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HISTOLOGY, DEVELOPMENT, AND INDIVIDUAL VARIATION OF COMPLEX MUROID BACULA

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ABSTRACT

Bacular development, morphology, and variation was studied in *Microtus*, *Ondatra*, *Sigmodon*, *Mesocricetus*, and *Rattus*.

Bacular shaft development is essentially similar in all forms in which it was studied. A synovial joint is described as present between the shaft and the distal processes of the baculum. The distal processes were observed ossified only in *Rattus*. In all other forms studied, the cartilage of these processes calcifies when sexual maturity is reached.

The total length of the baculum and the bacular index (a summation of the length times the width of the shaft and the product of the length of the median process times that of a lateral distal process) shows no correlation with known-age of 96 *Microtus montanus*, but, rather, is related to the total length of the individual. The development and absolute form of the baculum presumably is controlled in part by hormonal and genetic factors, and chronological age is not as important as physiological age in its development.

Individual variation in the baculum of *Microtus montanus* is described. The "os clitoridis" of *Mesocricetus* is not homologous to that of *Ondatra* as each

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bone or cartilaginous element is apparently homologous to a different part of the complex baculum.

The similarity observed in the development, histology, and general form of the baculum of *Rattus* and the cricetids studied herein, suggests that murids and cricetids represent but a single family.

I. Introduction

The baculum of many muroid rodents consists of a proximal shaft and three distal processes (Figure 1). It has been recognized for a long time (Gilbert, 1892; Tullberg, 1899), and considered characteristic of the

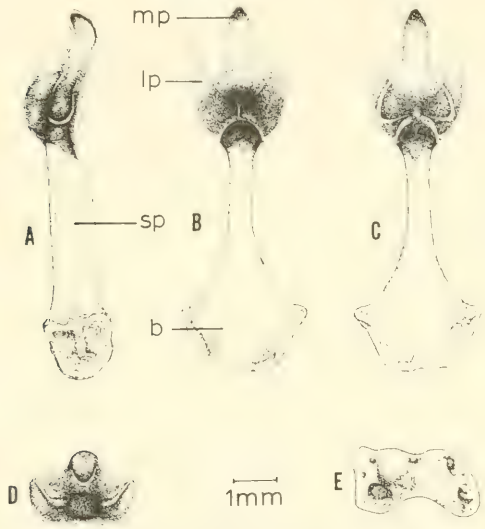


Figure 1. Views of the complex baculum of *Sigmodon hispidus*. The parts of the baculum are: median (mp) and lateral (lp) distal processes; the spine (sp) and base (b) of the shaft. The views illustrated are: A. lateral, B. dorsal (anti-urethral), C. ventral, D. distal (urethral uppermost), E. proximal (anti-urethral uppermost).

Microtinae, the Cricetini, and certain Neotropical or neotropically derived Hesperomyini (Cricetinae) and some Muridae (Hooper and Musser, 1964).

Hamilton (1946) described the baculum in numerous Microtinae, as well as in *Sigmodon* and *Oryzomys* (Cricetinae), and pointed out the similarity of the structure in such supposedly diverse groups. He also illustrated a series of bacula of *Microtus pennsylvanicus* and showed the general change in form associated with the assumed age of the animal. Callery (1951) illustrated series of bacula from a few known-age hamsters *(Mesocricetus auratus)* produced by inbreeding from a single pair of animals. Anderson (1960) figured a growth curve in which length of the bacular shaft of *Microtus ochrogaster* was plotted against total length of the animal. Elder and Shanks (1962) discussed bacular changes in a limited series of known-age muskrats *(Ondatra zibethicus)*. To our knowledge, no study is available describing changes in the morphology of the baculum in a large series of known-age animals, or considering the histology and changes occurring in the distal processes of this element.

II. Materials and Methods

This report is based on histological observations of the bacula of 6 muroid genera (Table 1), and approximately 50 locally collected hystricomorphs *(Myocastor coypus)*. One-hundred and thirty-eight *Microtus montanus* (including 97 known-age males and 21 known-age females) used in this study for growth and development data were taken from a laboratory breeding colony maintained by one of us (Negus). This colony originated from about 100 *Microtus montanus* live trapped in Jackson Hole, Wyoming. These animals were maintained

Table 1.
Muroid species and number of specimens (in parentheses) examined in this study. Supergeneric groupings follow Simpson (1945).

Superfamily Muroidea	
Family Cricetidae	
Subfamily Cricetinae	
Tribe Cricetini	
Mesocricetus auratus (males 3; females 2)	5
Tribe Hesperomyini	
Sigmodon hispidus (males 3; females 1)	4
Peromyscus gossypinus (males 4; females 2)	6
Subfamily Microtinae	
Tribe Microtini	
Ondatra zibethicus (males 5; females 3)	8
Microtus montanus (males 143; females 33)	176
Family Muridae	
Subfamily Murinae	
Rattus norvegicus (males 5; females 2)	7
Total Specimens Examined	206

as pairs in the laboratory, and fed a basic diet of rabbit chow supplemented every few days with lettuce and other greens. A constant photoperiod of 18 hours per day was maintained and room temperature was maintained by air conditioning. No inbreeding was permitted in the colony. Individuals were weaned at 15 days of age, at which time the litters were placed in separate cages, weighed, measured and sexed.

III. Results and Discussion

A. *Histology*

The bacular shaft of all forms we have examined is true bone. It consists of a laterally enlarged basal area to which the M. corpus cavernosus attaches and a spine-like distal projection (Figure 1). In all respects, the structure in cricetids is similar to that of *Rattus* (Ruth, 1934). In small species (i.e. *Microtus montanus*) and small individuals of large forms (*i.e., Sigmodon*) the shaft is formed by a single haversian system identical to that of the simple baculum of *Peromyscus* and other Nearctic cricetines (Figure 2). The spine may be composed of several haversian systems in larger forms (e.g. *Ondatra*). In cross-section the spine

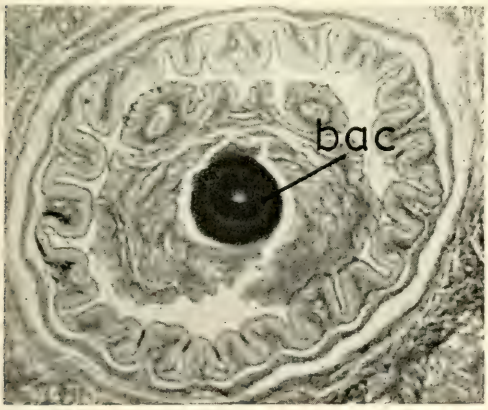


Figure 2. Cross-section of the phallus of *Peromyscus gossypinus*, illustrating the nature of the spine of the baculum (bac).

is circular, oval, or dorso-ventrally flattened. This spine is generally characteristic of the species, but much variation and overlap exists.

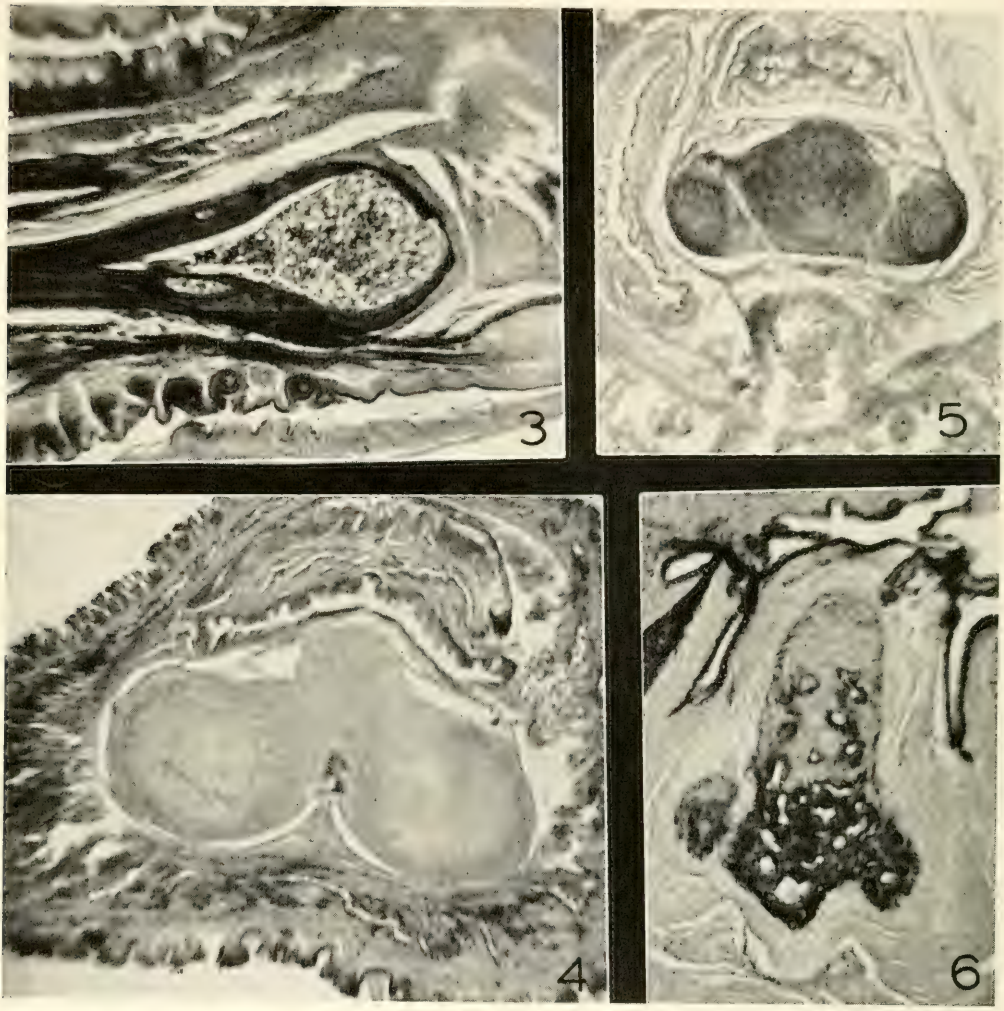
Ruth (1934) termed the bony development of the shaft of *Rattus* an endoblastemal ossification in which osteogenic cells become active in laying down osteoid substance before any marked differentiation of surrounding tissues can be observed. Although we have not sectioned pre- or neo-natal cricetids, the bony formation in one-week-old *Microtus* is similar to that described by Ruth (op. cit.). Diameter increase is by means of an active periosteum. An endosteum is seen in young animals. Maximum shaft length is achieved near breeding age.

Hemopoietic bone marrow and fatty tissue are present in the enlarged basal area of the shaft (Figure 3). Cancellous bone is present in some species. In large individuals of *Microtus,* and in most individuals of larger forms (e.g. *Ondatra*) these tissues extend into the medullary cavity of the spine for more than one-half its length.

The several elements of the complex baculum (the shaft and the distal processes) are not of the same origin or histological nature. The distal processes, often referred to as cartilage, ossifying in adults, have not been described histologically. The cartilaginous nature of these processes in young individuals has been described by many (Hamilton, 1946; Callery, 1951; Dearden, 1958; Anderson, 1960; Elder and Shanks, 1962; and others), but the subsequent "bony" development often described is usually considered to be typical endochondral ossification. In only one form *(Rattus)* have we observed this to be the case.

The "ossifications" of the distal processes of the complex cricetid baculum seen are only calcifications of either hyaline or fibrocartilage. In *Mesocricetus* (Figure 4), *Microtus* (Figure 5) and *Sigmodon,* no true ossifications were found. Only in *Rattus* (Figure 6) were true ossifications of the distal processes observed. An apparent reason for this oversight in previous work is that most studies on bacular morphology employ clearing (in KOH and glycerin) and staining (with Alizarin Red) of the whole glans penis in which the bony structure is found. Staining by Alizarin Red is not specific to bone, however, but calcium specific, and differentiation between an ossification and a calcification is not discernible with this technique.

The baculum of *Rattus* is usually considered to consist of but two osseous portions (Taylor, 1961) and although Hooper (1960) and Hooper and Musser (1964) do consider the glans penis of murines to represent the complex type, the presence of the lateral



Figures 3-6. Histological preparations of phalli. 3. Longitudinal section through the phallus of *Microtus montanus* showing hemopoietic tissue present in the enlarged basal area of the baculum. 4-6. Cross-sections through the distal regions of the phalli showing the relative sizes and nature of the distal processes. 4. *Mesocricetus auratus* 5. *Microtus montanus* 6. *Rattus norvegicus.*

distal processes is often overlooked. Whereas these structures are not as free as are those in the cricetids examined by us, their presence is obvious (Figure 6). This fusion of the lateral processes to the median may represent a condition derived from the pattern typically seen in cricetines, as some cricetines show trends in this development (Figure 7).

An unusual histological feature of the bacula studied is the presence of a synovial joint (diarthrosis) between the shaft and the distal processes (Figure 8). We have observed this in *Microtus, Ondatra, Sigmodon, Mesocricetus,* and *Rattus.* Associated with this joint, but not included in the scope of this report, are tendons and muscles in the soft tissues of the glans penis affecting the movement of the distal elements. The functional morphology and possible adaptive significance of this joint and associated structures will be reported in a later paper.

The distal processes are functionally not separate entities. They develop from cartilaginous anlagen, as three elements fused, or nearly fused, near the synovial joint. The distal processes exist essentially as a single

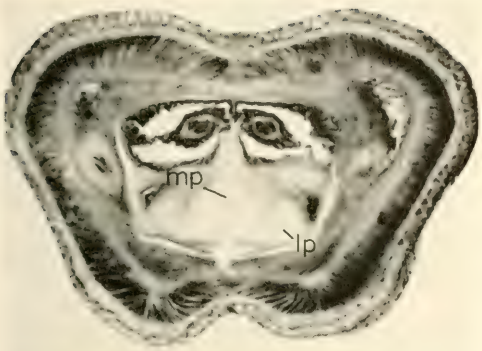


Figure 7. Cross-section of the phallus of *Sigmodon hispidus*, slightly distal to the level of the synovial joint, showing the fusion of the lateral processes (lp) with the median process (mp) near their junction with the shaft.

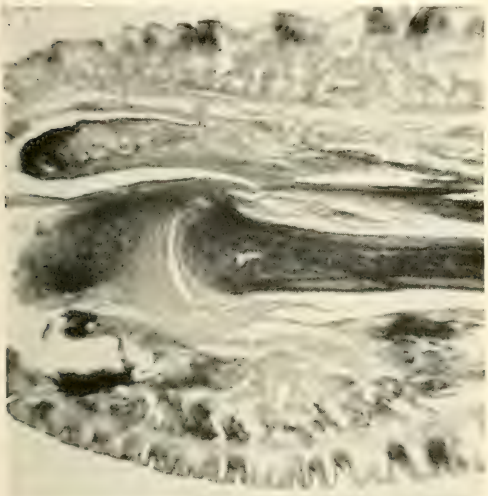


Figure 8. Longitudinal section through the phallus of *Microtus montanus* showing the synovial joint present between the distal and proximal elements of the baculum.

unit, with varying degrees of fusion, culminating in the ankylosed condition seen in adult *Rattus*.

Different degrees of calcification of the distal processes are seen in different species. It is most complete in the larger forms, or large individuals of smaller species. Large *Microtus montanus* develop sequelae. Such deposits in this region are visible in *Microtus* as anteriorly directed "spurs" (Figure 9). Extra calcification in the distal processes near the region of the synovial joint are evident in the illustrations of adult *Ondatra* (15 months of age and older) provided by Elder and Shanks (1962). If freedom of the synovial joint is essential in the reproductive activities of these forms, continued calcification may mark termination of the reproductive activity on the part of the individual. On the other hand, since most mice have short lives, such a problem may be only of academic interest.

The rod-like baculum of many Nearctic cricetines (e.g. *Peromyscus, Neotoma,* and others) is capped by a tip of hyaline cartilage which is adnate with the shaft, but

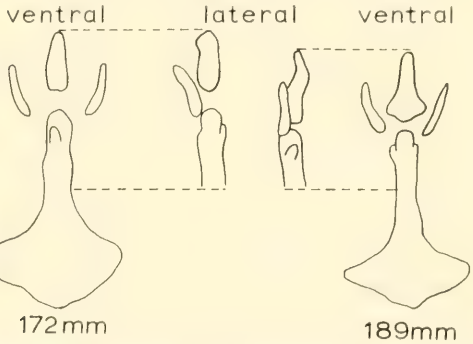


Figure 9. Excessive calcification in the bacula of large *Microtus montanus*. The "spurs" in the region of the joint between the shaft and distal processes are calcium deposits. Also note the variation in the shapes and angles of the median and lateral processes of the two bacula illustrated. The total lengths of the animals from which the bacula were obtained are given.

not joined by a synovial joint. This tip is possibly homologous with the medial distal process of the complex bacular form. Though only a small number of such bacula have been examined by us, no calcifications or ossifications in this distal tip have been noted. Hooper (1960) did report that the cartilaginous spine (i.e. tip) is one of four *Ototylomys* examined was partly osseous (calcified?).

B. *Development and Individual Variation*

The shaft of the baculum begins to develop in *Rattus* when the animal is one-day old, and within three days the definitive osseous character of the shaft is established (Ruth, 1934). The youngest *Microtus* examined by us was 7 days old (72 mm total length), and the osseous shaft of the baculum was 0.9 mm long. No basal enlargement is evident at this stage. By 15 days the basal area is well developed and cancellous. Late

development does not occur in all rodents, however. We have observed prenatal ossifications in nutria *(Myocastor coypus),* a large hystricomorph possessing a long (25 mm), simple, rod-like baculum in the adult. Such late development in the Muroidea perhaps is associated with the general altricial condition of the young.

After the first two weeks the shaft increases in length and breadth. The diameter of the spine of the shaft increases by active periosteal deposition. Calcifications are not evident in the cartilaginous distal processes until somewhat over one month (with some obvious, expected variation). Until calcifications occur, the cartilaginous limits of the distal processes are not always clearly visible in cleared and stained specimens. Calcification of the distal processes and expansion of the basal region of the shaft occur rapidly after approximately 35 days of age (Figure 10). All animals examined that were over 40 days of age had some calcification of the distal processes and only one less than 35 days of age demonstrated calcification. This rapid change in the structure of the baculum coincides with other changes of an endocrine nature occurring at the same time. Calcification of the median process appears to be more rapid (in *Microtus*) than that of the lateral elements. Generally by 50-60 days calcification of all three processes is underway.

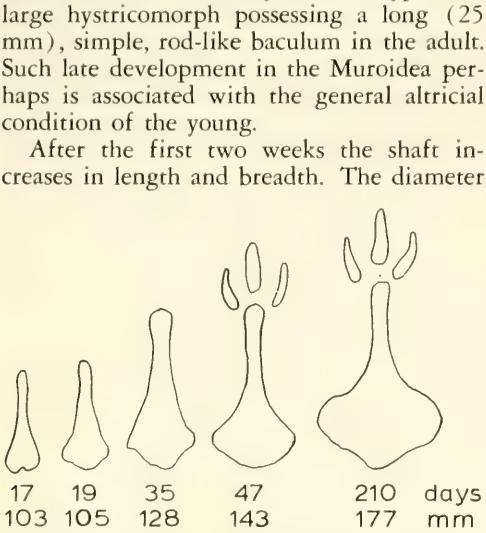


Figure 10. A selected series of bacula of *Microtus montanus* arranged by age and total length of the individual from which each was obtained, illustrating the general pattern of growth. Only calcified and true osseous elements are figured.

It is difficult to choose a single measurement that satisfactorily demonstrates the increase in size of a complex baculum. Figure 11 compares the total length of the baculum (i.e. maximum length of bone and cal-

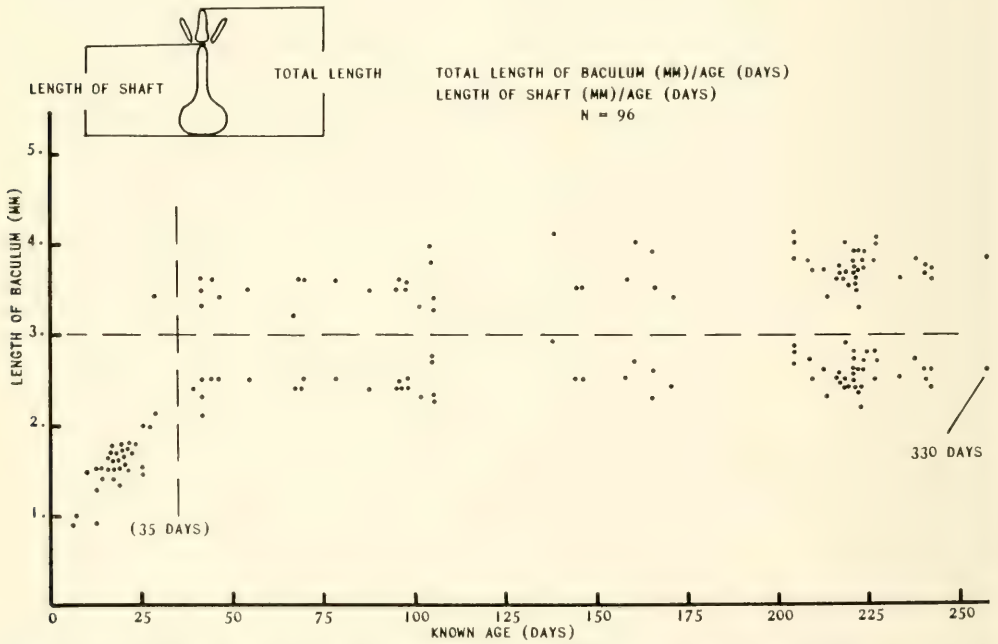


Figure 11. Comparison of the known age of 96 *Microtus montanus* to the length of the shafts of the bacula (below horizontal interrupted line) and to the total calcified length of the baculum (above horizontal interrupted line). The vertical interrupted line marks the approximate age at which the latter measurement is obtainable.

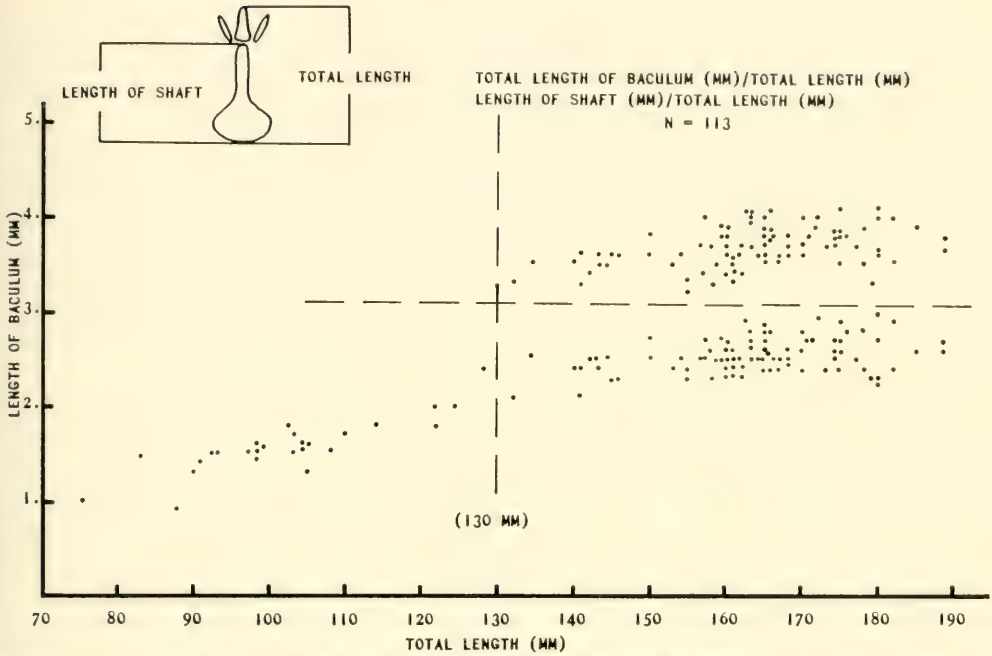


Figure 12. Comparison of the total lengths of 113 *Microtus montanus* to the lengths of the shafts of bacula (below horizontal interrupted line) and to the total calcified lengths of the bacula (above horizontal interrupted line). The vertical interrupted line marks the approximate total length at which the latter measurement is obtainable.

cified median distal process), and the length of the shaft only, against the known age of 96 *Microtus montanus*. Little or no change can be noted in either measurement after 35 days of age. The same bacular measurements are plotted against the total length of the animal (the same known age specimens plus several unknown age individuals) in Figure 12. Although a somewhat closer association is seen, the change is slight and much variation exists. Separation of individuals into age and size groups above 130 mm total length, or above 35 days of age is not possible utilizing either of these parameters (Figures 11 and 12).

Although simple lengths of the bacula do not correlate with known age or total length of the individual, subjective differences in massiveness and rugosity are evident between the bacula of young and old or small and large animals. Such impressions have, of course, been noted before. Hamilton (1946) illustrates 14 bacula of "immature", "subadult", and "mature" *Microtus pennsylvanicus*. Elder and Shanks (1962) illustrate similar changes in the bacula of twelve *Ondatra* classified as "juvenile" (5-8 months) and "adult" (15 months or more) individuals. Even though the observations concerning bacular form may be suggestive of juvenile age, *Ondatra* eight months old may be in breeding condition. The animals in their "juvenile" class (5-8 months old) were trapped in December, and born between April and July. Those born earlier in this period probably were in breeding condition during the latter part of the summer, whereas those born in July had far less chance to enter the breeding population their first year. Not all 5-8 months old *Ondatra* are juveniles, and if, as we suspect, the development of the baculum is controlled in part by hormonal factors, chronological age is not as important as physiological age. This consideration, as Elder and Shanks (1962) point out, is often ignored in taxonomic studies.

> "It seems unwise for authors comparing various species of the Microtinae to claim that only the middle, or only the lateral digital processes are calcified when only 3-4 specimens of a species have been examined. It also seems likely that disagreements as to which of the digital processes

are calcified at all in a genus such as *Phenacomys* (Dearden, 1958; Hamilton, 1946), are due to the fact that one man has examined bacula of juveniles, the other those of adults."

Of concern also is the unexplored possibility that bacular sizes and forms may differ within a population as the chronological and physiological age composition of the population changes. This could occur during a season, a year, or in a classic microtine four year cycle. It would be interesting to compare samples of bacula collected from a single population at different seasons or from year to year.

A number of attempts were made to measure the subjective impression of robustness alluded to above, that we, as well as others, note in viewing series of bacula from mice of different ages and sizes. The most successful approach is the utilization of an index, obtained by summing the product of the length times the width of the shaft and the product of the length of the median distal process times that of one (the longest) of the lateral distal processes. Plotting such an index against known age reveals considerable variation following the critical 35 day old point, indicating that, although the index tends to increase with age, the curve is not steep enough to allow separation of animals 50-75 days old from those 225 days old (Figure 13).

Plotting the same indices against total lengths of the animals reveals a closer correlation (Figure 14). The index is seen to be closely related to the size of the animal but enough individual variation is present to preclude separation of the 116 animals examined into size groups based on bacular index with any practical degree of probability.

Anderson (1960) notes that in *Microtus ochrogaster,* "sexual maturity is reached rather abruptly when the total length of most individuals is 140 to 150 millimeters." This probably corresponds to the 130 mm size we denote as critical in *M. montanus.* Anderson (op. cit.) also notes that maximum individual variation would occur in animals of this total length (140-150 mm). Our data demonstrate, however, that the greatest variability is evident in old (circa 225 days) and large (above 160 mm) voles (Figures 13 and 14).

A further indication that bacular size is

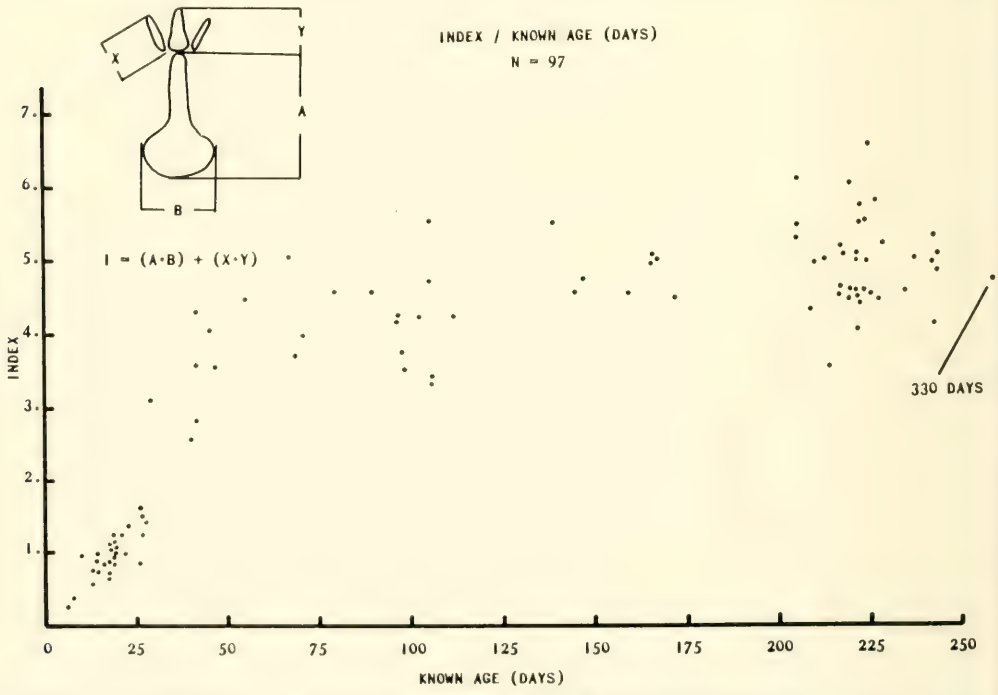


Figure 13. Comparison of the known age of 97 *Microtus montanus* to their bacular indices.

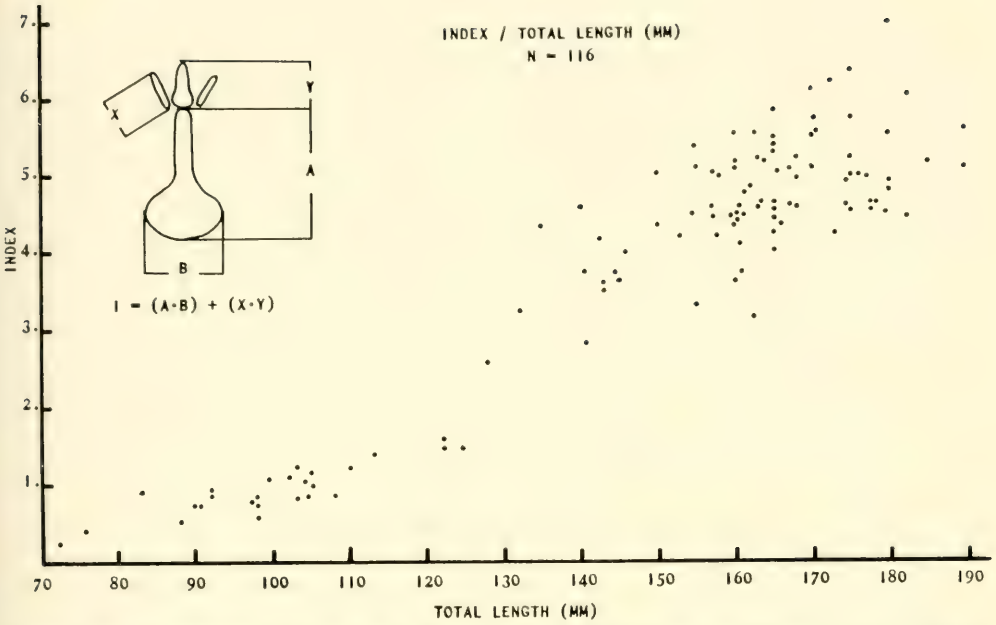


Figure 14. Comparison of the total lengths of 116 *Microtus montanus* to their bacular indices.

dependent more upon total length than upon chronological age of the animal, is summarized in data presented in Table 2. Data on animals of two size classes (160-165 mm and 180-189 mm) were selected from the known age *M. montanus* material and known age and total lengths were compared with the lengths of the bacular shafts and the bacular indices. Although the length of the shaft was essentially the same in both size classes, the bacular index of the larger size group was significantly greater than that of the smaller group of animals ($t=3.85$ at 27 degrees of freedom; significant at .001 level). Further, the average age of the 160-165 mm group was 186 days, whereas that of the 180-189 mm group was only 152 days (Table 2). The small number of animals in the respective classes disallows significant statistical results, however.

In our laboratory stock of *Microtus montanus*, both males and females reach sexual maturity at about 5 weeks of age at which time the average total length is approximately 130 mm. That total length of the baculum shows much greater variation after 35 days of age, suggests that physiological factors may influence bacular development This is further implied by closer relation of the bacular index to body length than to age (Figure 12). Apparently, individual differences in physiology and genetics may account for the greater variability in bacular size once sexual maturity is reached. Perhaps the gonadotropic hormones of the adenohypophysis or the gonadal hormones

TABLE 2.

Comparison of the length of the shaft of the baculum and the bacular index (see text for explanation) in two size classes of adult Microtus montanus.

Size Class (Total length of the individual)	Number of individuals in size class	Number of known-age individuals	Length of the shaft of the baculum	Bacular Index	Age (Days)
160-165 mm	20	13	2.3-2.9 mm ($\bar{x} = 2.5$)	3.1-5.5 ($\bar{x} = 4.6$)	79-243 ($\bar{x} = 186$)
180-189 mm	9	4	2.3-3.0 mm ($\bar{x} = 2.6$)	4.4-7.2 ($\bar{x} = 5.4$)	105-172 ($\bar{x} = 152$)

may exert some influence on bacular development. The general body size attained by an individual is regulated largely by genetic factors, but individual variations in size within a species may well be based more on physiological differences. Thus, an individual possessing a more active (or larger) anterior pituitary (producing more somatotropin) may grow faster and larger than another of its own species. Similarly, a more active pituitary might also release greater amounts of gonadotropins and release of more adrenal androgens may influence the possible relationship of bacular growth to sexual maturity and total length (as a measure of size of the individual) in *Microtus*. Presumably, elucidation of endocrine relationships to bacular development can be readily accomplished for many mammals by experimental procedures in the laboratory using known-age animals.

It is perhaps surprising that endocrine effects on such a taxonomically important element as the baculum have not been noted by mammalogists before, as they are well recorded in the literature. A response in baculum size (associated with general massive development of all parts of the male reproductive tract) in *Rattus* to androgens has been recorded by Korenchevsky et al. (1932) and Thyberg and Lyons (1948).

Howard (1959) referring to gonadectomized mice *(Mus)* states: "not only is there an increase in lengths of the bone (i.e. baculum) with DHA (dehydroepiandrosterone), but the changes in shape and thickness are striking." A similar response is produced by administration of 11-hydroxy-androstenedione (an adrenal androgen) to gonadectomized mice (Howard, op. cit.).

These data suggest that chronological age cannot be ascertained in *Microtus* by measurements of a number of parameters of the baculum. We suspect that the same is true for other rodents with the complex type of baculum. Total bacular size (as indicated by the index herein employed) appears to be possibly a function of hormonal activity and physiological, rather than chronological, age.

Other than differences directly attributable to size, considerable individual variation was noted in the bacula of *M. montanus*. Figure 15 illustrates a series of bacula demonstrating the extremes of variability observed in the 117 males studied. The base of the shaft is usually a crudely shaped diamond without a basal notch. In some (Figure 15E), a notch is present. In others the shape of the base varies from roughly triangular (Figure 15D) to oblong (Figure 15H), often with an irregular, rugose proximal edge (Figure 15G). The spine of the shaft is more constant in form than the base, though occasional medial or terminal swellings are evident (Figures 15B and 15I). The "spurs" or sequelae, mentioned above, are often present near the synovial joint associating shaft and distal processes (Figure 15B and 15J). These latter elements are highly variable. The calcified portion of the median process may be simple rod-like (Figure 15C, 15E, and 15G) or may be expanded near its base (Figure 15A, 15F, 15H, and 15J). Although this expansion is generally associated with greater age or total length of the individual, exceptions were noted.

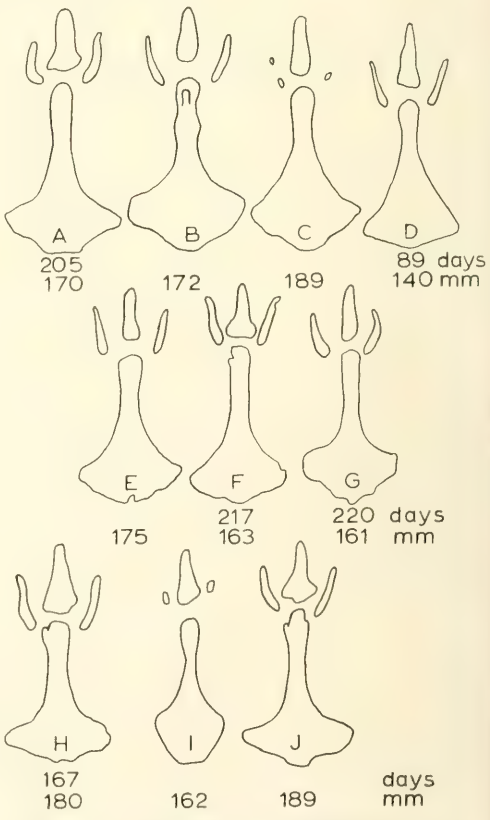


Figure 15. Ten bacula of *Microtus montanus* illustrating individual variation. Ages and total lengths of the individuals from which the bacula were taken are given below the figures.

The lateral distal processes vary greatly between individuals and sometimes between members of the same pair. Calcification, even in large, adult animals, may be complete or incomplete, and may, in each process, result from one or occasionally two, centers of calcification (Figure 15C). If fully calcified, these processes may curve inward (Figure 15A and 15G), or remain straight (Figure 15D and 15E). The tips occasionally curve outward. Viewed laterally the lateral processes vary in their relation to the median process and the shaft, sometimes lying in the same plane as the shaft or declinating by as much as a 45° angle (Figure 9).

In the *Microtus* studied, the lateral processes are the last to calcify and occasionally they may not do so. In large microtines (e.g.*Ondatra*) these elements are large and usually well calcified. *Pitymys,* one of the smaller microtines, is often characterized by the poor development of these processes. Possibly the different degrees of calcification seen in a group such as the microtines may be more a function of the average or maximum size obtained by the form than a morphological characteristic, per se.

C. *Os Clitorides in Muroid Genera with Complex Bacula*

As homologs of the penis, clitoral elements are of interest as they often demonstrate what may be interpreted as either rudimentary or reduced conditions of the male structures. In some rodents, especially the sciurids, the os clitoridis is a small, clearly homologous, version of the baculum (Layne, 1954). This is not the case in the muroids examined.

In muroids the clitoris forms a small replica of the penis. The urethra is enclosed within the clitoris in *Mesocricetus, Ondatra* (Figures 16 and 17) and *Microtus.* Distally the clitoris terminates in three lobes of tissue, homologous with the anlagen of the three distal processes of the baculum. Cartilaginous tissue is present in these lobes in the genera examined. In *Ondatra* the fibrocartilage of the median lobe calcifies in large individuals (Figures 17 and 18A), and although we have not observed calcifications in the lateral processes, they possibly may occur in some individuals. The only other microtines in which the os clitoridis has been reported are *Microtus californicus* and *M. longicaudus* (Ziegler, 1961). The illus-

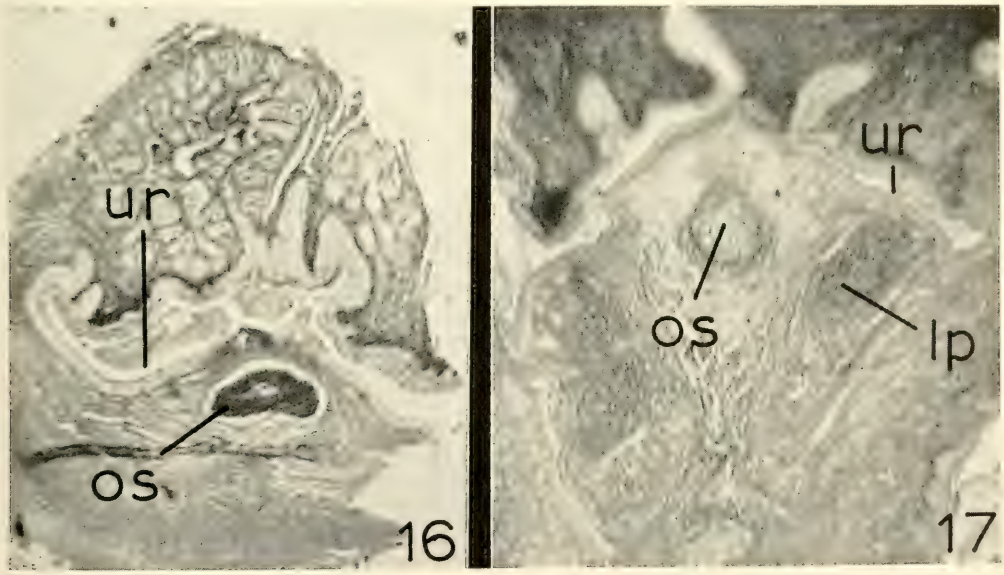


Figure **16.** Cross-section of the clitoris of *Mesocricetus auratus* showing the true bony nature of the os clitoridis (os). Figure **17.** Cross-section of the clitoris of *Ondatra zibethicus,* showing the homologs of the lateral processes of the baculum (lp), and the median process with a calcified fibro-cartilage "os clitoridis" (os). The urethra (ur) is visible in both Figures 16 and 17.

trations of these specimens suggest that they are of the same type as that of *Ondatra.* We have examined 21 female *Microtus montanus* ranging in total length from 145-166 mm, and in age from 212-245 days, but have observed no calcification following Alizarin Red staining. Fibro-cartilage is present in the median lobe, however, and under favorable conditions might calcify. Ziegler (1961) suggests that the occurrence of the os clitoridis in *Microtus* may not be associated with age, as it is found in both young and old animals.

The os clitoridis of *Mesocricetus* is quite different from that of the microtines. In *Mesocricetus* the element is located more proximally and has a more definitive shape (Callery, 1951). Sectioning reveals that this is true bone (Figure 16), histologically identical to the shaft of the baculum. Its proximal location in the clitoris confirms this homology (Figure 18B). No calcifications were noted in the three large, loosely cartilaginous lobes of tissue present distally in *Mesocricetus.*

The "os clitoridis" of *Mesocricetus* is not homologous to those of *Ondatra* and *Microtus,* as each is homologous to a different part of the complex baculum. The "os clitoridis" of *Mesocricetus* is the only one observed that can properly be termed a bony element.

D. *Taxonomic Implications*

The continuing use of the baculum and other phallic structures in mammalian, especially muroid, systematics, suggests the desirability of much more information on the development, individual variability, microstructure, and physiological and chronological relationships of these elements before sound taxonomic interpretations can be based on them.

From the data presented above, bacular structures obviously are subject, at least at the population and infraspecific levels, to considerable variability. Such observable differences may be dependent upon a plethora of variables, including the endocrine state of the individual, chronological age, genetic background, etc.

The degree of such variability, and the importance of the endocrine state, as well as the nature of the calcifications observed in the distal processes in this study, cast doubt on the utility of minor differences in

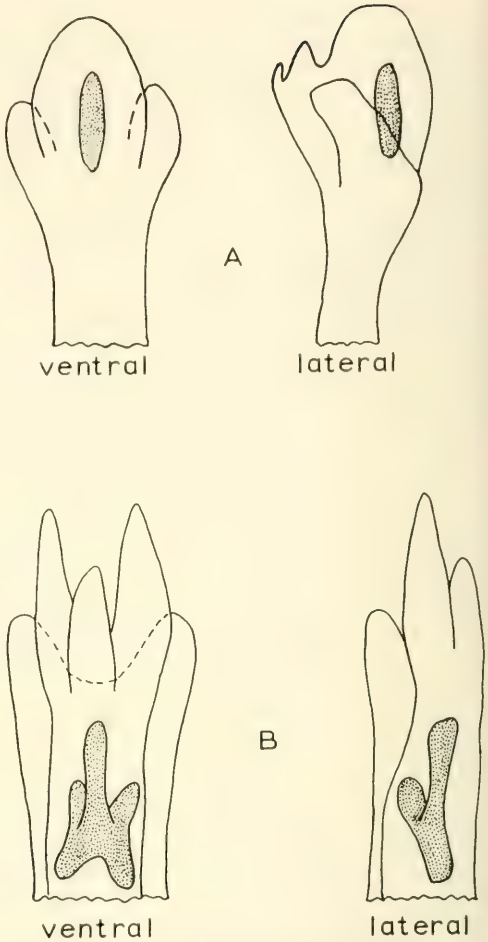


Figure 18. Clitorides of two cricetids, *Ondatra zibethicus* (A) and *Mesocricetus auratus* (B), illustrated in ventral (urethral) and lateral views. The "os clitoridis" of each is stippled.

form and size of the complex baculum in systematic studies at the lower taxonomic levels in those rodents in which it occurs.

The source of specimens employed in such studies also seems to be of considerable importance. Unfortunately, many specimens available in collections, and often used in morphological and systematic studies, have been aged on such criteria as the condition of the pelage and/or the size of the testes and epididymides. Whereas such criteria may determine "ecologically adult" individuals (i.e. individuals functioning as sexually mature entities in a population), they provide no reliable information on the true chronological or physiological age of the

individual. Since only a small percentage of rodents seem to achieve full morphological adulthood under natural conditions, laboratory colonies of known age animals can perhaps provide better material for comparative morphological studies of male reproductive organs and systematic studies based on these elements than can be obtained in the field.

This does not mean to imply that observable differences do not exist between the bacula of different muroid rodents, particularly at, and above, the generic level. At these levels gross differences in proportions and/or dimensions can generally be substantiated as has been shown by Hooper (1960 and other papers) and Hooper and Musser (1964). Even at these levels, however, it would seem imperative to understand something of the development of the baculum, or at least to select bacula from individuals of large size as these may represent the maximum, and therefore characteristic development of the form involved, reducing the variability caused by the endocrine state, diet, and other factors.

Above the generic level basic anatomical patterns of bacular development and form, as well as association with other structures of the glans penes should be similar within phylogenetically related groups. Within the Rodentia such information is currently only available within the myomorphs, and the similarity of the baculum or the complete glans penis in diversely classified muroids has been noted for some time. Hamilton (1946) compared *Oryzomys* and *Sigmodon* to the microtines. Hooper and Musser (1964) in a study of the glans penes, considered cricetids and murids to represent a single family (Muridae). Arata (1964), studying the male accessory reproductive glands, demonstrated that a basic pattern existed in murids and cricetids, and suggested that only one family was represented. Hershkovitz (1962) discounted the commonly accepted differences in dental pattern between the murids and cricetids and recognized only a single family (Muridae), preferring the evidence afforded by the phallus.

The similarity of bacular form in *Rattus* and the cricetids examined in this study supports the thesis that murids and cricetids represent but a single family. The development of the baculum of *Rattus* described by Ruth (1934), and the presence of a movable joint between proximal and distal elements of the baculum of *Rattus* and the cricetids noted in this report suggests that basic homologous morphological forms are represented.

Although all cricetids examined by us have calcified fibro-cartilage distal elements as contrasted to the bony distal processes of *Rattus*, far too many muroids remain unexamined, and little systematic significance can be placed on this difference at this time.

The fusion of the distal elements seen in *Rattus* is greater than that observed in the cricetids, but is probably derived from the basic cricetid pattern. Hooper and Hart (1962) note similar trends in microtines, and Hooper and Musser (1964) point out that this trend may have occurred several times, and is evident in microtines, murines, South American cricetines and Old World cricetines, producing secondarily simple penes, derived from an ancestral complex stock. Bittera (1918) previously suggested that such reductions were secondary. The evidence produced by a study of the male accessory reproductive glands (Arata, 1964) also suggests that certain glandular complements, usually present along with the complex baculum occurs in muroids (including cricetines, microtines, and murines), and is variously reduced in different subgroups.

Thus, the data presented above reinforce the importance of the baculum and associated phallic structures in studies of muroid rodents at the generic level and above, and suggest caution concerning the utilization of the baculum alone at specific and subspecific levels in rodents in which the complex type is present.

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