding life of more than three years (total span not recorded), and second, M_2 and M_3 would share the dental burden and thereby lessen the rate of adult attrition. Figure 13 bears this out: the average tooth heights seem to shift about 0.5 mm. in successive stages; the graph of total numbers also shows successive lows and highs on approximately 0.5 mm. modes. If we accept 0.5 mm. as an average annual rate of wear for M_1 during adult life, and 3.5–3.7 mm. as the average height of M_1 at the end of the first year of life, the two aged individuals with all enamel worn off must be seven to eight year-olds. These assignments to years reduce the probability that the abnormal young-adult death rate is an artifact produced by improperly-interpreted age stages.

Much of the spread in stage 4 is due to difference in overall size of individuals. Although we could not work out a quantitative ratio, we were unable to detect by inspection any proportional difference in stage due to size; a large individual would achieve successive stages about at the same rate as a smaller one. This is reflected on the M_1 graphs by the general parallelism of the upper and lower envelopes to the central trend lines, throughout stages 4 and 5.

Summarizing, *Leptomeryx* is postulated as an animal with seasonal breeding and fawning times, producing one young per birth with occasional twins. The period of gestation was probably 120–160 days. Full size was attained in six to eight months; the total life span was about eight years. As a corollary to these propositions, the young were produced, almost certainly, one per year per doe; taking into account decline of fertility with senility, the average doe certainly could not have produced over six live fawns during her lifetime.

Collating these assumptions regarding the life history of *Leptomeryx* with the paleoclimates of Middle Oligocene time (Clark *et al.*, 1967, pp. 72 and 97), explains the apparently minuscule infant-juvenile mortality.

The climate is described as temperate, with winters slightly too cool to permit habitation by alligators. The present wind system of prevailing westerlies was establishing itself. Presumably the summers were warm and dry, with showers somewhat more frequent than

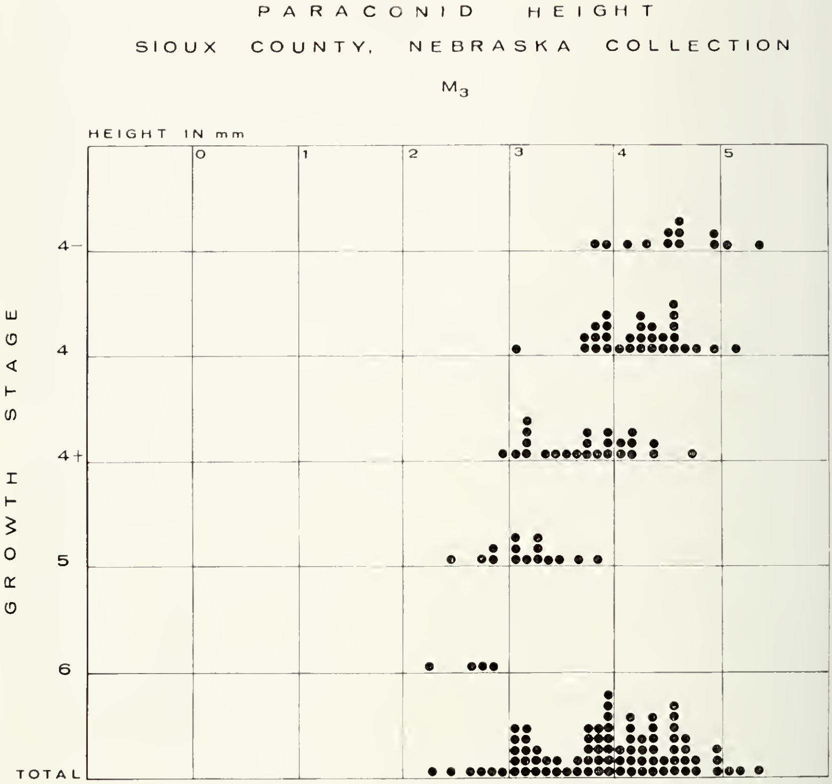

FIG. 10. Sioux County Collection: paraconid height, M_3.

at present; winters were frosty, with little or no snow; and the major rains occurred in November, February, or March; the year's crop of fawns reached full size by October, and bred in late October or early November. This is, of course, the approximate breeding cycle of most temperate-latitude cervids of small-to-medium size.

However, streams under a depositional regimen would, necessarily, flood during the major rainy season. Sedimentation, and hence burial, would occur when all of the year's normal crop of fawns were full grown, and before the next year's fawning season occurred. The only infants and juveniles available for death and burial would be the very few abnormally late or extremely early births. Voorhies (1969) suggested such a mechanism.

The junior author has experimented with bodies of adult muskrats, skunks, rabbits (*Sylvilagus*), and domestic cats in the area around Rockford, Illinois. He finds that in average dry woodland and forest border, summer perthotaxic processes completely remove the flesh of animals within three weeks, and destroy the bones in about three more weeks. The climate of Rockford is considerably drier than that of Virginia, where Payne (1965) studied perthotaxy in baby pigs, and the adult animals naturally have more resistant bones, but perthotaxy still progresses to destruction within six to seven weeks.

It is safe to presume, therefore, that any *Leptomeryx* who died before October would be completely destroyed before perthotaxy was halted by cold late in November. The collections represent a perthotaxic assemblage of animals who died after the onset of autumn, not a representation of an annual or longer incrementation of corpses. The proportion of infants and juveniles is low because the corpses resulting from juvenile mortality on the regular annual cohort were destroyed by perthotaxy before annual sedimentation occurred.

Even a cursory examination of Figure 1 reveals that the death rate among post-juveniles cannot possibly represent a normal mortality rate in a stable population. In a stable population, the life table of any one cohort yields the same statistics as a vertical sample of the whole population. A mortality rate of 76 per cent among young adults, who could not have produced an average of more than one young before death, added even to the minimal juvenile mortality of our biased sample, would result in extirpation of the population within about eight years. With the addition of a probable infant-juvenile mortality at least three times as great as the recorded one, the population would be extirpated much more quickly.

The collection of *Poebrotherium* recorded in Figure 1 probably does represent, by contrast, a normal mortality in a relatively stable population (except for the usual absence of juveniles). The young-adult and middle-age stages are low, with a large number of aged individuals. This graph, it may be noted, is almost the inverse of that of *Leptomeryx*. It further tends to validate the wear stages as accurately representing the age stages assigned to them.

Deevey (1947, p. 288) pointed out that vertical population samples such as this one have no statistical validity unless they represent samples of populations stable in time. In that case, the actual age distribution and the life table age distribution would be identical. Since these collections obviously do not represent mortality in a population stable in time, we must forego the usual statistical analyses and approach them from a basis of observation and cautious induction.

The possibility that this might be a natural, stable population, misinterpreted due to a misinterpretation of age stages, has been mentioned above but must be more carefully considered. Certainly there is justification for assuming that all animals up to and including stage 4– died in the first year of their lives. The amount of wear on M_1 during the time, less than six months, between stages 2 and 3 is much greater than the amount between stages 3 and 4– (see figs. 2, 5, 8), therefore, the interval between stages 3 and 4– cannot have been longer than six months. Using the Sioux County collection, and counting all individuals with wear equal to the maximum of stage 4 as yearlings, one arrives at 31 yearlings and under, from a total of 78 individuals. Accepting the natural breaks in the graph to demarcate years thereafter (fig. 8) gives 20 two-year olds, 15 three-year olds, 10 four-year olds, and two much older. Wear from the first through the fourth year apparently averages 0.5 mm. per year. By projection of this rate to the aged individuals with enamel completely worn off, seven or eight years is seen to be the life span of the most aged individuals represented.

Figure 13 shows that the South Dakota assemblage consisted of 30 yearlings, 11 two-year olds, six three-year olds, three four-year olds, six five-year olds, and two six-year olds.

Therefore, stages 4, 4+, and 5 very apparently do not include senile individuals. The stages have not been misinterpreted; we are forced to seek explanation for an abnormally high death rate in young adults. Conversely, since the South Dakota collections represent animals who died, and presumably lived, on the actual acres where their bones were collected, we are forced to explain a population with a minuscule proportion of middle-aged to senile individuals. This collection does not represent normal mortality in a stable population. It also does not represent catastrophic death, i.e., a life sample, in a stable population.

Figure 12 contrasts the survivorship curve of a relatively stable population of *Ovis dalli* (Deevey, 1947, p. 289) with those of the Nebraska and Dakota populations of *Leptomeryx*. Significantly, the average age in *Ovis dalli* is 7.06 years, almost exactly half of the 14-year life span. In *Leptomeryx* (Table 4), with a seven- to eight-year life span, the average age is 2.14–2.18 years. This is not merely a population with a high mortality of young adults; it is definitely a life population with a high number of young adults.

The similarity of the *Leptomeryx* growth-stage data to those reported by Child and Wilson (1964, p. 866) for duikers is striking and, we believe, significant. The duiker population had been heavily hunted for several years with a respite of 28 months preceding sampling. Child and Wilson collected a grab sample of 61 individuals, by shooting every one they saw within a restricted area during one week. Despite a very low number of infants, which they attribute to hunting problems in high grass, they found 45 individuals, or 74 per cent of their sample, under 22 months old. This would be the equivalent of our stages 1 through 4 (duiker first calve at 12 to 14 months) but probably not 4+.

Child and Wilson's data represent a catastrophe (hunting) producing a rough life sample of a population undergoing rapid growth following an earlier similar catastrophe (hunting for tse-tse fly control). The general pattern of the sample certainly corresponds with that of our samples of *Leptomeryx*. We suggest, therefore, that our collections represent a catastrophically slaughtered sample of a life population which was undergoing rapid expansion following a similar catastrophe a few years earlier. The Nebraska population presumably suffered its previous catastrophe five years earlier. With the Dakota collections the evidence is not so sharp, but any time from four to seven years previously is possible.

Biostratonomic evidence makes determination of the nature of these catastrophes possible by elimination.

First, the animals were not killed by flood. The bones are generally dissociated and partially destroyed by perthotaxy, showing clearly that the individuals died weeks or a few months before they were buried.

Kurtén's (1953, pp. 69–75) discussion of various factors leading to mass accumulations of fossils is of great interest here, but does not directly apply because our collections represent fossiliferous areas rather than mass accumulations. Kurtén does not always clearly separate mechanically-transported assemblages from herd assemblages, nor perthotaxic processes from taphic[1] ones. It is also possible that the rarity of fossilization in an environment subject to

---

[1] Taphic Factors—"Factors determining whether or not an animal's bones will be buried." Clark *et al.*, 1967, p. 155.

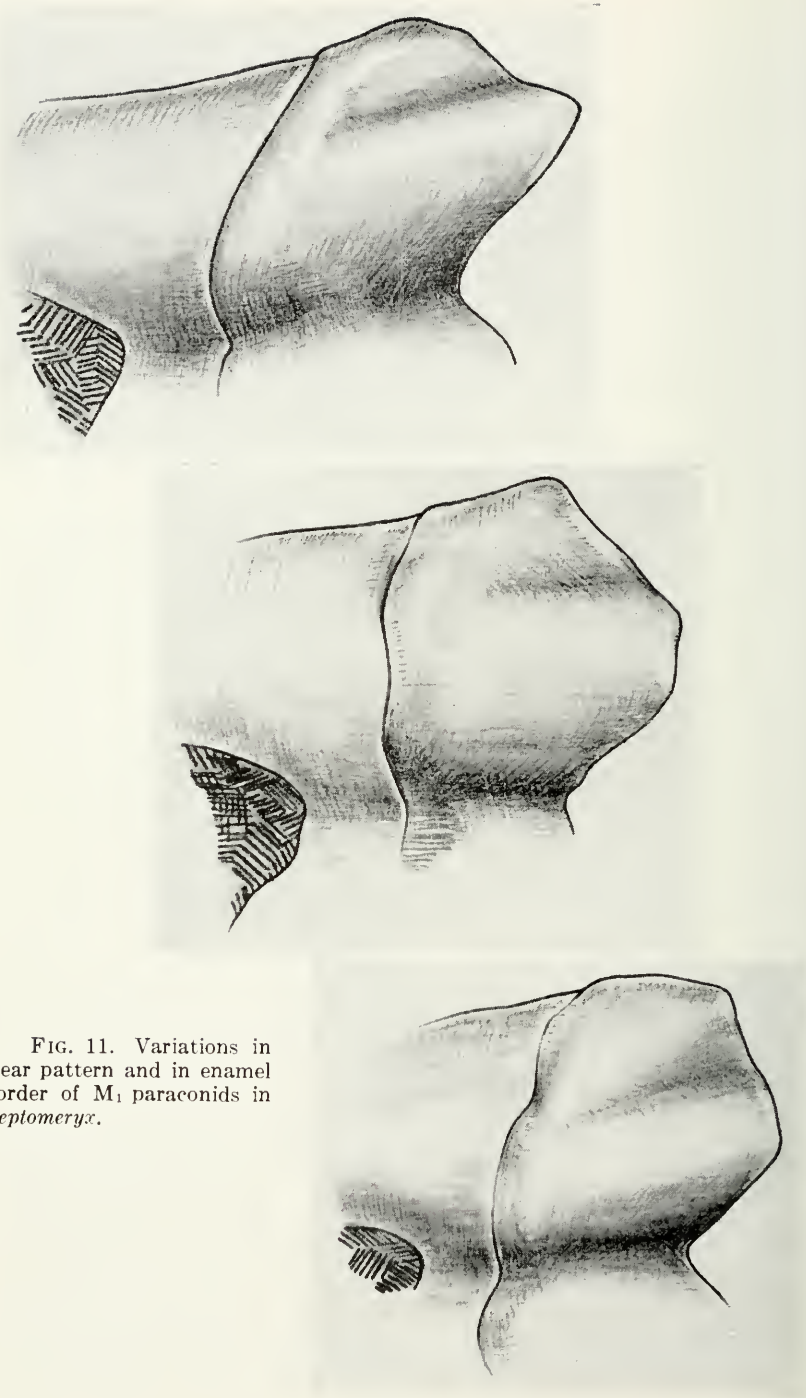

FIG. 11. Variations in wear pattern and in enamel border of M_1 paraconids in *Leptomeryx*.

successive depositional episodes may have been over-stressed, both by Kurtén and by his predecessors. In such environments, fossilization of bone which has survived perthotaxy may indeed be more nearly the rule than the exception.

Second, ash falls and dust storms were not the cause of death. There are no ash beds, loessic sediments, or indications of wind action within the sediments of the Lower Nodular zone. The specimens were buried by thin mudflows (Clark *et al.*, 1967, pp. 82, 113) passing over a surface presumably grass-covered. Wind-transported material in any quantity would certainly have accumulated on such a surface and been buried by the next mudflow.

Third, lightning-induced fire is so improbable an agent of death as to be almost impossible. The climate is believed to have resembled that of present eastern Nebraska, Kansas, and Oklahoma (save for warmer, rainier winters), where lightning-induced grass fires are unheard of. The sediments include no trace of the carbonized wood which should have been abundantly present on the surface, if a swampy savannah were burned over.

Fourth, drought is also extremely improbable as a cause of death. Both the Nebraska and the South Dakota populations lived within two miles of permanent, through-going streams. The Dakota streams had their sources in the Black Hills; the Nebraska stream originated in the Medicine Bow and other high ranges which presently nourish the North Platte. Periodic drying of two such stream systems is highly improbable. In the event of a severe drought, the vigorous, young-adult population of *Leptomeryx* would certainly have made its way to these streams.

Collection 26, from a swamp environment, gives added evidence that drought was not the cause of death. Ostracods, pond snails, fishes, and five individuals of the aquatic rhinoceros *Metamynodon* have been found associated. It is extremely unlikely that such a fauna would inhabit an ephemeral swamp. The sediments are both calcareous and stained with ferrous iron, showing clearly that no prolonged drying (and thus oxidation) occurred. Therefore, drought becomes improbable.

The well-known herd assemblage of over 20 skeletons of *Leptomeryx*, FM P12320, offers additional indirect evidence against drought as a cause of death. Field data give the locality as "lower Brule, Cain Creek, South Dakota," which of itself would not be helpful because Cain Creek is 20 miles long. However, the specimen is listed in series with a group of many, all coming from Chamberlain

Pass (SE-$\frac{1}{4}$ sec. 25, T3S, R 13E, Pennington Co., S. Dak.), between Bear Creek and Cain Creek, about $3\frac{1}{2}$ miles ESE of Scenic. This spot was a famous collecting locality during the early 20th century; it is one of very few fossiliferous localities within the Lower Nodular Zone of Cain Creek drainage. Brule stream No. 8 (Clark *et al.*, 1967, fig. 33) lies within 500 yards of the outermost limits of the fossiliferous area.

It is, therefore, reasonable to presume that this herd of *Leptomeryx* died within 500 yards of a major, through-going stream which almost certainly did not undergo periods of complete cessation of flow. The skeletons are in an early stage of perthotaxy, with only a few limbs disarticulated. Although they have not been prepared sufficiently to allow accurate determination, the height of the teeth suggests that most individuals are in stages 4− or 4, with a few 4+ and one 5. We have here a herd essentially of yearlings and two-year olds which died, quickly and peacefully, within easy reach of a major stream, and lay exposed for a short time before burial.

Animals dying of drought usually jam themselves into a desperate heap actually within the drying mudholes. Representatives of all of the local species occupying the area congregate at such places (personal observation). Monospecific herds such as the one described, or the three known herd assemblages of *Hypertragulus,* actually constitute strong evidence against rather than for drought as a cause of death. Kurtén (1953, p. 72) has clearly expounded this.

Neither predation nor intraspecific strife could possibly be responsible for the deaths of such herd assemblages. Either could have caused some of the deaths at Sage Creek and Sioux County. However, predation selection of young adults at a catastrophic level is practically impossible: this age group would be best equipped to escape predators. Genocidal intraspecific strife, especially among hornless cervids with inadequate canine teeth, is almost equally impossible.

The one remaining cause of death, epidemic disease, perfectly fits the evidence, and becomes almost the inevitable explanation by default of all others. Repetition of the epidemics every few years would be a normal phenomenon, and would explain both the catastrophic death recorded and the general youth of the population. It would also make any such computations as life expectancy, deviation from average age, or any more complex figures, completely meaningless; for this reason we have in Table 4 constructed only those portions of

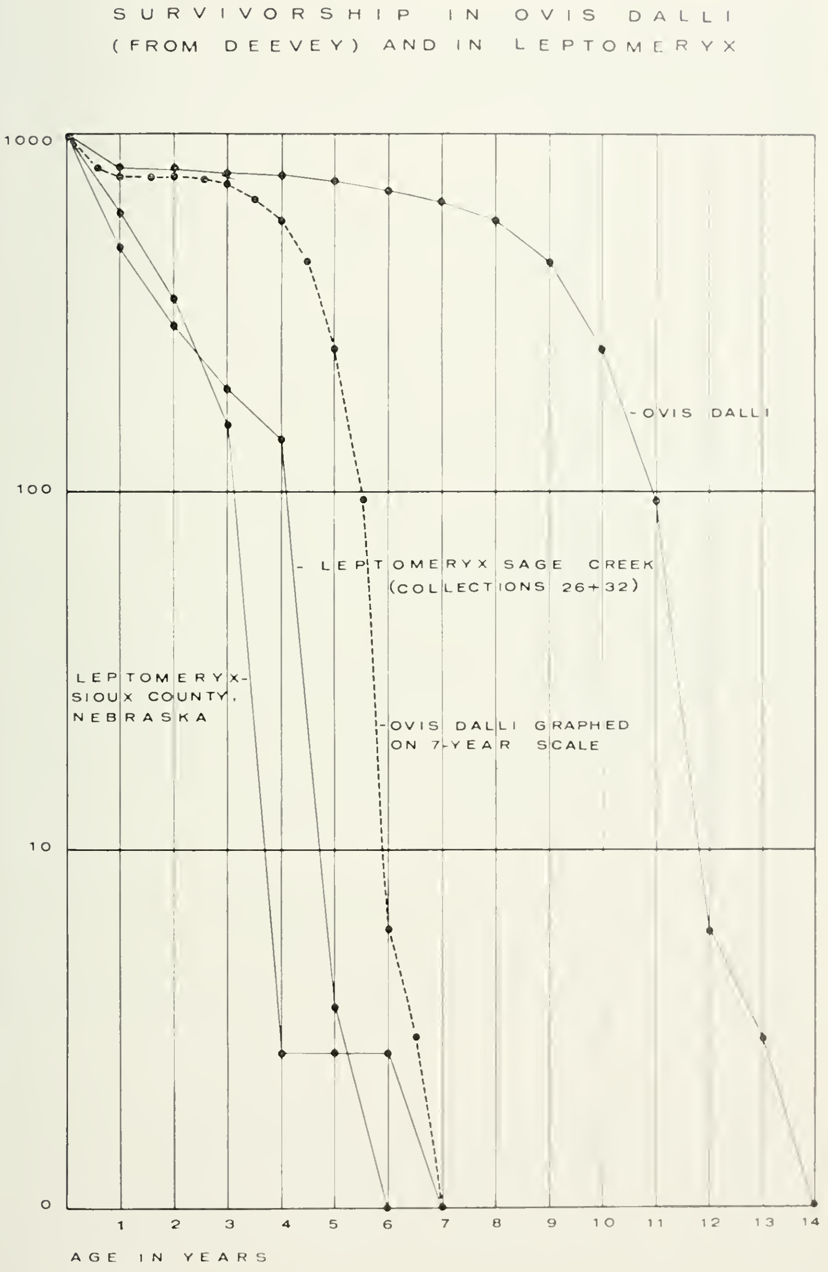

FIG. 12. Survivorship in *Ovis dalli* (from Deevey) and in *Leptomeryx*.

the life tables which the data justify. It is of interest in this connection to note that the average age, 2.16 years, probably is not represented by any individual in the collection. If fawning time was in March, and time of death in late autumn, practically all of these individuals would be ± 0.6, or 1.6, or 2.6 years old, and so forth.

We therefore conclude that the collections of *Leptomeryx* studied represent populations killed by an epidemic disease, and that epidemics recurred at intervals considerably shorter than the life span of *Leptomeryx*. The cause of the disease and its mode of transmission are unknown. Presuming that the cause of death in the herd assemblage is the same as that in the collections, the herd assemblage testifies that it must have been highly contagious and run a very rapid, debilitating, fatal course, and that death was not attended by delirium or convulsions. A slower course would have allowed the less weakened individuals to wander away from those already incapacitated. Convulsive death would have thrown the animals out of the comfortable, resting positions in which most of them lie.

Clark *et al.* (1967, p. 128) have already indicated that the same general situation of a high percentage of young adults occurs in *Hypertragulus calcaratus*, from the same horizon and localities. Two herd assemblages of *Hypertragulus* also exhibit the phenomenon of 20 to 30 young adults lying in moderately close proximity to each other and in comfortable poses. One might presume that the same disease which affected *Leptomeryx* also struck its smaller relative. The much more distantly related *Poebrotherium*, on the other hand, apparently was not affected.

Presence of the same death rate in herds and non-herd collections of two genera which, though not closely related, are closer to each other than to other members of the community, increases the probability of disease as the cause of death. It also decreases somewhat the probability of such disturbing factors as age-specific disease or herds of selected age, which are much less likely to occur in two genera than in one.

Speculation regarding the nature of the disease is almost pure guesswork. One might suppose that transmission was probably not by insects or ectoparasites, since such diseases are more usually pandemic than epidemic. By consideration of usual modes of transmission, rate of development, and high mortality, one might also suppose that the disease was more probably viral or bacterial than epizootic or fungal. Further pursuit of this line of supposition seems utterly futile.

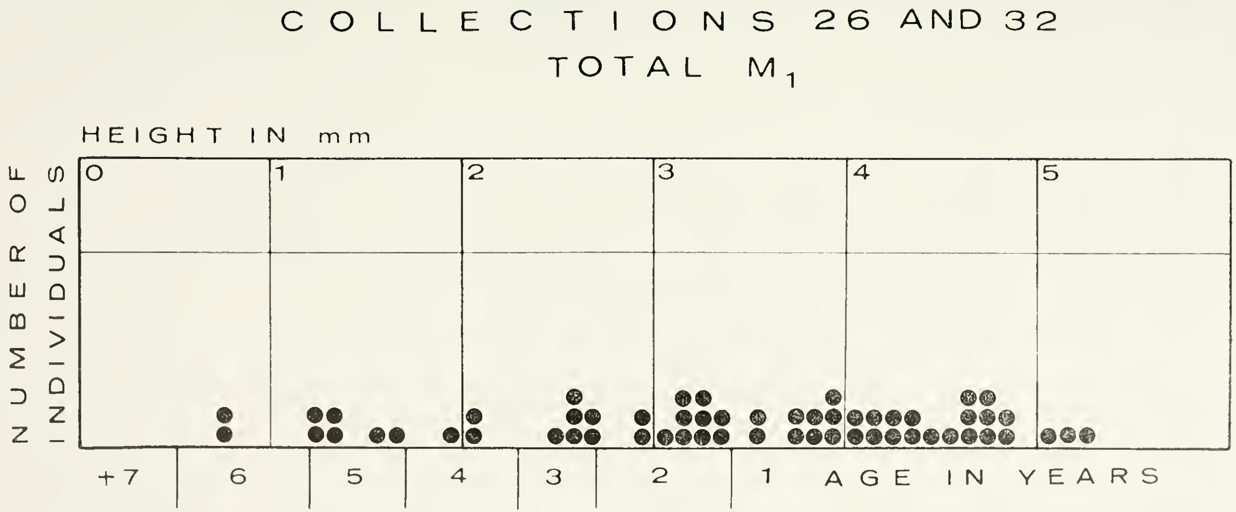

FIG. 13. Paraconid height and age in years, collections 26 plus 32.

In summary, direct evidence indicates that *Leptomeryx* populations pulsated violently in response to highly lethal epidemics which struck every four to six years. The disease, whatever its nature, was debilitating, rapidly fatal, and not attended by terminal convulsions. The total life span of *Leptomeryx* was seven to eight years, but due to the epidemics very few individuals lived out their lives.

Wear on lower molars was approximately 0.5 mm. per year after the first year during which M_1 lost 1.0 mm. of its height.

Indirect evidence suggests that *Leptomeryx* had an annual cycle of spring fawning, six months' growth to maturity, a late autumn breeding and a 120–160-day gestation period. Probably only one young was produced per birth, and the average doe could not have produced more than five or six young during her lifetime.

The graphs of paraconid height in M_2 and M_3 (figs. 3, 4, 6, 7, 9, 10) reveal the same general rate of molar attrition relative to growth stage as that shown by M_1. The slope of the median line through each closely parallels the slope of the median line in the graphs of M_1.

Detailed analysis of these graphs must await final curating of the extensive collections from the Sage Creek locality. It is hoped that this will make available enough specimens including all three molars on one jaw to yield statistically significant samples without inclusion of isolated teeth. Variations in the relationship of tooth height to enamel pattern can then be studied in detail. At present, such studies would be premature.

General Conclusions

This study presents an hypothesis which offers an internally consistent explanation for a surprising age distribution in three collections. It does not by any means achieve proof, or even demonstration to a high degree of probability. To quote Kurtén (1953, p. 85) "the calculations leading to this datum are riddled with subjective assumptions."

We do not actually know, for example, the life span, period of gestation, number of young per birth, duration of juvenility, proportion of males to females in the adult population, actual seasonality of either the life cycle or the weather, or the relationship of these two cycles to each other. The graphs of mortality and tooth wear relative to growth stage are highly suggestive, but the samples are too small to give a reasonable degree of confidence in the age determinations.

However, paleoecologic literature reveals a growing number of studies based upon data less satisfactory and assumptions fully as subjective. This paper demonstrates the necessity for differentiation between:

1. Mass death caused by a catastrophic agent of deposition, as at Pompeii. This yields a virtual life census.

2. Mass death caused by catastrophe not related to deposition, producing a dilated perthotaxy, such as the herd assemblage of *Leptomeryx*. The life census killed will have been modified by perthotaxy.

3. Perthotaxic assemblages developed from normal mortality in continuing populations. Accuracy of representation of mortality depends upon timing and frequency of depositional episodes interacting with differential perthotaxy.

4. Mechanically transported assemblages.

The last of these is absolutely unsuited for census studies or studies of population dynamics, unless it can be demonstrated that the transporting medium has taken a single, contemporaneous death or perthotaxic assemblage and has carried it without selective abrasion or selective transport. Both of these requirements constitute almost impossible situations. Mechanically transported samples, therefore, are strongly but unpredictably biased samples of unknown universes or combinations of universes. Each quarry assemblage constitutes a unique sample of a separate universe of unknown size. The combination of bias, uniqueness of sample, and unknown size of universe makes statistical analysis indefensible. Since many analyses of fossil mammal collections have been made upon just such samples, let us consider certain of the weakness inherent in even the more carefully reasoned ones.

Shotwell's (1958) method of arriving at a distinction between "animals living together in a community from those also appearing in the site but representing other communities" makes four basic assumptions which are stated.

"1. Reasonably large collections from quarry assemblages are a random sample of what is present in the quarry providing all specimens are retained from the volume of sediment worked." This assumption contains the subjective element of what constitutes a "reasonably large" collection, plus a very much more serious error in understanding of sedimentation. A quarry assemblage such as Shotwell envisages is usually a lens-shaped accumulation of assorted sizes and shapes of disarticulated bone in a sandstone matrix. Depending upon local situations and sizes of bone, there may be placering out of smaller bones in the lee of larger ones, concentrations of larger bones at the upcurrent side of the deposit, size separation near the edges of the lens, separation of partially flesh-covered bone from bone dry before transportation, and many other sedimentary situations precluding a random distribution of elements from animals of different sizes throughout the lens. No one portion of this non-randomly assembled mass can give a random or a representative sample of the whole; collection of the whole is necessary.

"2. An indication of the relative density of mammals of the proximal community may be obtained from the use of the minimum number of individuals." This depends, naturally, upon three non-random variables. (a) The depth and velocity of the transporting currents may be such that all elements above a certain size and shape are left relict in the area from which bones are being washed, and all elements below a certain size are transported on through the particular site later quarried. (b) Differences in shape between the same element in different taxa strongly influence distance of transport. Among Oligocene bones, for example, the astragulus of a *Mesohippus* would roll much farther than the more angulated astragulus of a *Dinictis* of the same size. (c) Sullegic[1] and trephic[2] factors militate in favor of identification of bones belonging to monospecific genera or monogeneric families, in any collection.

"3. If a community other than the proximal one is represented in a quarry sample, that community must be present in the region of the quarry." This, accepting the subjective decision of what constitutes a region, depends upon the well-established fact that water transport destroys bone in distances never over a few miles. It is generally true, with only the unusual exception of flotation of gas-inflated corpses.

"4. Mammals whose community in life was close to the site of deposition will be more completely represented than will those whose community was farther away." This depends upon the assumption that all areas of a stream or beach system are equally subject to erosion of equal power. Consider, for instance, a river-bank flood-plain community immediately upstream of a large tributary whose current is bringing in numerous bones from an erosional area five miles away. A bar at the confluence would receive most of its bones

---

[1] Sullegic—Those factors influencing the collecting of fossils which determine whether or not any particular fossil at the surface will find its way into a collection.

[2] Trephic—Factors incident to curating and identifying a specimen which determine whether or not a fossil in a collection becomes available for use—Both footnotes [1] and [2] in Clark *et al.*, 1967, pp. 118–120.

from the tributary; only those single bones which adventitiously fell into the main stream would represent individuals of the proximal community. Since every site of erosion and of deposition is a configurational rather than an imminent phenomenon (Simpson, 1963, p. 24), and since every quarry site must be interpreted in terms of its individuality, this fourth assumption becomes untenable.

Shotwell's method also necessitates two other basic assumptions, implicit but unexpressed: (a) that a quarry assemblage is always a transported assemblage. This is usually but not universally true; (b) that all elements of skeleton and dentition will respond equally to abrasion and will be transported equal distances in the same current. Thus one sees in his table (p. 273) rabbit molars equated with proboscidean skulls, and an equid astragulus equated with its pelvis. Voorhies (1969, appendix) presents careful experimental evidence of extreme differences in rate and mode of transport. To anyone possessed of knowledge of stream transportation, Voorhies' evidence belabors the obvious: Shotwell's basic assumption is mechanically unsound. Since his population analyses are based upon purely mechanical assemblages of clastic objects which happen to be fossil bones, the analyses are equally unsound.

Van Valen (1964) carries this one step further by stating that "the species present in the matrix may not have been in the same proportions when alive. This could be due to differential destruction or transportation prior to burial, which will be ignored because it cannot be corrected for and because the faunas are balanced . . ." His statement: (1) overlooks the fact that Shotwell's purpose, no matter how much in error, was specifically to determine the difference between the proportionate abundance of species in the matrix and the proportions in life; (2) states that a major known bias shall be ignored because it cannot be evaluated. Surely this is peculiar mathematics—data known to be seriously inaccurate may be regarded as accurate, provided that the error cannot be evaluated; (3) states that the faunas are balanced—an impossible conclusion, since no census of any recent mammalian population has ever been taken for comparison.

The majority of paleoecologic analyses of recent years have been performed upon mechanically-transported assemblages no more reliable than the two cases cited above. It is to be hoped that realization of the considerable biases and subjective opinions necessarily involved in a study of even so definite a perthotaxic assemblage as ours will in the future engender distrust of transported assemblages before, rather than after, the fact of publication.

A second major conclusion of this paper is the necessity for detailed field observation by persons trained at sedimentation. Voorhies' (1969) excellent analysis bears witness to this. The contributions from study of the sediments to the present interpretation of population dynamics in *Leptomeryx* are obvious. Differentiation between the types of fossil assemblage suggested above depends upon study of field evidence. The seasonality of incrementation helps to determine the age distribution which will be preserved. Environment of deposition, *e.g.*, the swamp represented by Collection 26 of this report, inevitably influences any paleoecologic interpretation and can be determined only by field study. Use of the Nebraska collection in this report is justified solely, in our opinion, by its close correspondence with the Dakota collections. Otherwise, its inadequate field data fail to establish contemporaneity, and the purpose of collection militates against completeness of the sample.

A third major conclusion relates to infant-juvenile mortality. Kurtén's careful analysis (1953, pp. 83–87) seems to indicate a general rate of 55–81 per cent, with a suggested usual rate around 70 per cent. We believe that this is too high for mammals bearing generally single young, one per annum, with life spans under eight or nine years.

Over a period of years long enough to include both population explosions and minima, an average female must produce somewhat more than two individuals who survive to maturity, if the population is to continue. Assuming, as in the case of most cervid populations not subject to human predation, that the proportion of males and females is approximately 1 : 1, the amount above two young must equal the number who survive to maturity but do not themselves live enough longer to produce two young who live to maturity. Admittedly, the assumption of a 1 : 1 sex ratio is highly debatable.

Leptomeryx, if our presumptions are correct, had a life span of seven to eight years and a birth rate of one per year. A doe during a full life span could not have produced more than six fawns; due to still-births and occasional missed pregnancies, the actual maximum was probably between five and six. Seventy per cent of six is 4.2; that is, a doe producing the absolute maximum number of fawns would under this mortality rate have seen only 1.8 live to breeding maturity. This would not have maintained the population, even if the resulting fawns had all lived full life spans and themselves had produced the maximum possible number of young. Either one of our assumptions is wrong, or juvenile mortality was highly selective against males, or the juvenile mortality rate was much less than 70 per cent. On entirely subjective grounds, it seems most probable that *Leptomeryx* underwent a smaller juvenile mortality.

The very fact of numerous, large litters is usually equated with a high infant-juvenile mortality. Conversely, single births and short life span must equate with lower juvenile mortality. Were it not for this, *Leptomeryx* producing at most six young per doe could not possibly have maintained populations stable relative to such animals as *Eumys* and *Paleolagus,* in which a female of full but shorter life span probably produced 30 to 50 young.

As a fourth major conclusion, probably very few fossil assemblages represent pure life-samples, pure samples of catastrophic death, or pure samples of normal mortality in relatively stable populations.

Let us accept, for the moment, our hypothesis of catastrophic death due to epidemic in the case of *Leptomeryx.* Assuredly the sample includes also those individuals dying under conditions of normal mortality. The sample is therefore a life census population taken by catastrophe, plus a normal death population, and no one system of statistics is directly applicable. Any one collection will be weighted toward a mortality sample or a life census by the interaction of the size of the total life population, the virulence of the epidemics or other catastrophes, the rate of natural mortality, the nature and rate of perthotaxy, and the timing and nature of incrementation of sediment.

Finally, this study seems to demonstrate the necessity for developing and maintaining multiple hypotheses. Clark *et al.* (1967, p. 128) proposed as a reason for the high number of young-adult deaths in *Hypertragulus* the action of an age-specific epidemic. A second alternative explanation might be either a seasonal immigration to the areas of sedimentation by young adults, or an emigration by all others.

The combination of perthotaxy removing infant and juvenile corpses, plus repeated general epidemics producing a young-adult population and catastrophically sampling it, seems more probable than an age-specific epidemic striking two genera. However, this does not at all remove the possibility of age-specific epidemics.

The herd deaths seem to us conclusive evidence of death by epidemic. Once again, however, this does not remove the possibility that large herds of older individuals were either dying of the same disease or surviving without it in areas other than the sites of deposition.

Finally, the possibility that x, the factor one has overlooked or misinterpreted, leads inevitably to y, the hypothesis one has not even considered, should never be forgotten.

We have thus at least three possibilities in addition to the one preferred. Because choice between the four is based upon a subjective weighing of probabilities, we feel that none of the four can safely be entirely discarded. We believe that a factor which cannot be evaluated must never be ignored.

We wish to thank Professor J. R. Beerbower of McMaster University for critically reviewing the manuscript of this paper.

TABLE 1.—Paraconid Height

Collection: 26

Number	Teeth	Class	M_1	M_2	M_3
14068	P_4-M_1	1	4.8		
14074	LP_4,M_3	5−			
14130	P_4-M_3	4+	3.1	3.7	4.2
14132	LP_4-M_1	4	2.9		
14133	LM_{1-2}	6	1.3	2.5	2.5
14134	LM_{1-2}	4	2.9	3.7	
14135	LM_{1-2}	4−		4.9	
14136	RM_{2-3}	4		4.6	5.4
14146	RM_1	4	4.8		
14147	RM_1	4	3.0		
14148	RM_1	5			
14149	RM_1	4			
14150	RM_1	4			
14151	RM_1	1+	4.7		
14152	RM_1	4	3.9		
14153	RM_1	4	3.8		
14154	RM_1	4	4.7		
14155	RM_1	4			
14156	RM_1	4−			
14157	RM_1	5−	2.0		
14158	RM_1	4−	5.0		
14159	RM_1	4−	3.5		
14160	LM_1	4+			
14161	RM_2	4		3.2	
14162	RM_2	5		3.0	
14163	RM_2	6		2.5	
14164	RM_2	4+		3.9	
14165	RM_3	4+			3.9
14166	RM_3	4+			3.3
14167	RM_3	4+			4.0
14168	RM_3	4			3.3
14169	RM_3	5−			2.9

TABLE 1.—Paraconid Height

Collection: 26

Number	Teeth	Class	M$_1$	M$_2$	M$_3$
14170	RM$_3$	4+			
14171	RM$_3$	4+			
14176	P$_4$–M$_3$	5	1.2	2.6	
14180	LP$_4$–M$_1$	4	3.8		
14181	LM$_{1-2}$	3+	4.3		
14182	LM$_{1-2}$	4−	4.1	4.8	
14183	LM$_{1-2}$	4	3.9	4.0	
14184	LM$_{1-2}$	4+		3.4	
14185	LM$_{2-3}$	4		2.9	3.4
14186	LM$_{2-3}$	4			4.9
14187	LM$_{2-3}$	3		4.7	4.9
14193	LM$_1$	4	4.0		
14194	LM$_1$	4+	4.2		
14195	LM$_{1-2}$	6	1.5	2.2	
14196	LM$_1$	4			
14197	LM$_1$	4	4.2		
14198	LM$_1$	4	4.4		
14199	LM$_1$	4			
14200	LM$_1$	4−			
14201	LM$_1$	2−	4.7		
14202	LM$_1$	4	3.3		
14203	LM$_1$	3	4.3		
14204	LM$_2$	4		3.9	
14205	LM$_1$	4+			
14206	LM$_2$	4		5.2	
14207	LM$_2$	4		3.4	
14208	LM$_2$	4−			
14209	LM$_2$	4			
14210	LM$_2$	4		4.9	
14211	LM$_2$	4		4.5	
14212	LM$_3$	4			
14213	LM$_3$	4+			
14214	LM$_3$	4+			
14215	LM$_3$	4+			3.2
14216	LM$_3$	4−			
14217	LM$_3$	4−			5.4
14218	LM$_3$				3.7
14219	LM$_3$				
14220	LM$_3$	6−			
14221	LM$_3$	5			
14222	LM$_3$	4+			
14224	LM$_{1 \text{ or } 2}$	4			

TABLE 2.—Paraconid Height

Collection: 32

Number	Teeth	Class	M_1	M_2	M_3
14557	RM_{1-3}	4		4.6	5.0
14558	RM_{1-3}	5+		2.5	
14559	RP_4–M_3	4	3.2	3.9	4.1
14560	RP_4–M_3	5+	1.9	2.1	2.5
20287	RM_1	3+	4.6		
20288	RM_1	1	5.1		
20289	RM_1	4+	2.5		
20290	RM_1	4	3.1		
20291	RM_1	4+	2.6		
20292	RM_1	4+	2.5		
20293	RM_1	4			
20294	RM_1	1−			
20295	RM_1	4			
20296	RM_1	2−			
20297	RM_1	4+			
20298	LM_1	5+			
20299	LM_1	4−			
20300	LM_2	4		3.3	
20301	LM_1	4	3.9		
20302	LM_1	4			
20303	LM_1	4			
20304	LM_1	4	3.2		
20305	LM_1	4	4.5		
20306	LM_1	4	3.1		
20307	LM_1	3−	3.7		
20308	LM_1	1−	5.2		
20309	LM_1	4	4.2		
20310	LM_1	6			
20311	LM_1	4			
20312	LM_1	4−	2.4		
20313	LM_2	2−		5.2	
20314	LM_2	2		5.1	
20315	LM_2	2			
20316	LM_2	4		4.4	
20317	LM_2	3−			
20318	LM_2	3−		5.4	
20320	LM_2	5−		2.9	
20321	LM_2	4			
20322	LM_2	4−		3.2	
20323	RM_2	4−		4.0	
20324	RM_2	5−		2.6	
20325	RM_2	4		4.2	
20326	RM_2	4−		4.0	
20328	RM_2	3−		5.1	
20329	RM_2	4		4.8	
20330	RM_2	4−		4.7	
20331	RM_2	3−		5.3	
20332	RM_2	4−		3.4	
20333	RM_2	3−		4.7	
20334	RM_2	4		4.9	
20335	RM_2	4			
20336	RM_2	4			
20337	RM_2	4			
20338	RM_3	4			
20339	RM_3	4+			
20340	RM_3	4+			3.2
20341	RM_3	4−			

TABLE 2.—Paraconid Height

Collection: 32

Number	Teeth	Class	M_1	M_2	M_3
20342	RM_3	5−			
20343	RM_3	3+			
20344	RM_3	2+			
20345	RM_3	4+			4.1
20347	RM_3	4			4.0
20348	LM_3	4			5.4
20350	LM_3	4			4.4
20351	LM_3	3+			6.1
20352	LM_3	4+			
20353	LM_3	4+			5.8
20354	LM_3	5+			
20355	LM_2	4+			2.7
20356	LM_3	4+			3.7
20357	LM_3	5−			3.9
20358	LM_3	4+			3.5
20359	LM_3	5			
20360	LM_3	4+			
20361	LM_3	4−			
20362	LM_3	4−			5.1
20363	LM_3	4			
20364	LM_3	5−			
20374	RM_{1-2}	6		1.7	
20458	LM_{1-2}	4+		3.9	
20459	RP_4–M_2	5−	1.6	2.7	
20460	P_4 – M_2	4+	3.3	4.1	
20470	LDP_4–M_1	2−	4.6		
20471	RDP_4–M_1	2−	4.6		
20472	RM_1	4			
20473	RP_4–M_1	4	3.2		
20474	RP_4–M_1	3			
20475	RP_4–M_1	6	0.7		
20476	LP_4–M_1	5−			
20477	LP_4–M_1	5+			
20478	LP_4–M_1	4+	2.6		
20479	LM_{2-3}	6		1.7	
20480	LP_4–M_1	4+	2.5		
20481	LM_{1-3}	6			
20482	LM_{1-2}	4	3.7	4.7	
20483	LM_{1-3}	4−	4.1	4.9	5.0
20484	LM_{2-3}	6		1.3	1.8
20485	LM_{1-2}	4+		2.7	
20486	LM_{1-2}	4−	4.0		
20487	LP4–M_1	4			
20488	LM_{1-2}	4			
20489	RP_4–M_1	4			
20490	LM_{1-2}	2−		5.4	
20491	LM_{2-3}	3			
20492	LM_{2-3}	6			
20493	RM_{1-2}	5	2.0		
20494	LM_{1-2}	2+			
20495	RM_1	4	3.5	4.1	
20496	RM_1	2+	5.0		
20497	LM_{2-3}	6			2.0
20498	RM_{2-3}	5			
20499	RM_{2-3}	4+			4.5

Table 2.—Paraconid Height

Collection: 32

Number	Teeth	Class	M_1	M_2	M_3
20500	LM_{1-3}	4+			
20501	LM_{2-3}	4+			
20502	LM_{2-3}	4		3.8	
20503	LM_{2-3}			5.5	
20504	LM_{2-3}	5		2.8	

Table 3.—Paraconid Height

Collection: Sioux Co., Nebraska

Number	Teeth	Class	M_1	M_2	M_3
450	LM_{1-3}	5+	2.4	2.7	2.7
480	LP_3–M_3	5−		3.0	3.6
497	RP_3–M_3	4	3.0	3.6	3.9
498	LM_{2-3}	4		3.6	3.8
902	RP_3–M_1	4			
903	P_3–M_3	5	2.8	3.1	3.0
913	P_3 & M_{1-3}	4−	3.5	4.4	4.6
914	P_{2-3} & M_{2-3}	4+		3.3	4.3
915	P_3–M_1	4−	3.6		
916	P_3–M_3	4	3.3	3.4	4.7
917	P_3–M_3	4+	2.5	3.5	4.3
918	P_3–M_3	4+		3.4	3.7
924	M_{1-3}	4	2.5		
925	P_4–M_2	4−	4.0	4.8	
926	DP_4–M_1	1+	4.8		
928	M_{2-3}	4		4.5	4.1
929	DP_4–M_1	2−	4.8		
930	P_4–M_3	5	2.0	2.8	3.2
931	P_4–M_2	4+	2.8	3.5	
935	P_2–M_2	4+	2.4	2.7	
936	P_3–M_1	4	3.8		
938	P_3–M_3	4+	2.9	3.6	3.8
939	P_2–M_1	4+	2.5	2.7	3.1
940	P_2–M_1	5+	1.7		
942	RM_{2-3}	4−		3.7	4.1
943	LP_2–M_3	4+	3.1	3.8	4.0
944	LP_4–M_2	4	3.0	3.5	4.3
945	LM_{2-3}	4−		4.0	4.6
946	LDP_4–M_1	4+	2.3	3.2	
947	LP_3–M_3	2−	4.6		
987	LP_2–M_2	4+		3.2	
988	LP_2–M_3	4+	2.1	2.8	3.0
989	RP_2–M_3	4	2.6		3.7

TABLE 3.—Paraconid Height

Collection: Sioux Co., Nebraska

Number	Teeth	Class	M_1	M_2	M_3
990	RP_3–M_3	4−	3.9	3.9	4.5
991	RP_3–M_3	4	3.3	4.1	4.6
992	RP_3–M_3	4+	2.8	3.7	3.7
993	RP_3–M_3	4	2.9	3.5	3.0
994	RP_3–M_1	5−	2.6		
995	LP_3–M_3	5+	1.7	2.3	2.8
996	LP_3–M_3	6			2.2
997	LP_3–M_3	4	3.1	3.3	3.9
998	LP_3–M_3	4	3.0	3.0	3.8
999	LP_{2-3} & M_{1-3}	4−	3.8	4.4	4.7
1000	LP_3–M_2	4	3.3	3.9	4.5
1001	LP_3–M_1	4+	2.3		
1002	LP_3–M_1	4+	3.3		
1004	RDP_3–M_2	2	4.7		
1031	RP_1–M_3	4−	3.6	4.3	4.3
1032	RP_4–M_3	4+	3.0	3.6	3.9
1033	RP_4–M_3	4+	2.4	3.0	3.5
1034	RP_4–M_3	4+	3.3	3.9	4.2
1035	RP_4–M_3	4	3.1	4.0	4.4
1036	RP_4–M_3	4		4.0	4.3
1037	RP_4–M_3	4	4.0	4.3	4.5
1038	RP_4–M_3	4	3.1	3.7	4.1
1039	RDP_4–M_3	3−	4.0	4.9	
1040	RP_4–M_3	5−	2.1		3.3
1041	RP_4–M_3	4	3.7	3.8	4.3
1042	RM_{1-3}	4−	3.2	3.6	3.9
1043	RM_{1-3}	4−	3.2	5.0	5.3
1044	RM_{1-3}	4		3.6	3.7
1045	RM_{1-3}	4	3.4	4.1	4.2
1046	RM_{1-3}	4+	2.8	3.3	3.4
1047	RM_{1-3}	5+	2.0	2.4	2.4
1048	RM_{1-3}	4	3.0	3.5	3.9
1049	RM_{1-3}	4	3.4	3.7	3.8
1050	RM_{1-3}	4+	3.0	3.7	3.9
1051	RM_{1-3}	4	3.6	3.5	3.9
1052	RM_{1-3}	6			2.6
1053	RM_{1-3}	4−		4.5	4.9
1054	RM_{1-3}	4−	3.5	4.5	4.9
1055	RM_{1-3}	4	3.0	4.0	4.2
1056	RM_{1-3}	5+	1.9	2.8	3.2
1057	RM_{1-3}	5	2.2	2.7	3.1
1058	RP_4–M_2	4+	3.3	3.9	
1059	RP_4–M_3	4−	3.7	4.2	4.6
1060	RP_4–M_1	4−	3.8	4.8	
1061	RP_4–M_3	4−	3.7	4.0	4.5
1063	RM_{2-3}	4−		4.7	5.0
1064	RM_{2-3}	4		3.3	4.0
1065	RM_{2-3}	5−		3.1	3.2
1066	RM_{2-3}	4−		3.7	
1067	RM_{2-3}	4+		2.9	2.9
1068	RM_{2-3}	5		2.9	3.0
1069	RM_3	4+			4.2
1070	RM_3	4+			4.0
1071	RM_3	6			2.7

TABLE 3.—Paraconid Height

Collection: Sioux Co., Nebraska

Number	Teeth	Class	M_1	M_2	M_3
1072	RM_3	4+			3.9
1073	RM_3	4+			4.2
1074	LP_3–M_3	4−	6.1	4.2	
1075	LP_4–M_3	4	3.3	3.9	4.5
1076	LP_4–M_3	4+	2.9	3.0	3.1
1077	LP_4–M_3	4+	2.5	3.3	3.7
1078	LP_4–M_3	4+		2.9	3.1
1079	LP_4–M_3	5+	2.1	2.8	3.4
1080	LM_{1-3}	6		1.9	2.8
1081	LM_{1-3}	4+	2.5	2.8	3.1
1082	LM_{1-3}	4+	2.4	2.8	3.4
1083	LM_{1-3}	4		4.2	4.2
1084	LM_{1-2}	4		4.1	4.5
1085	LM_{1-3}	4+	2.9	3.2	3.6
1086	LM_{1-3}	4	2.6	3.3	3.8
1087	LM_{1-3}	5−		2.7	3.8
1088	LP_4–M_2	4	2.9	3.3	
1089	LP_3–M_1	4+	2.6	3.0	
1090	LP_4–M_2	4+		3.4	
1091	LM_{1-2}	5		2.6	2.8
1092	LM_{1-3}	4+	No measurements possible		
1093	LM_{1-2}	4		4.0	4.7
1094	LM_{2-3}	4		4.0	4.2
1095	LM_3	4			4.4
1406	P_3–M_1; M_3	4	3.8		5.1
1409	RP_2–M_3	5−	2.1	2.6	3.0
1425	RP_2–M_3	4−	3.8	4.6	4.9

TABLE 4.—Partial Life Table

Leptomeryx. Sioux County, Nebraska

Age	d_x	l_x	1000_{qx}
0–1	397	1000	397
1–2	256	603	425
2–3	192	347	553
3–4	128	155	826
4–5		27	0
5–6		27	0
6–7	2.6	27	1000

Average age 2.18 years.

Leptomeryx. Sage Creek—Coll. 32–26

Age	d_x	l_x	1000_{qx}
0–1	517	1000	517
1–2	189	483	392
2–3	103	294	350
3–4	51	191	267
4–5	103	140	736
5–6	37	37	1000

Average age 2.14 years.

REFERENCES

ASDELL, S. A.

1964. Patterns of mammalian reproduction. Cornell University Press, pp. 1–670.

BLANFORD, W. T.

1891. The fauna of British India. Part 6, Mammalia.

CHILD, GRAHAM AND WILSON, VIRGINIA

1964. Delayed effects of tsetse control hunting on a duiker population. J. Wildlife Mgt., **28**, no. 4, pp. 866–868.

CLARK, JOHN, BEERBOWER, J. R., AND KIETZKE, K. K.

1967. Oligocene sedimentation, stratigraphy, paleoecology, and paleoclimatology in the Big Badlands of South Dakota. Fieldiana: Geol. Mem., **5**, pp. 1–158.

DAVIS, J. A.

1965. A preliminary report on the reproductive behaviour of the small Malayan chevrotain, *Tragulus javanicus*, at the New York Zoo. Int. Zoo Yearbook, **5**, pp. 42–44.

DEEVEY, E. S., JR.

1947. Life tables for natural populations of animals. Quart. Rev. Biol., **22**, no. 4, pp. 283–314.

KURTÉN, BJORN

1953. On the variation and population dynamics of fossil and recent mammal populations. Acta Zool. Fennica, **76**, pp. 1–122.

PAYNE, J. E.

1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. Ecology, **46**, no. 5, pp. 592–602.

PHILLIPS, W. W. A.

1935. Manual of the mammals of Ceylon. Ceylon J. Sci.

SHOTWELL, J. A.

1958. Intercommunity relationships in Hemphillian (mid-Pliocene) mammals. Ecology, **39**, no. 2, pp. 271–281.

SIMPSON, G. G.

1963. Historical Science. *In* C. C. Albritton, Jr., ed., The Fabric of Geology, Addison-Wesley Publishing Co., Inc., Reading, Mass.

TABER, R. D. AND DASMANN, R. F.

1957. The dynamics of three natural populations of the deer *Odocoilus hemionus columbianus*. Ecology, **38**, no. 2, pp. 233–246.

TICKELL,

No date. Calcutta J. Nat. Hist., **1**, p. 420.

VAN VALEN, LEIGH

1964. Relative abundance of species in some mammalian faunas. Amer. Nat. **97**, no. 899, pp. 109–116.

VOORHIES, M. R.

1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Contr. Geol., Spec. Paper No. 1, Univ. Wyoming.