VARIATION OF THE BACULUM IN THE WOODRAT

NEOTOMA MICROPUS CANESCENS

by

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CHAPTER I

INTRODUCTION

The baculum (os penis, os priapi, os genitale) has long been considered a useful taxonomic character in the systematic studies of mammals (see Burt, 1960). However, because no careful analyses of large series of bacula have been made in the past, its worth as a taxonomic character in mammals has been dubious. Recent literature concerning the baculum may be categorized into two groups: (1) Anatomical descriptions and (2) very brief biometric analyses. The most detailed account of the baculum of North American mammals is by Burt (loc. cit.). He did not include the Chiroptera, but these have been adequately covered by Hamilton (1949). Friley (1949, 1951) and Elder (1951) have made use of the baculum in age determinations. Lidicker (1960) used both anatomical and biometric analyses of the baculum to determine superspecific groupings in Dipodomys. White's (1943) analysis of the taxonomy of chipmunks (Sciuridae) is based upon the anatomical relationships of the baculum. Hooper (1958, 1959, and 1960) and Hooper and Musser (1964) utilized both the hard and soft anatomy of the penis in a systematic reevaluation of the taxonomy of cricetid rodents.

The origin and development of the baculum was

discussed by Ruth (1934) for the laboratory rat, and Callery (1951), for the golden hamster. The bone was found to be heterotopic in type and of endoblastemal origin, the most simple type of bone growth.

Arguments against using the baculum as a taxonomic character are based upon the following reasons: (1) The baculum is an external character and, (2) it is too variable to make it useful in mammalian taxonomy. Each statement seems fallacious. The baculum is not externally oriented. Because of its location, the baculum is, in fact, less subject to those stresses of the external environment which act on externally oriented characters to express measurable variability. If anything, one would expect low variability and the tendency towards the preservation of more primitive characteristics in the baculum. That a morphological character is variable does not rule against its use. The importance lies in understanding the limits of variability with concomitant evaluation of the character in a population.

The purpose of this study was to analyze variation of bacula taken from two distant populations of the woodrat, Neotoma micropus canescens. Biometrical methods and comparative anatomical techniques were employed to analyze the nature and degree of variability within the populations and between them. Studies of

this nature are essentially lacking and should prove useful in establishing to what degree the baculum may be employed in mammalian systematics. A description of the male reproductive tract of N. m. canescens is included in this report.

CHAPTER II

MATERIALS AND METHODS

Sampling Technique and Locality Data

A total of 28 bacula were taken from specimens trapped 6.8 miles southeast of Kermit, Winkler County, Texas, from October, 1963 to January, 1964. 18 bacula were obtained from 36 specimens (18 males, 18 females) trapped on oil lease property 23 miles southwest of Gail, Borden County, Texas, from January to May, 1964. These two areas are approximately 200 miles apart. Both are included in the Mixed-grass Plains district of the Kansan biotic province as described by Blair (1949). The dominant mammalian fauna has been described by Davis (1960) and includes at least 59 species in 6 families.

Preparation of Specimens

Animals were captured in Victor 4-way rat traps baited with peanut butter and rolled oats. The specimens from Kermit were either preserved in a solution of 10% formalin or prepared as museum study skins according to methods outlined by Hall (1955). All specimens from Borden County were prepared as museum skins.

The bacula were removed from the penis by maceration

in 4% KOH (potassium hydroxide) and stained with Alazarin Red-S according to methods outlined by Baldauf (1960). Staining permitted more detailed observation of the characteristics and morphology of the bone. The bacula were examined under a binocular microscope at 10X. All illustrations of the bacula were drawn free hand. The male reproductive tract was dissected from a freshly killed animal and photographed during the dissection.

Age Categories

In order that accurate comparisons be made from field captured samples, age categories were constructed. These criteria were used in determining the categories:

(1) Adults: High degree of tooth wear; dentine lakes bordered by a band of enamel on occlusal surfaces of cusps; palatine not cancellous.

(2) Subadults: Little tooth wear; lakes not nearly as evident as in adults; palatine cancellous.

On the basis of these criteria, bacula were grouped into adult or subadult categories. Only adult bacula were used in statistical analyses unless otherwise stated.

Measurements

All measurements were taken with a single Helios dial caliper. These are given to the nearest tenth of a millimeter and include:

(1) Total length, the distance from the tip of the shaft, excluding the cartilaginous cap, to the proximal edge of the base.

(2) Width, the distance across the widest portion of the base.

(3) Depth, the dorsoventral distance measured at the thickest portion of the base.

Each measurement was taken three times on three alternate days in order to eliminate error. The average of the three was taken as the final reading. Body measurements, when given, are also in millimeters.

Statistical Methods

Statistical analyses were performed according to methods outlined by Arkin and Colton (1960) and Cazier and Bacon (1949). The Student's *t* test was run in order to compare the sample means. The Pearson coefficient of variability (CV) was also performed to take into account not only the sizes of the means but the variation of compared characters from the means in terms of standard deviations. The standard deviation then becomes expressed as a percentage of the mean.

These values give a clearer comparison of the variation of each sample (loc. cit.). Figures 1, 2, and 3 illustrate the means (horizontal lines), the observed ranges (vertical lines), two standard errors (small black boxes), and one standard deviation (large clear boxes) to either side of the mean. Figures 4, 5a, and 5b are scatter diagrams illustrating the correlation of length, width, and depth of the baculum with body length. Black circles indicate Kermit adults, white circles, Borden adults; black triangles, Kermit subadults, white triangles, Borden subadults. All age classes were used in this case.

Anatomical Study

Comparative anatomical studies of both samples were made. These samples were also compared with bacula taken from other species of *Neotoma* in the Texas Technological College Collection of Mammals and from drawings by Burt (1960). The following characteristics of the bone were studied and figured in plate II:

(1) Degree of development and variation of the base as interpreted by the presence of tuberosities, ridges, depressions and depth of paired posterolateral fossae.

(2) Length of the shaft, presence or absence of a keel and the character of the tip of the shaft.

(3) Presence or absence of an elongate, conical cartilaginous cap.

These characteristics are described in plates II and VII.

CHAPTER III

DATA AND RESULTS

Quantitative Variation

The statistical data are summarized in tables 1-5. The Kermit sample was broken down into 14 adult and 14 subadult specimens for study of ontogenetic variation. Little overlap in ranges of adult and subadult samples was observed for length measurements. Some overlap was observed for width and depth measurements between these samples. (see figures 1-3). High *t* values (see table 4) indicate that a biologically significant difference exists between the age categories. High coefficients of variability for the subadult group reflect the effect of age in testing the measurements of the samples (Simpson, *et al*, 1960). Further analysis of ontogenetic variation is given in figures 4, 5a, and 5b. Width and depth again appear most variable and length, the least, when compared with increasing body length. It appears that the length of the baculum increases with increase of body size. When the adult stage is reached, growth in length of the baculum diminishes considerably.

In comparing samples of the same age groups, variation was considerably lower. Overlap of ranges between samples was noted in all cases. Low *t* values

(table 5) indicated that no biologically significant difference existed between the two samples. Coefficients of variability for each measured character were also low. Length, width, and depth varied similarly, little difference existing between their respective magnitudes of variation. The high coefficient of variability for width and the overlap of width and depth in subadult and adult comparisons is due to the allometric growth of the base. This is discussed later. The measurements for all characters of the baculum are in full accord with those found by both Burt and Barkalow (1942) and Burt (1960), albeit their sample sizes were considerably smaller (2 and 5 respectively).

Anatomy of the Baculum

The baculum of *Neotoma micropus canescens* is drawn in three views in plate I. The morphological characteristics are described and labeled in plate II. The degree of ridging on the dorsal proximal edge of the base and the depth of the paired posterolateral fossae in the base were alike in bacula taken from each population. The base is moderately flared in comparison to other species of *Neotoma* (see plate III). It is slightly depressed in the dorsomedial aspect and highly concave ventrally, this concavity forming and inverted

"U" (see plates I and II). The paired posterolateral fossae are distinctly ovoid and deep. The base is not hollow. The shaft is slightly constricted at its attachment to the base. It is slightly compressed laterally, resulting in a rounded, dorsal keel. The tip is slightly curved to the dorsum and rounded to form a small knob. An elongate, conical cap of cartilage rests on the tip of the shaft and is frequently lost in the macerating process. It has not been reported by other workers. These anatomical features remained constant in the samples from Borden and Winkler Counties.

Anatomy of the Male Reproductive Tract

The reproductive tract from a male approaching breeding season is shown dissected from the body and labeled in plates IV and V and represented *in situ* in plate VI. The seminal vesicles were greatly distended with sperm and seminal fluid, appearing translucent and crowding the other organs posteriorly. Three sets of prostate glands (one dorsal, two ventrolateral) were present. These are situated dorsally to the bladder. The location of these glands is similar to that in the laboratory rat (*Rattus*: Muridae). The paired Cowper's or bulbourethral glands are located at the base of the penis and connect to the urethra

by short ducts.

The testes were partially descended through the inguinal canal (epididymal portion proceeding first) to the scrotum. They were highly vascularized and appeared bright pink.

Within the penis, the corpus cavernosum (vascular erectile tissue) ends at the proximal portion of the glans and is strongly attached to the base of the baculum (see plate VII). The baculum comprises the remainder of the support for the glans. It occupies the posterior two-thirds of the glans. During erection, the baculum is forced forwards by the corpus cavernosum to supply rigidity and added length to the glans. A cartilaginous cap protrudes beyond the tip of the glans and is enclosed in a thin layer of skin. The surface of the glans is evenly covered with spines. The nature of these spines and the systematic value of the soft tissues of the glans penis in general have been discussed by Hooper (1960) for this genus.

CHAPTER IV

DISCUSSION

Ontogenetic variation of the baculum occurs in size and, to a lesser degree, in shape. The anatomy of the baculum is distinctive at an early age. Variation in length decreases noticeably in the adult age categories. Width and depth of bacula were more variable in adults than length. Such allometric growth is expected. Constant deposition of bone occurs on the base throughout the life of the animal seemingly due to the stresses placed upon the base by the corpus cavernosum. This structure is anchored securely on the base, the major contact points being the dorsal proximal ridge and the posterolateral fossae (see plate VII). The morphology of the shaft is distinctive in subadult groups. Anatomically and biometrically, the shaft is the least variable component of the baculum.

Analyses of adult specimens show that no biologically significant difference exists between bacula taken from the Kermit and Borden populations. The degree of overlap in observed ranges (see figures 1, 2, and 3) for all adult characters and the low *t* values for these characters indicate that if similar samples were drawn at random, they could not be differentiated

by biometric analysis. Furthermore, low standard deviations as interpreted from the variances from the sample means would indicate concomitantly low variations from an expected mean, a clustering of values about the means and, therefore, very low variation in these characters within each population. The reasons for lack of variability in internal anatomical elements have been suggested by Anderson (1960, see also Hoffmeister, 1951, and Burt, 1960). External anatomical features tend to be more variable and greater difficulty is encountered in establishing the limits of their variation. Such anatomical elements may reflect more readily genetic responses of the organism to environmental changes through adaptation. Conversely, internal elements, such as the baculum and cranial features, may tend to retain more primitive characteristics. These would then be of greater value in determining phyletic trends.

The shaft of the baculum is the least variable component. Its length comprises more than one-half the total length of the bone and varies little in the adult stage. Few osseous deposits occur here during this period. The outlines of the base are consistent, both within and between the populations. From examination of all age groups, the characteristics of the base are formed at an early age. Nonetheless, these

characteristics of the base are more easily distinguished in adult animals. The "U"-shaped depression on the ventral surface of the base (see plates I and II) and a similarly shaped depression along the longitudinal axis of the ventral surface of the corpus cavernosum (see plate VII) allow for the passage of the urethra. Embryonically, the baculum originates as a solid osseous mass of endoblastemal origin, oriented dorsally to the urethra (Ruth, 1934, Callery, 1951). The base partially envelopes the urethra. Such an arrangment has not been noted in mammals other than woodrats.

The baculum of Neotoma micropus is easily distinguished from other species of woodrats. Comparisons of N. micropus with other species of Neotoma are given in plate III. In general appearance, the bacula of Neotoma somewhat resemble the bacula of microtine rodents. However, the bacula of Neotoma lack the complex digital ossifications at the tip of the shaft and the extremely broadened and complex base which are characteristics for the microtine rodents. Anderson's (1960) study of the bacula of microtine rodents, a more primitive group of rodents than the cricetines, revealed that a more complex baculum was a primitive character. This concept would be useful in the determination and clarification of phyletic trends, especially in cases where these trends in other characters

may have been masked by convergence (see also Blair, 1942, White, 1953, Rainey and Baker, 1955, and Hooper, 1959).

Burt and Barkalow (1942), on grouping species of Neotoma, place N. micropus intermediate between the albigula group and the floridana group on the basis of complexity of structure of the baculum. Burt retained this same grouping in his later monograph on bacula from North American mammals (1960). The major differences between these two groups are:

(1) N. floridana: Base highly sculptured, paired posterolateral fossae moderately oval, dorsum of base not depressed, width of base compared with length of shaft considerably greater than in either N. micropus or N. albigula; shaft straight, prominently constricted proximally, moderate dorsal keel.

(2) N. albigula: Base smooth, not depressed dorsally, posterolateral fossae shallow and circular, length of shaft compared with width of base considerably less than in N. floridana or N. micropus; shaft strongly curved dorsally with moderate keel and smooth tip.

The baculum of N. micropus was previously described. On the basis of Anderson's conclusions and the findings of other authors, the intermediate placement of

N. micropus on the basis of relative complexity is valid. Furthermore, the validity of these conclusions is enhanced by the non-variable nature of the adult bone as found in this study.

The anatomy of the male reproductive tract does not differ from that found in the laboratory rat (Davis and Golley, after Turner, 1960, and Grasse, 1959). The testes are retained in the abdominal cavity except during the winter months. During the breeding season, the scrota are prominent but never fully exposed. The adaptive significance of this is correlated with the proximity of the body to the ground. Although the adaptive significance of the baculum has never been stated, the structure appears to have evolved as a more efficient method of sperm deposition and perhaps, in conjunction with the cartilaginous cap and spiny structure of the glans, vaginal stimulation.

CHAPTER V

SUMMARY AND CONCLUSIONS

Variability is an inherent property of animal populations. The mere cognizance of this fact is not enough. It must be thoroughly analyzed as far as the scope of biological knowledge will permit in order to understand its meaning and value to these populations. The result of such study will enhance our understanding of the mechanisms which relate to the evolution of animals and, hence, a development of more accurate methods of taxonomy.

These statements summarize the findings of this study:

(1) There is no biologically significant difference between adult bacula taken from two distant populations of Neotoma micropus canescens.

(2) If similar, random samples were taken, the bacula could not be differentiated biometrically, thus it seems likely that the two populations are justifiably grouped into the same subspecies.

(3) Bacula taken from subadults showed a high degree of variability in measurements, and would not be useful in systematic evaluations.

(4) Anatomical details of the baculum are evident at an early age but are more clearly noted in adult specimens.

(5) In adult groups, the shaft is the least variabile component of the baculum, the base, the most variable. Variability of the base is due to continued deposition of bone resulting from the stresses caused by the attachment of the corpus cavernosum.

(6) Anatomically, no difference was noted between bacula taken from each population.

(7) In adult specimens, all characteristics of the baculum were surprisingly consistent in orientation and detail.

(8) Compared with bacula from other species of Neotoma, the bone of N. micropus is distinctive for this species.

(9) Low variability, in conjunction with consistent anatomical detail, point to the reliability of this structure as a character of taxonomic relevance in mammalian systematics. Phyletic analyses will be aided by the use of the baculum owing to its non-variable nature.

(10) The anatomy of the male reproductive tract does not differ markedly from that found in the laboratory rat.

(11) The baculum has evolved as an efficient method of sperm deposition. The cartilaginous cap and spine covered glans aid in vaginal stimulation.

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TABLE 1

Variant	Range	X	SD
length	4.1-5.8	4.8 ±.38	.77
width	1.3-2.5	2.0 ±.18	.37
depth	0.5-1.9	.87 ±.16	.35

Tabulated statistical data
for Kermit subadult sample

TABLE 2

Variant	Range	X	SD
length	6.0-8.1	6.8 ±.34	.61
width	1.7-3.6	3.1 ±.32	.51
depth	0.9-2.2	1.5 ±.04	.09

Tabulated statistical data
for Kermit adult sample

TABLE 3

Variant	Range	X	SD
length	5.9-7.8	6.8 ±.2	.50
width	2.3-3.5	2.7 ±.18	.40
depth	1.0-2.0	1.6 ±.02	.04

Tabulated statistical data
for Borden adult sample

TABLE 4

Variant	Subadult CV	Adult CV	t value
length	17.8	10.1	9.2
width	16.4	15.4	6.0
depth	6.0	4.2	7.0

Coefficients of variability and t values for Kermit subadult and adult samples

TABLE 5

Variant	Kermit CV	Borden CV	t value
length	10.1	8.0	1.01
width	15.4	14.3	1.35
depth	4.2	2.5	1.50

Coefficients of variability and t values for Kermit and Borden specimens

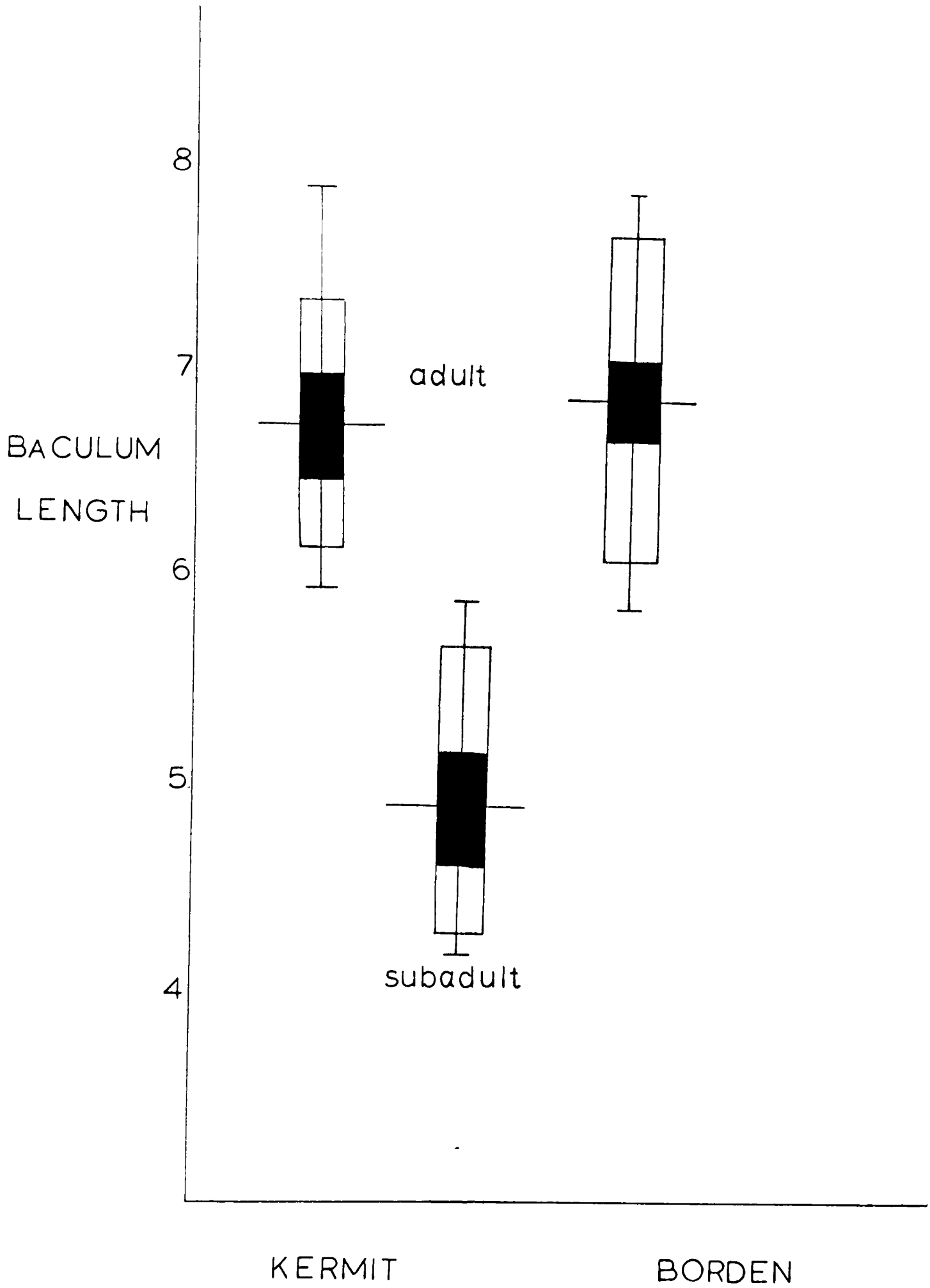


Figure 1. Compared variation of length

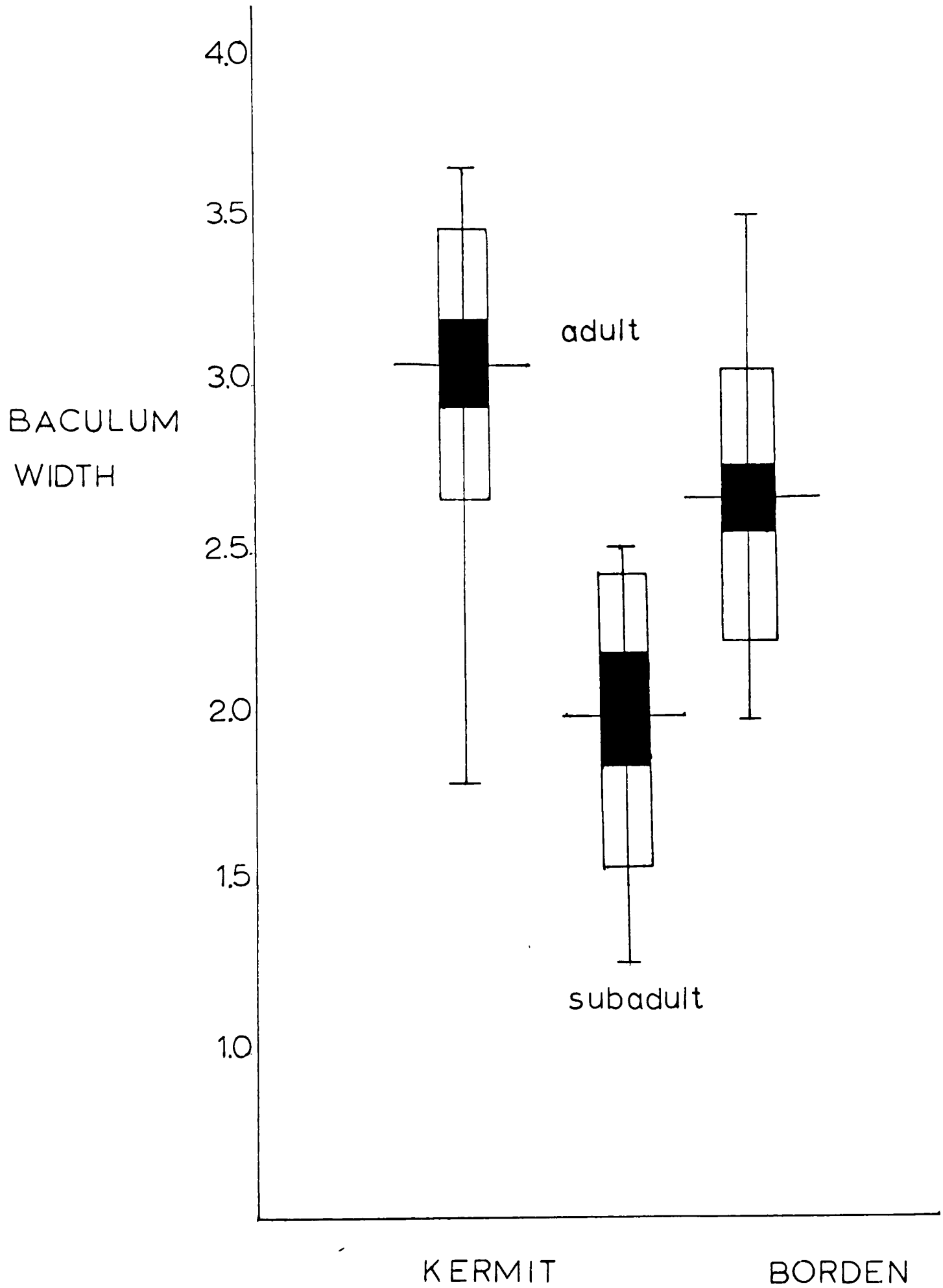


Figure 2. Compared variation of width

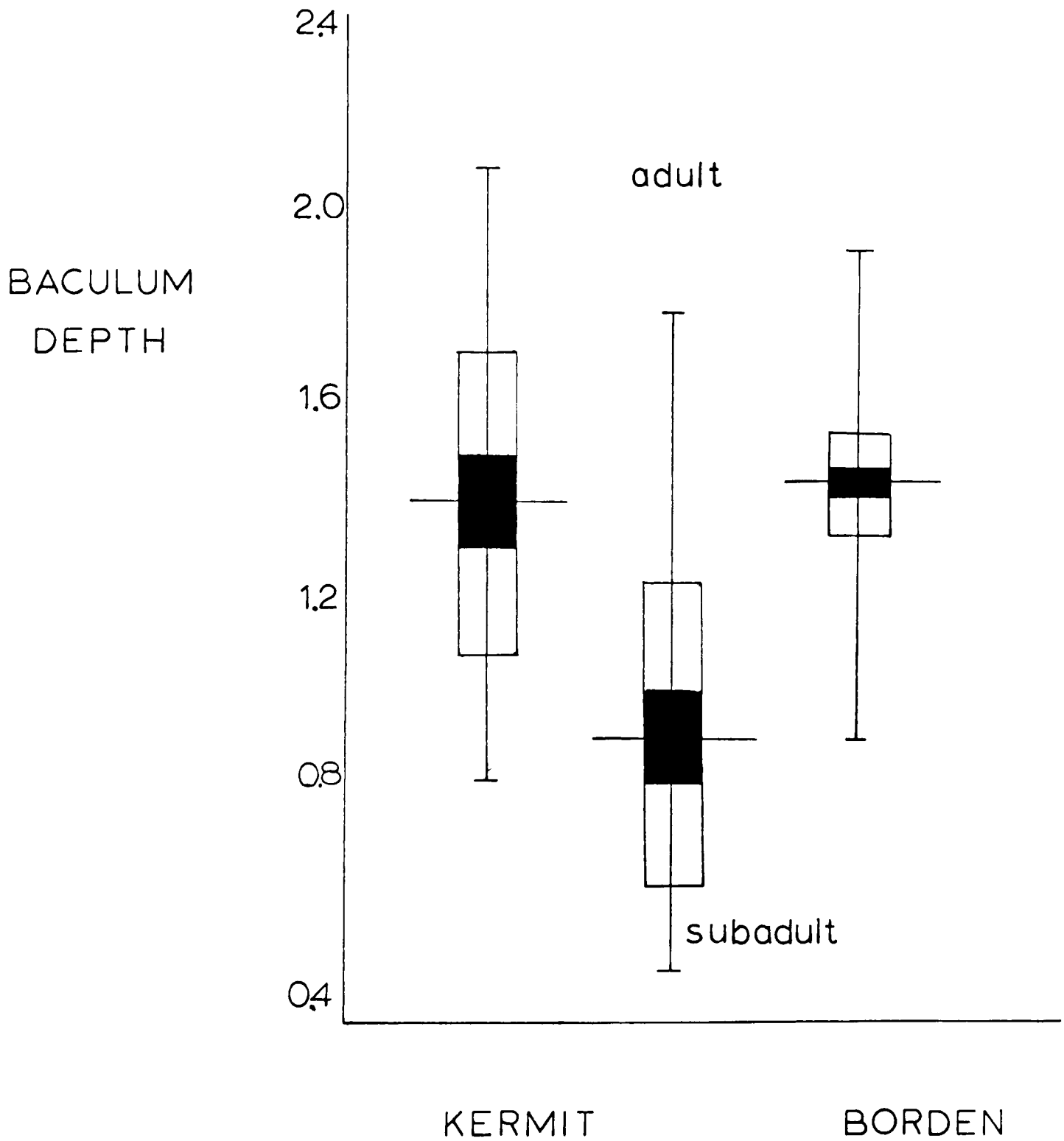


Figure 3. Compared variation of .
depth

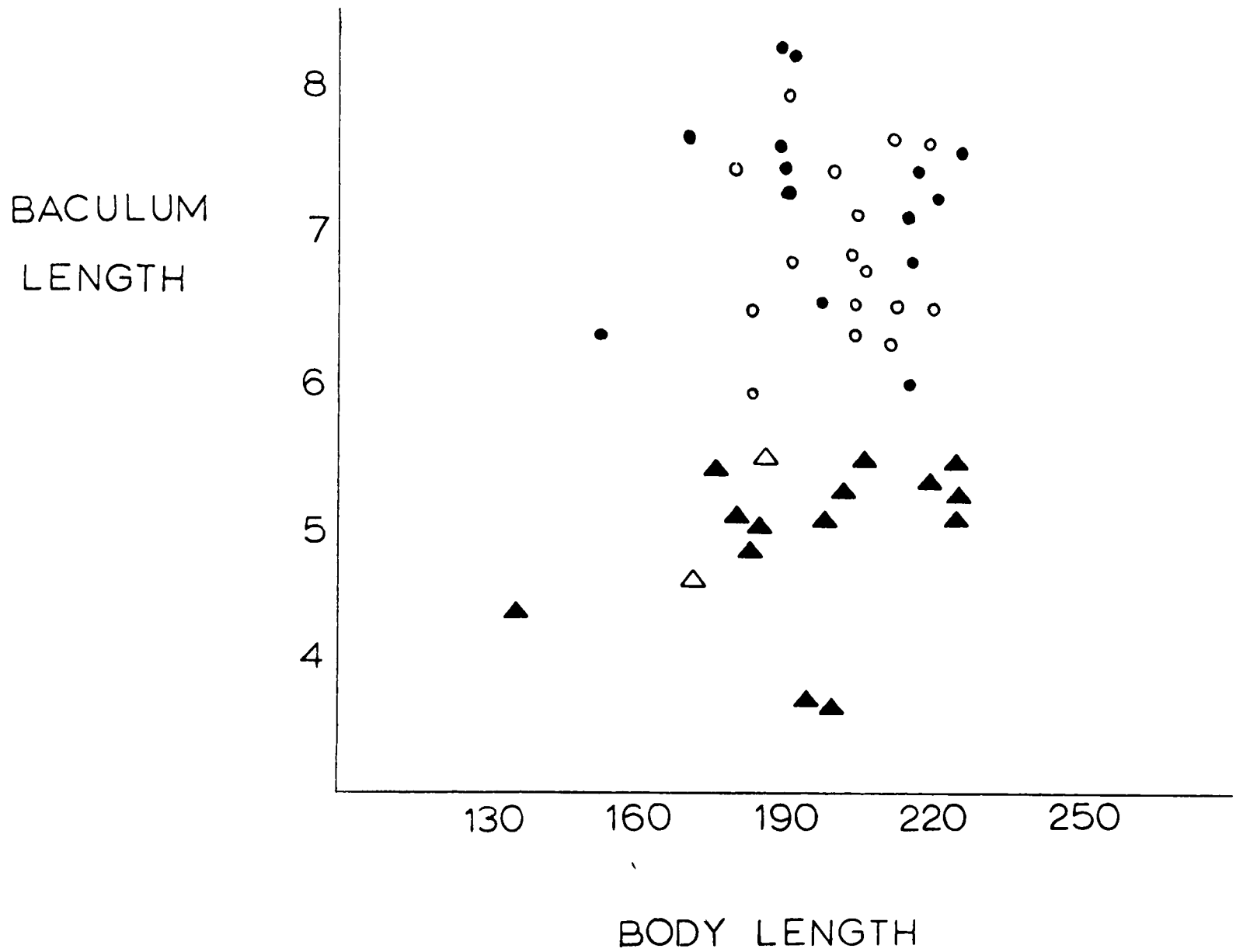


Figure 4. Correlation of baculum length with body length

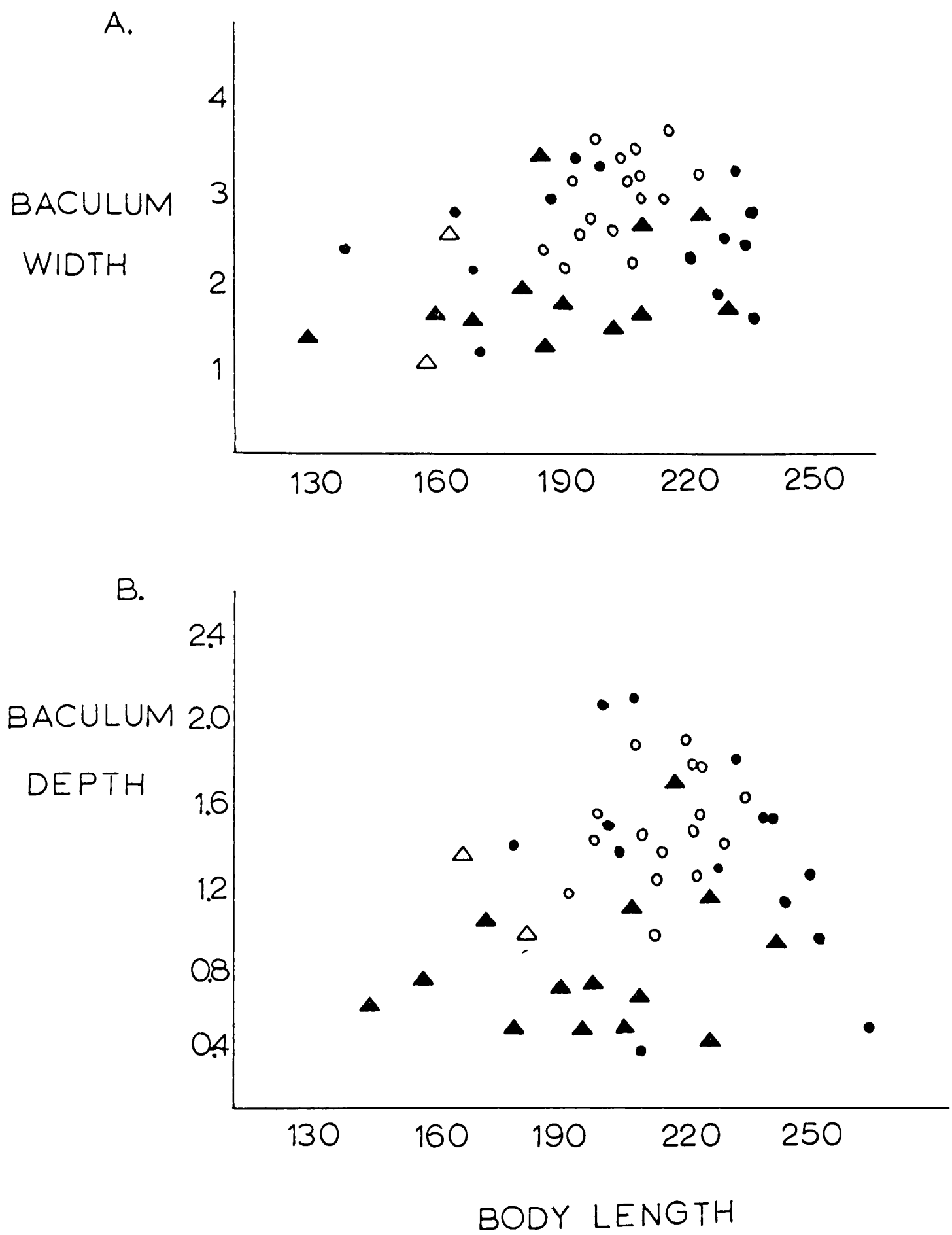
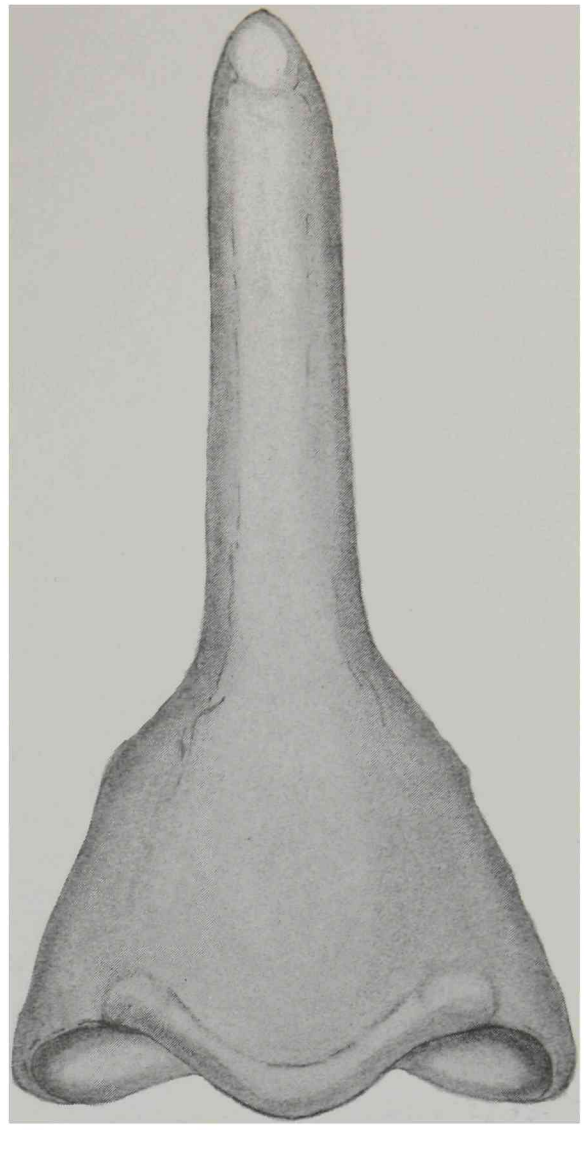
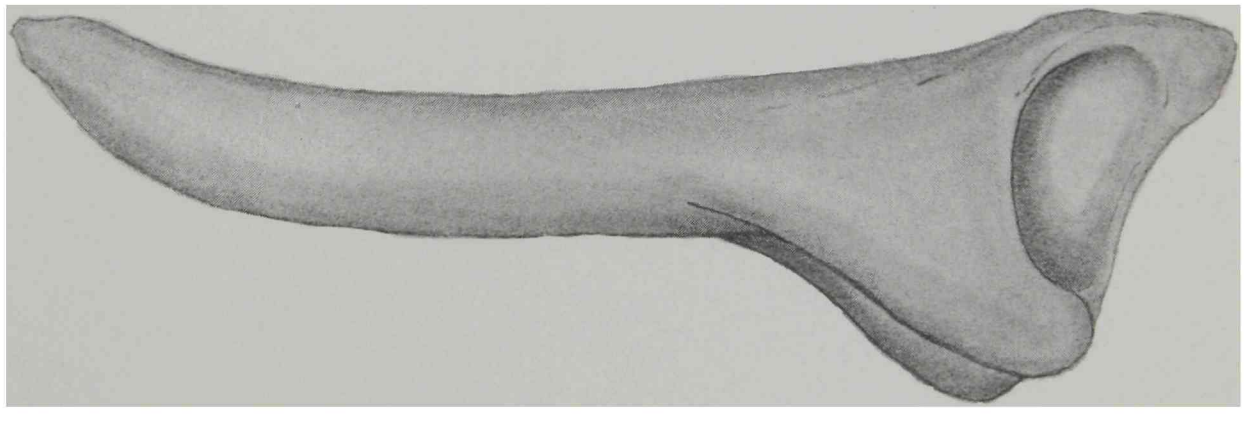


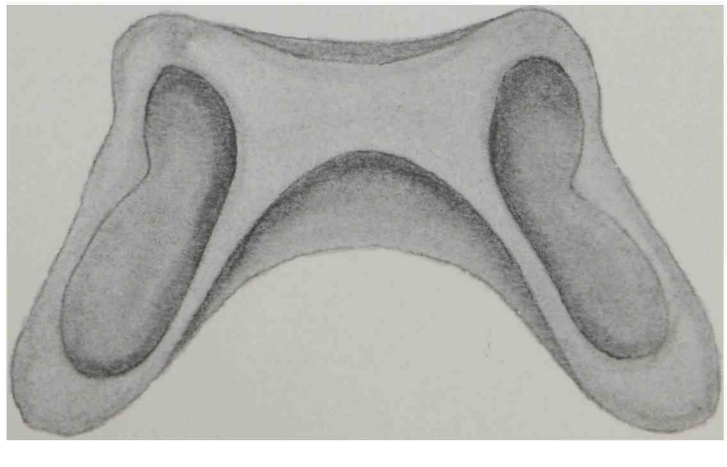
Figure 5. A. Correlation of baculum width with body length; B. Correlation of baculum depth with body length

EXPLANATION OF PLATE I

Baculum of *Neotoma micropus canescens* illustrated in dorsal, lateral, and proximal end views respectively.

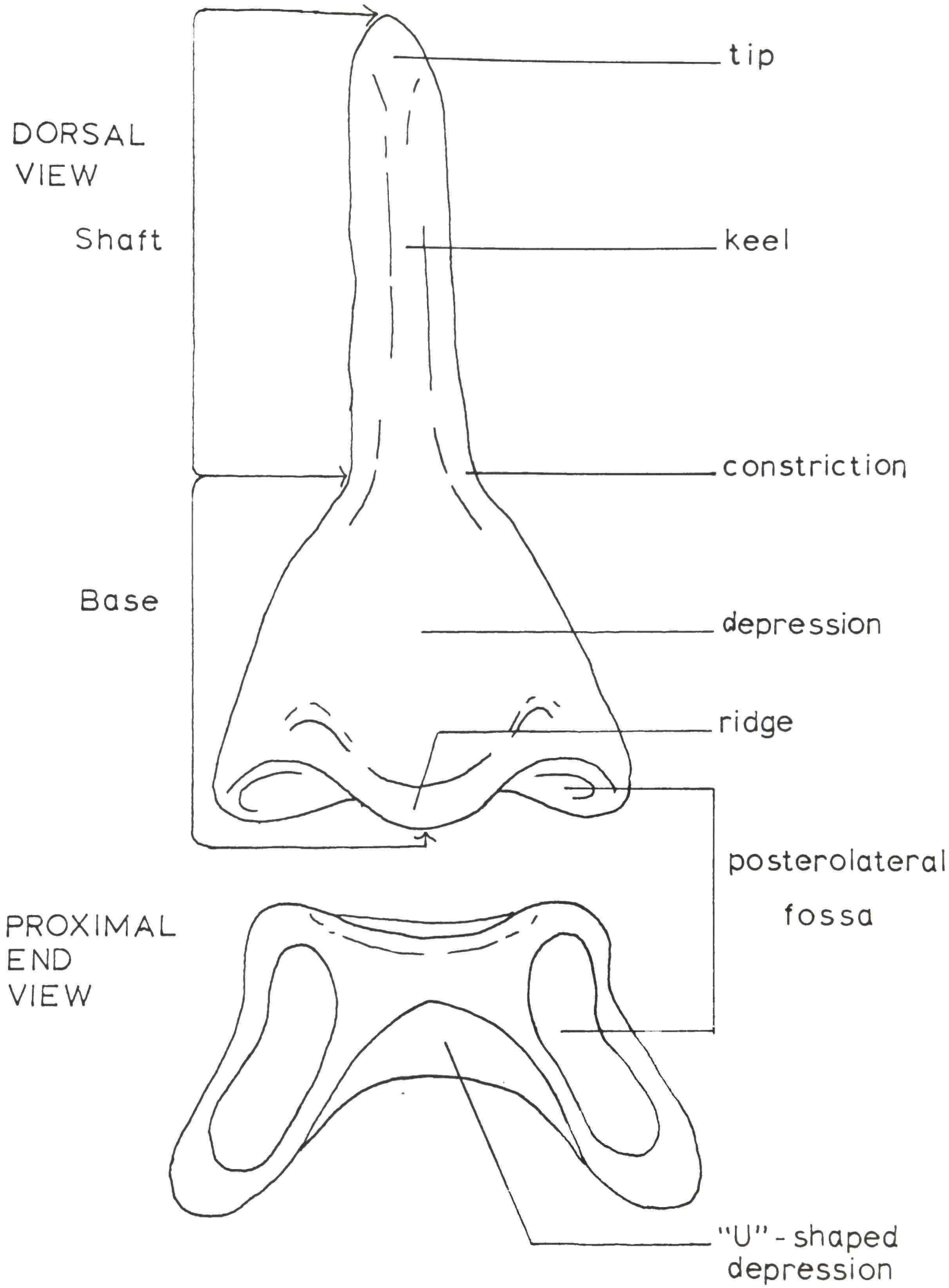






EXPLANATION OF PLATE II

Morphology and characters of the baculum of *Neotoma micropus canescens* used in this study.


DORSAL VIEW
Shaft
Base
tip
keel
constriction
depression
ridge
posterolateral fossa
PROXIMAL END VIEW
"U" - shaped depression

EXPLANATION OF PLATE III

Comparison of woodrat bacula:

a. *Neotoma floridana*, dorsal view

b. *Neotoma mexicana*, dorsal view

c. *Neotoma albigula*, lateral view*

d. *Neotoma fuscipes*, lateral view*

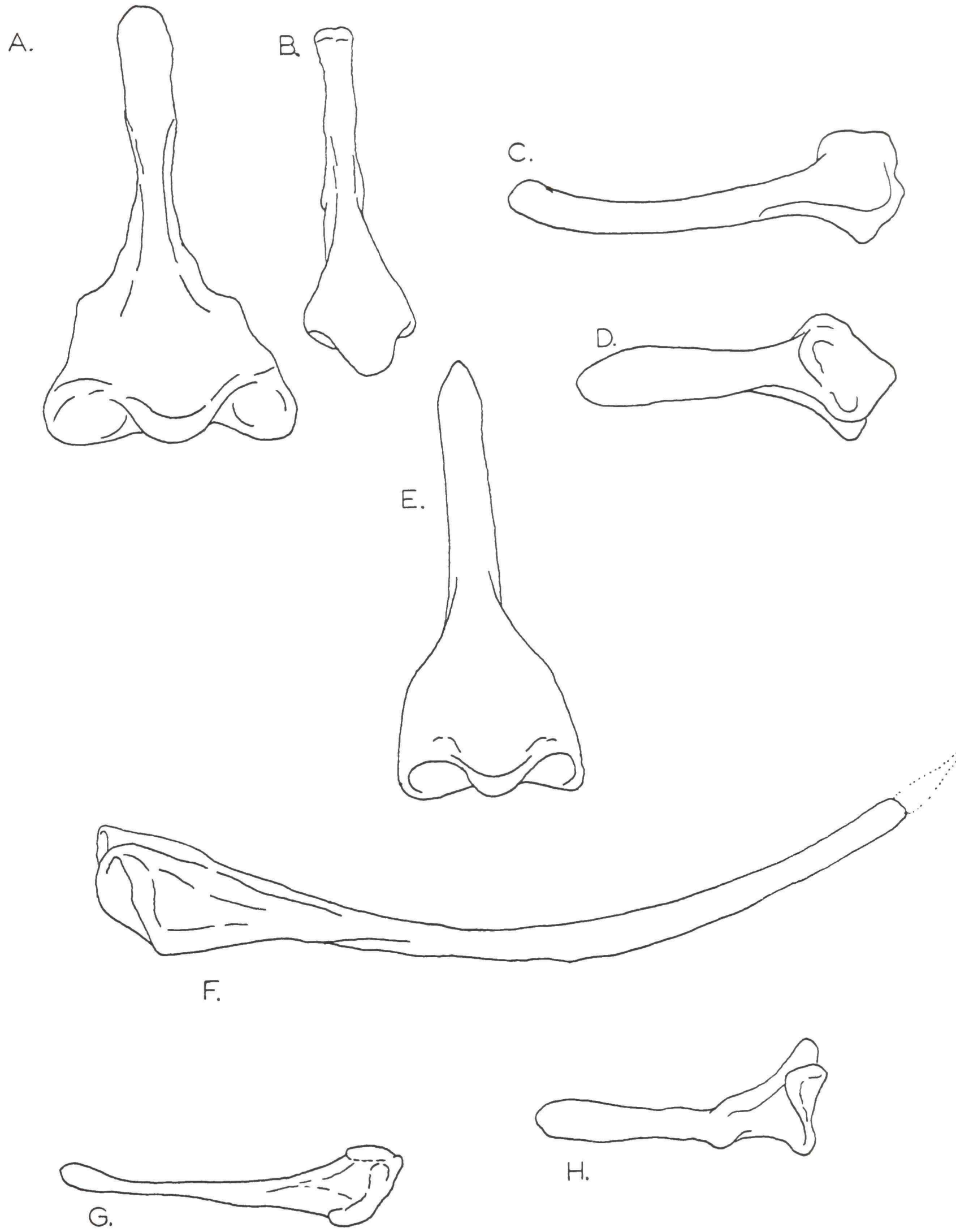
e. *Neotoma micropus*, dorsal view

f. *Neotoma lepida*, lateral view

g. *Neotoma alleni*, lateral view*

h. *Neotoma cinerea*, lateral view*

(* indicates sketched from Burt, 1960)


A.
B.
C.
D.
E.
F.
G.
H.

EXPLANATION OF PLATE IV

Male reproductive tract of *Neotoma micropus canescens*, dissected from the body, ureters visible:

a. seminal vesicles

b. prostate gland, dorsal

c. prostate gland, ventrolateral

d. ureter

e. bladder

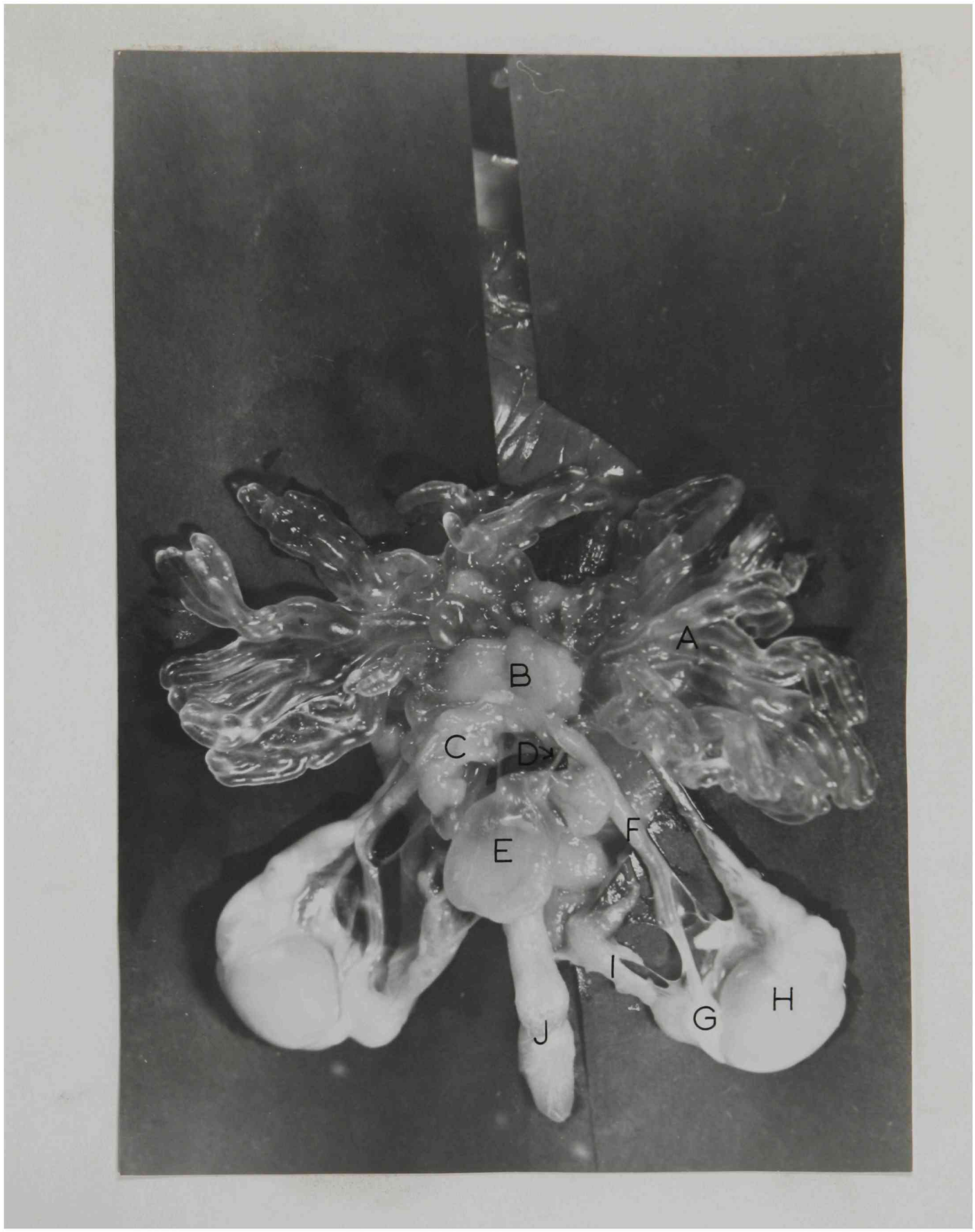
f. ductus deferens

g. epididymis

h. testis

i. inguinal canal

j. penis


A
B
C
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J

EXPLANATION OF PLATE V

Male reproductive tract of *N. m. canescens*, dissected from the body, Cowper's (bulbourethral) glands visible:

a. urethra

b. Cowper's glands

c. ducts from Cowper's glands


A
B
C

EXPLANATION OF PLATE VI

Male reproductive tract of *N. m. canescens*, *in situ*:

a. intestines

b. seminal vesicles

c. dorsal prostate gland

d. ductus deferens

e. bladder

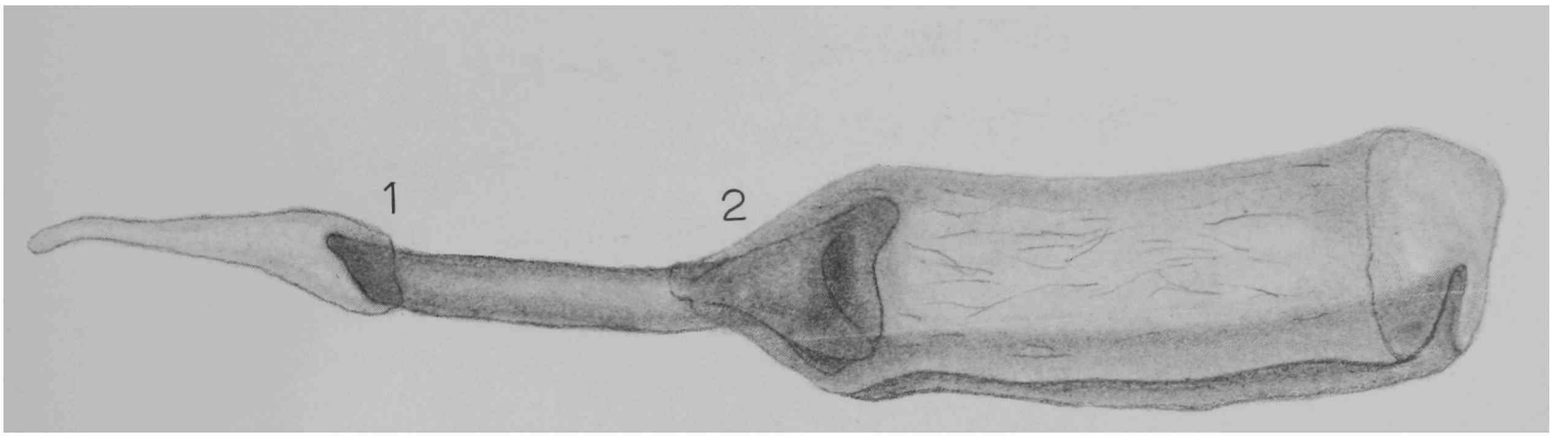
f. penis

g. testis


A
B
C
D
E
F
G

EXPLANATION OF PLATE VII

Attachment of the (1) cartilaginous tip and (2) corpus cavernosum to the baculum.


1
2