Glans penes and bacula of five species of *Apodemus* (Rodentia : Muridae) from Croatia, Yugoslavia

by

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Les pénis et les os péniens de cinq espèces d'*Apodemus* ont été examinés. Dans ce genre, le pénis est cylindrique et présente une crête dorsale, un sillon ventral, un processus apical et une constriction transversale. L'os pénien comprend une partie osseuse proximale et un cartilage trilobé à l'extrémité. La partie osseuse a la forme d'une flèche.

L'analyse des caractères morphologiques et des mensurations ne révèle pas de différences qui puissent être attribuées à une variation non géographique. Cependant, selon certains indices, il peut exister une variation géographique chez *Apodemus sylvaticus*. On note d'importantes différences spécifiques : *A. mystacinus* est facilement reconnaissable, notamment à cause de sa taille. Bien que les quatre autres espèces soient similaires, *A. agrarius* et *A. flavicollis* peuvent être différenciés l'un de l'autre et de *A. krkensis* et *A. sylvaticus*. Les ressemblances entre *A. krkensis* et *A. sylvaticus*, en plus des autres facteurs, rendent les relations taxonomiques et systématiques de ces deux formes très incertaines : d'après cette étude elles seraient synonymes.

A detailed study of glans penis and baculum of *Apodemus agrarius*, *A. flavicollis*, *A. krkensis*, *A. mystacinus*, and *A. sylvaticus* was conducted. Descriptions and comparisons of these structures were made of the different species and geographical samples within one species. Based on physical characters, measurements, and statistical analysis, comments were made regarding possible taxonomic and systematic relationships among these species.

INTRODUCTION

Previous investigations regarding the morphology of the glans penis and baculum have proven useful in understanding the systematic relationships of mammalian species (Hooper, 1958, 1959, 1960, 1961, 1962; Hooper and Musser, 1964; Layne, 1960; Lidicker, 1968). The comparative morphology of the male phallus has been particularly useful in differentiating closely related species (Genoways, 1973). Under these circumstances, the glans penis and baculum may serve as taxonomic indicators while functioning as a mechanical reproductive isolating mechanism.

Within the Republic of Croatia, Yugoslavia, there are five nominal species of *Apodemus* in which there are several taxonomic problems (Corbet, 1966). *Apodemus flavicollis* and *A. sylvaticus* are difficult to distinguish morphologically (Dulíc and Tvrtkovíc, 1972) in this region and often occur sympatrically in deciduous woodlands. In some parts of Europe they even have been known to interbreed (Corbet, 1966). *Apodemus agrarius* occupies not only deciduous woodlands but also broad-leaved woodlands (Corbet, 1966) and although similar to *A. flavicollis* and *A. sylvaticus* in size, it is easily recognized by its dorsal black stripe and distinctive cranium. *Apodemus*

krkensis is endemic to the island of Krk, where it is sympatric with *A. sylvaticus*. These species differ primarily in dorsal coloration, *A. sylvaticus* being rufous brown and *A. krkensis* gray (Miríc, 1968). *Apodemus mystacinus* inhabits rocky hillsides and dry, scrubby woodland, and is readily distinguished from other members of the genus by its larger size, gray pelage, and dentition (Corbet, 1966).

In an attempt to resolve the taxonomic problems in the Croatian species of *Apodemus*, we have examined and compared bacula and glans penes. Based on the following analyses, comments have been made regarding the systematic relationships of these species.

METHODS AND MATERIALS

Penes were removed from 122 specimens representing five species of *Apodemus* — *A. agrarius*, *A. flavicollis*, *A. krkensis*, *A. mystacinus*, and *A. sylvaticus*. Specimens were taken from selected localities in the Republic of Croatia in Yugoslavia. Penes were removed from freshly killed specimens and preserved in a solution of ethyl alcohol, formalin, and acetic acid (AFA).

Each sample was examined externally from dorsal, ventral, and lateral positions. In addition, terminal and epidermal structures were noted. These characters were compared among individuals, geographical regions, and species. Anatomical terminology used for descriptions generally follow that of Hooper (1958, 1960) and Lidicker (1968).

For purposes of final analysis and comparisons, only adult individuals were utilized, thus reducing the sample size to 62. For *A. agrarius*, *A. flavicollis*, *A. krkensis*, and *A. sylvaticus* the criterion used for determining adults was the amount of toothwear on the molars. Those individuals showing cusps that were totally or nearly worn smooth were considered to be mature adults and were incorporated in further examination. Because toothwear was not as evident in adult *A. mystacinus*, the criteria used in determining mature individuals were based on relative size and development of external and cranial features, such as pelage, total length, testes size, and condition of suture lines on the skull.

External examination and illustration of individual glans was made with the use of a Wild camera-lucida, dissecting scope. An illustration of the dorsal, ventral, and lateral aspects was prepared for each specimen. Measurements were taken from the illustrations and corrected for magnification.

Individual glans were subsequently cleared and stained (Hooper, 1958; Russell, 1973) so that the size, shape, and position of the baculum could be ascertained. Because of potential loss of epidermal structures and alterations in the general shape of the glans, caused by clearing and staining, such procedures were performed only after thorough examination of untreated specimens. Following clearing and staining, the baculum was removed for examination to avoid any distortion of the baculum size and shape, caused by light diffraction through the cleared tissue. Bacular measurements were taken in the same manner as that described for measuring external dimensions of the glans.

Using the technique described above, the following measurements of the glans and baculum were recorded.

Length of the distal tract. — Overall length of the phallus from the proximal margin to the distal projection (excluding urethral structures) as measured from the dorsal aspect.

Greatest width of proximal section. — Distance across widest portion of the proximal half of the glans as measured from the dorsal aspect and perpendicular to the long axis.

Greatest width of distal section. — Greatest width of distal half of the glans as measured from the dorsal aspect and perpendicular to the long axis.

Lateral width of the glans midsection. — Distance across the midsection of glans at the constriction as measured from a dorsal aspect and perpendicular to the long axis.

Dorsoventral height of glans midsection. — Distance across the midsection of the glans at the constriction as measured from a lateral aspect and perpendicular to the long axis.

Length of baculum. — Greatest length of the baculum, including cartilaginous structures.

Length of proximal section of baculum. — Greatest length of the baculum, excluding cartilaginous structures.

Lateral width of baculum base. — Greatest width across the base of the baculum, as viewed from a dorsal aspect.

Dorsoventral height of baculum base. — Greatest distance across the base of the baculum, as viewed from the side.

Relative size relationships among glans penes and bacula are often examined by utilizing the length of the hind foot (with claw) as a standard (Hooper, 1958, 1959, 1960, 1961, 1962). Because hind foot measurements often lack consistency and precision in documentation, this study substituted condylobasal length as a comparative measure. Hind foot lengths were documented, for the benefit of future investigators.

Statistical analyses of geographical samples of each species were performed on an IBM 370 computer. Univariate analyses were made with the use of a program, called UNIVAR (Power, 1970), which computes standard statistics (mean, variance, standard deviation, standard error, coefficient of variation, and range) and makes a single-classification analysis of variance (F-test, significance level .05) to test for significant differences between or among means. Significantly different means were used in a Sum of Squares Test Procedure (SS-STP) to determine nonsignificant subsets. Means (rounded off to one decimal place) of characters described above (excluding hind foot length) for each group were used in a NT-SYS multivariate analysis to determine phenetic relationships. These relationships were computed by cluster analysis from a distance matrix, and expressed in the form of a phenogram.

RESULTS

DESCRIPTION

The glans penis of *Apodemus* is generally cylindrical in shape and is two to three times longer than wide. Near the midsection of the distal tract there is a shallow constriction. This constriction varies in distinctness among species and divides the glans into definite proximal and distal sections. Generally, the distal section has a distinctive dorsal ridge and a ventral groove. The dorsal ridge tends to extend distally into the terminal crater. Proximally, the dorsal ridge may extend the entire length of the glans. The distal portion of the glans consists of a terminal crater

that encompasses various urethral craters and lappets. Also, within the terminal crater exists a bacular mound and lateral bacular processes which collectively maintain a trilobed shape created by the distal section of the baculum.

Epidermally, tubercles and spines are present. The tubercles tend to be more massive on the proximal section of the glans. The spines vary in size and number, with more numerous and larger spines occurring proximally and ventrally. Typically the spines occur around the terminal crater, on the dorsal ridge, and on the proximal section of the glans, and are either nonexistent or considerably reduced on the ventral and lateral sides of the distal section. No spines occur within the terminal craters except where the dorsal ridge extends into the outer crater. Individual spines are simple and consist of a single proximally oriented projection that originates from a depression in the epidermis.

The baculum is composed of two parts. The distal portion is cartilaginous and appears to be trilobed, particularly from a dorsal view. The middle lobe is generally the most prominent. The cartilage extends proximally along the lateral sides of the osseous portion of the baculum (proximal section of the baculum) which, when viewed from a dorsal aspect, consists of a distally tapering shaft that expands abruptly at the base. The proximal section of the baculum may possess faint dorsal ridges on the base and midsection of the shaft. From a lateral view it is curved slightly, so that the dorsal and ventral sides appear to be concave and convex in shape, respectively. The base is expanded dorsoventrally. The distal portion of the os baculum is slightly expanded.

Basically the description of the baculum is the same in each species of *Apodemus*, except for *A. mystacinus* where the primary difference is attributed to size. Individual species also possess other characters, or combinations of characters of other portions of the glans penis that may be used for differentiation. More detailed descriptions for each species are given below.

Apodemus agrarius.

The glans tapers distally and proximally when examined dorsally or ventrally. From the lateral view, the dorsal and ventral margins are almost parallel, with the exception that the dorsal side might be slightly concave. The dorsal ridge and ventral groove are well developed and extend from the midsection into the terminal crater. The proximal section of the glans is essentially featureless, whereas the distal portion is slightly tapered distally on the ventral side. The apex of the glans has two definite sets of processes which, in their natural position, may extend outside of the crater. The largest, and external, process opens ventrally and encompasses the internal process, which also opens ventrally but is reduced in size. Nodules and spines are present over the entire glans in a manner characteristic of the genus. The spines themselves tend to be smaller and more numerous than those of other species of *Apodemus* (Fig. 1).

Apodemus flavicollis.

The general shape and size is similar to that of *A. agrarius* with the exception that the proximal section of the glans is more bulbous, and that the distal section is somewhat more recurved and less tapered distally. A lateral examination of *A. flavicollis* reveals that the dorsal side is also more strongly recurved at the midsection. The dorsal ridge is larger, but not as distinct as that of *A. agrarius*. It appears that the ridge of *A. flavicollis* may extend onto the proximal section of the glans.

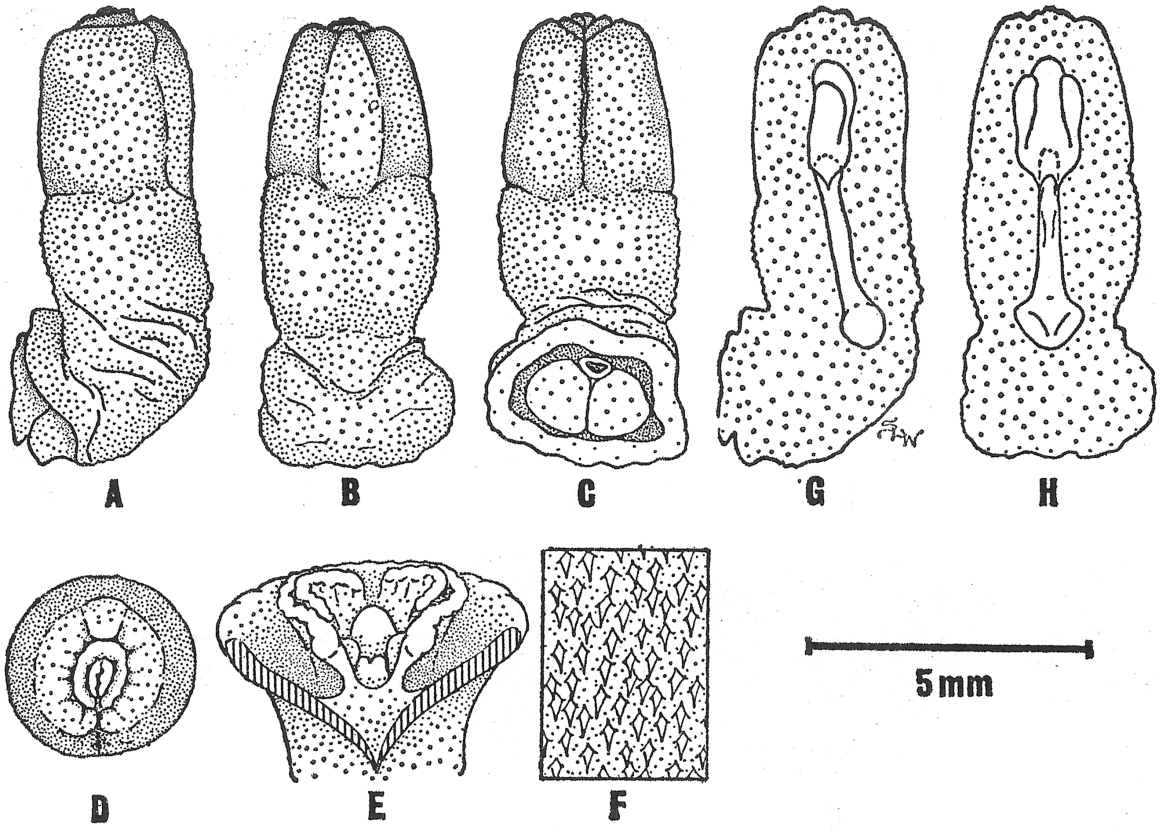

Fig. 1. — Glans penis and baculum of *Apodemus agrarius* from 6 km N, 1 km E Lekenik. Illustrated are the lateral (a), dorsal (b), and ventral (c) views of the entire glans penis ; apical views of the glans penis as it appears naturally (d) and incised midventrally to expose the apical processes and craters (e) ; epidermal structures of the midventral region (f) ; lateral (g) and dorsal (h) views of the baculum showing the respective positions within the glans penis.

Unlike *A. agrarius* (and other species discussed later in text) there is no apparent ventral groove present on the distal section of the glans. The apex of the glans is similar to that of *A. agrarius* except that the processes are not partitioned on the dorsal and ventral sides, and in their natural position, they are more enclosed within the margins of the outer crater. The spines of *A. flavicollis* tend to be larger than those of *A. agrarius* (Fig. 2).

Apodemus krkensis.

The general shape of the glans of *A. krkensis* is similar to that of *A. flavicollis*. In contrast to *A. flavicollis*, *A. krkensis* has a ventral groove and a dorsal ridge which is clearly defined for the entire length of the glans. The sides of the ridge expand slightly from the center of the proximal end of the glans, converge somewhat at the constriction, flare out strongly on the distal section of the glans, and finally meet at the terminal crater. Unlike *A. agrarius* the ventral groove is relatively wide and contains longitudinal folds that tend to bring the central part to the surface. Also, the groove extends almost the full length of the distal section and does not continue into the terminal crater. The apex of the glans contains processes similar to those of *A. flavicollis* except they tend to be less elaborate in structure and the external processes are not united ventrally. The inner processes are also relatively large, as compared to the external processes. *A. krkensis* has greater numbers of spines on the ventral side along the ventral groove. The size of spines is similar to that of *A. flavicollis* (Fig. 3).

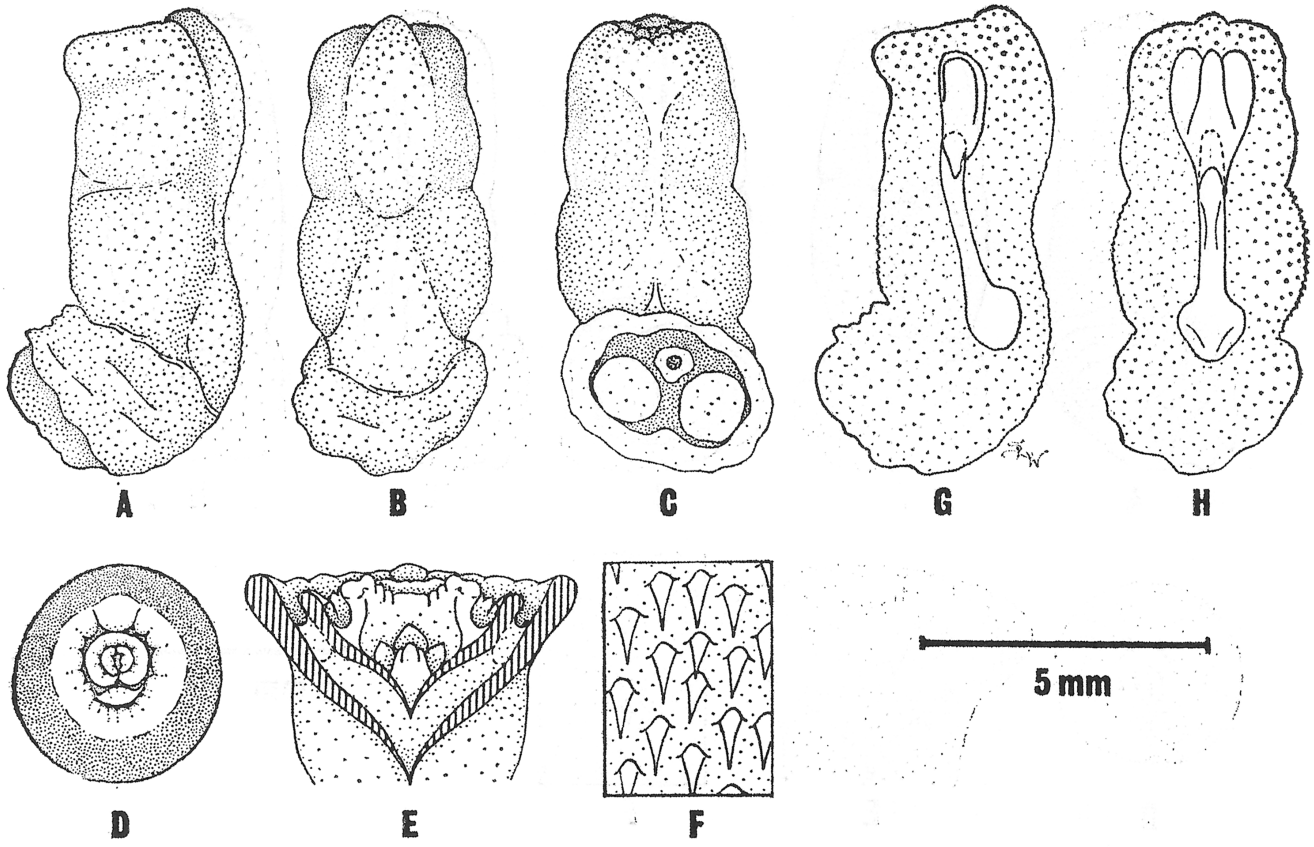

Fig. 2. — Glans penis and baculum of *Apodemus flavicollis* from 8 km W Lekenik, illustrated as in Figure 1.

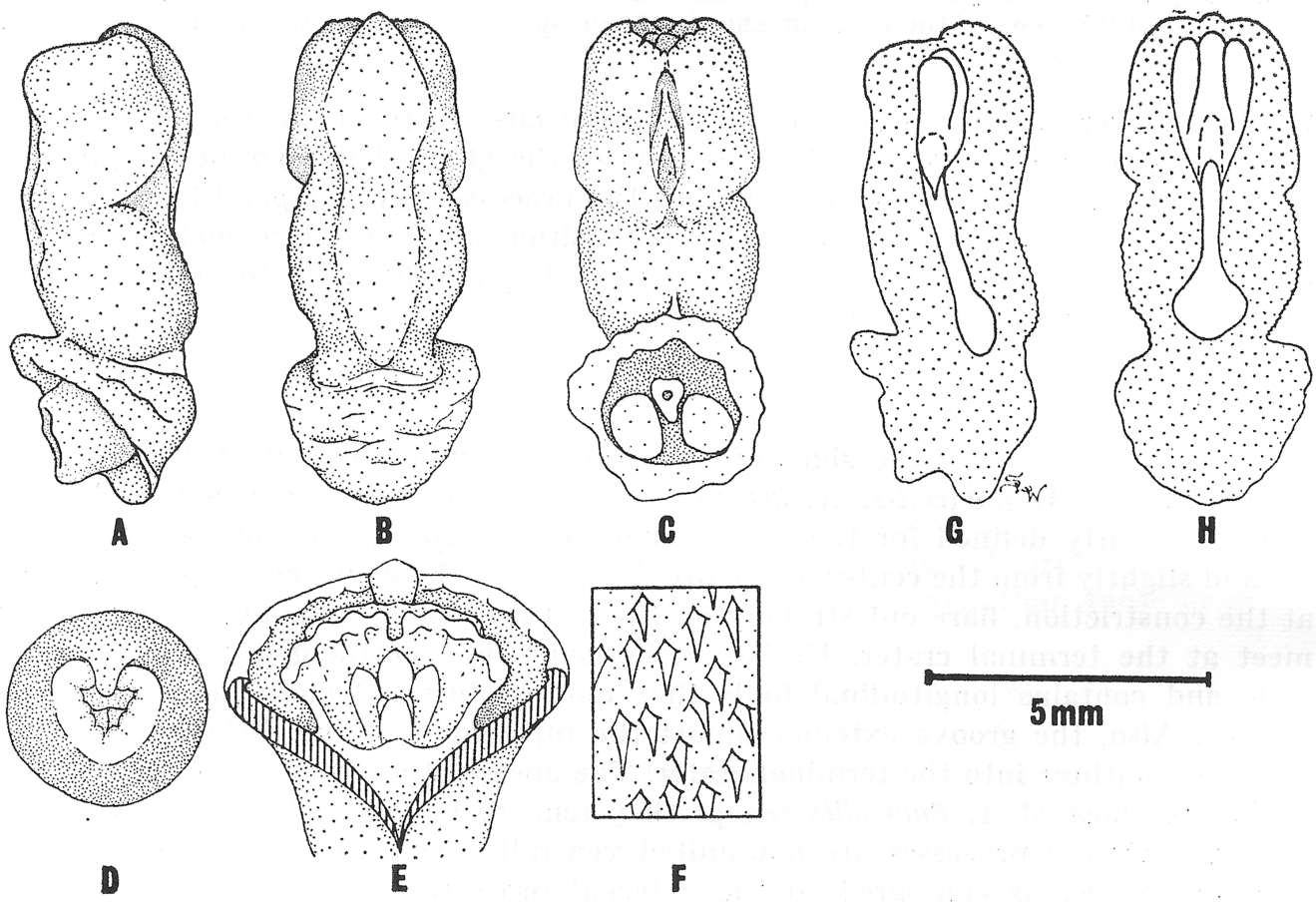

Fig. 3. — Glans penis and baculum of *Apodemus krkensis* from 3.6 km S, 4.3 km E Krk, illustrated as in Figure 1.

Apodemus mystacinus.

The glans of *A. mystacinus* is distinct from the other species by its larger size and modified shape. From dorsal and ventral views the proximal section of the glans is bulbous in shape and shorter than the distal section. Margins of the distal section are slightly recurved and are narrower than the margins of the proximal section. Lateral examination shows a greatly enlarged distal section and a tapering proximal section. The ventral margin of the proximal section is deeply curved inward, whereas, the dorsal margin is relatively straight and parallel to the longitudinal axis. Unlike other species of *Apodemus*, the dorsal ridge is essentially nonexistent. However, traces of the ridge do occur near the terminal crater. One distinguishing feature for this species is a ventral depression or groove in the middle of the proximal section. This groove is curved slightly and is oriented perpendicular to the longitudinal axis of the glans. Another distinguishing character of this species is the occurrence of a single process that creates a complete inner crater at the apex of the glans. Both the inner and outer crater walls of *A. mystacinus* possess smaller projections, and maintain margins which are more or less at the same level. Unlike other members of the genus epidermal spines are large, conspicuous, and occur on all parts of the glans, with the exception of the internal parts of the terminal craters (Fig. 4).

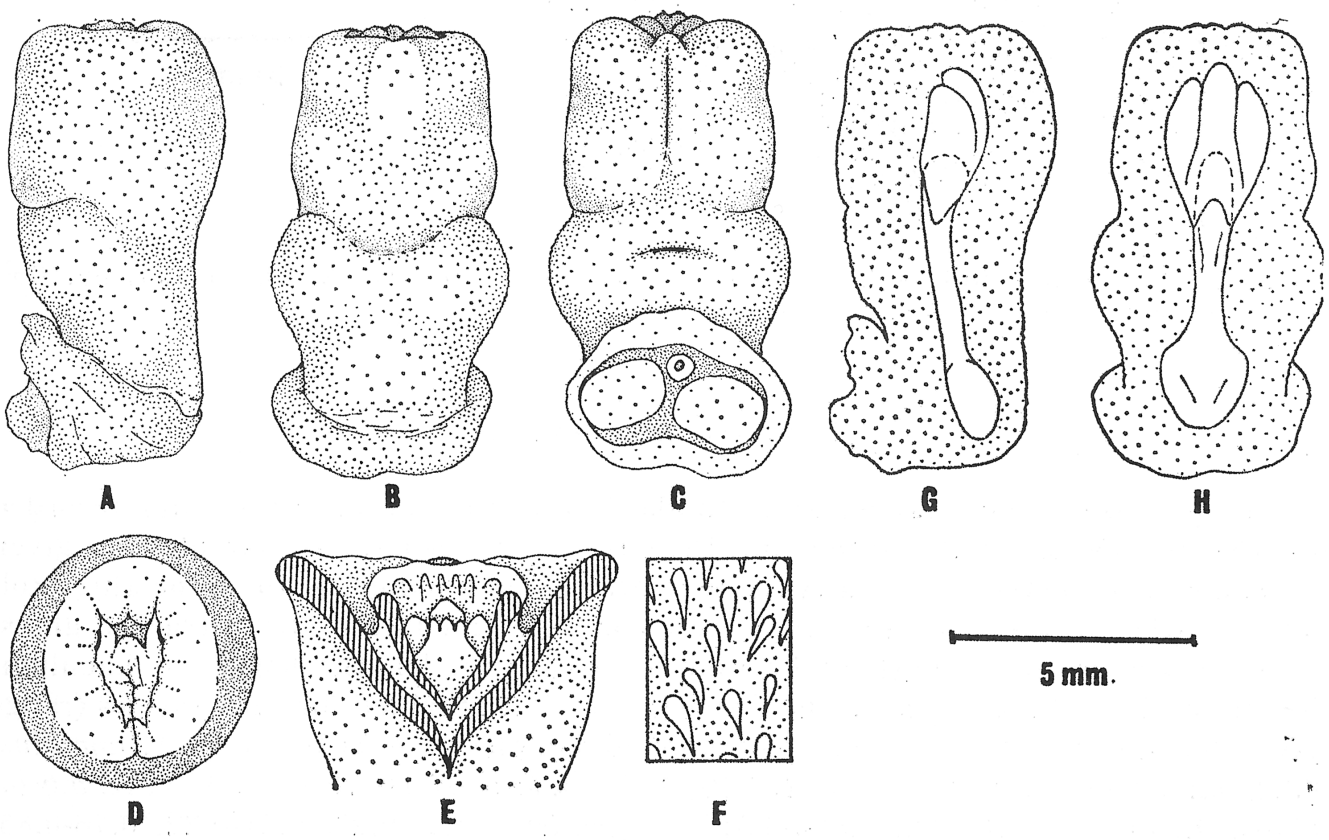

Fig. 4. — Glans penis and baculum of *Apodemus mystacinus* from 2 km N, 11 km E Posedarje illustrated as in Figure 1.

Apodemus sylvaticus.

Basically the glans of *A. sylvaticus* is the same as *A. krkensis*. Minor differences within the terminal crater and distinctness of the dorsal ridge and ventral grove

appear to be the only criteria that may differentiate the two species. Because individual variation may be responsible for some of the observed differences, and this possibility cannot be checked without additional samples of *A. krkensis*, no distinguishing characters can be defined at this time to separate the two species (Fig. 5).

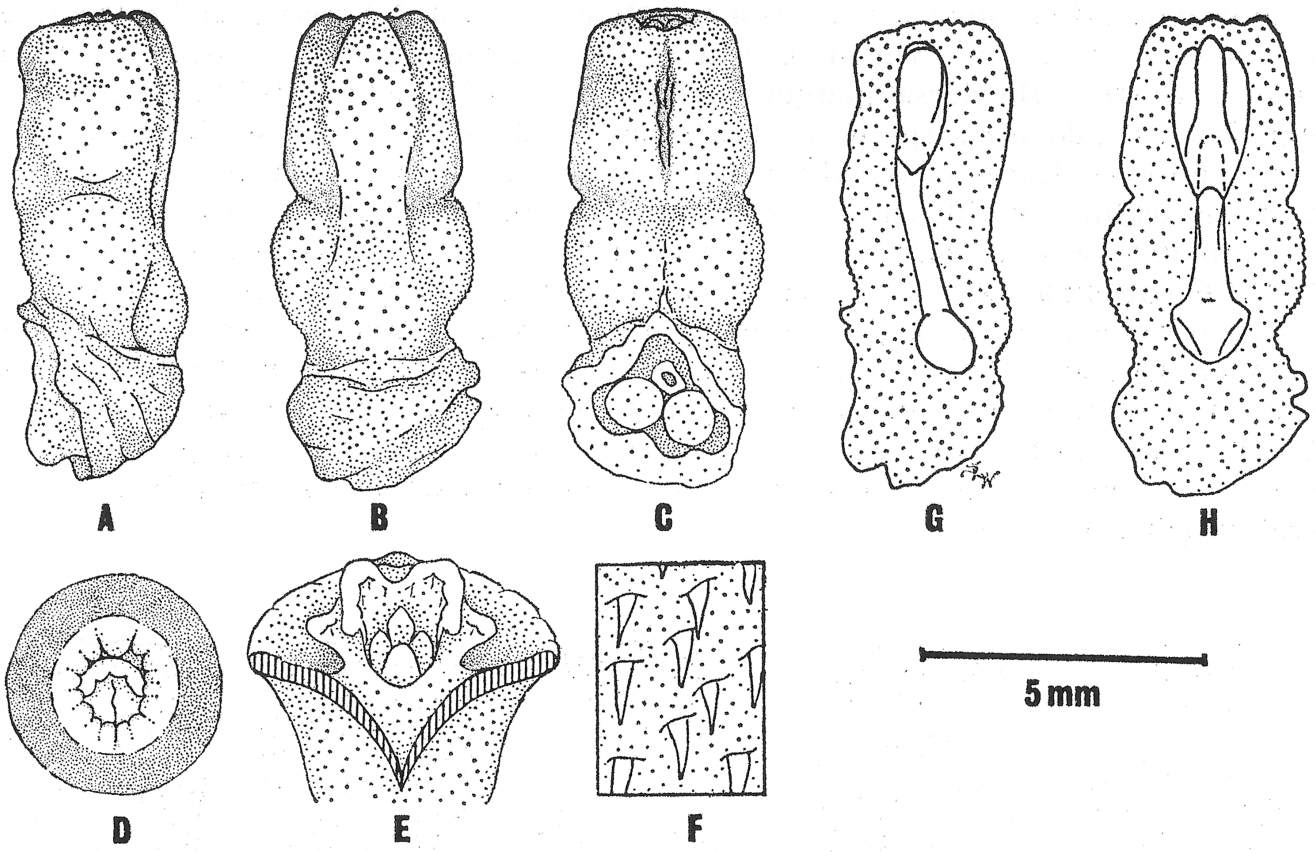

Fig. 5. — Glans penis and baculum of *Apodemus sylvaticus* from 6 km N, 1 km E Lekenik, illustrated as in Figure 1.

Statistical analyses

Sample size, mean, range, and standard deviation of measurements recorded for the five species of *Apodemus* and their respective geographic samples are given in Table 1. To determine relative size relationships among the taxa the three following ratios, based on mean values, were computed : length of distal tract of glans/condylobasal length; length of baculum/condylobasal length; length of baculum/length of distal tract of glans. The respective ratios, obtained for each species (range given for species with different geographical samples) are as follows : *A. agrarius*, 0.23, 0.21, 0.89; *A. flavicollis*, 0.22, 0.19, 0.83; *A. krkensis*, 0.24, 0.20, 0.81; *A. mystacinus*, 0.25-0.27, 0.21-0.22, 0.81-0.83; *A. sylvaticus*, 0.26-0.27, 0.21-0.22, 0.76-0.85.

Individual variation within samples was examined using samples of *A. agrarius* from Zagreb and *A. sylvaticus* from Krk. The coefficients of variation for condylobasal length in the two samples were 3.4 and 2.3, respectively. The average coefficient of variation of measurements taken of the glans was 5.4 for *A. agrarius*, with a range from 5.0 (width of proximal section of glans) to 5.9 (dorsoventral height of glans midsection). The same average for *A. sylvaticus* was 4.8, with a range of 3.6 (dorsoventral height of glans midsection) to 6.3 (lateral width of glans midsec-

tion). Bacular dimensions showed the greatest amount of variation with average coefficients of variation of 11.8 and 7.5 for *A. agrarius* and *A. sylvaticus*, respectively. The range of coefficients of *A. agrarius* was 9.1 (length of baculum) to 14.6 (lateral width of baculum base) and *A. sylvaticus* was 4.5 (length of proximal section of baculum) to 11.9 (dorsoventral height of baculum base).

Geographical variation of *Apodemus*, based on characters used in this study, was examined using five samples of *A. sylvaticus*. The sample from Zadar was excluded because of inadequate sample size. The five samples showed significant differences ($P \geqslant .05$) for all of the characters except for the width of the proximal section of glans, lateral width of the glans midsection, dorsoventral height of the glans midsection, and length of the proximal section of baculum. All of the characters showing significant differences, except condylobasal length and greatest width of the distal section of the glans, had overlapping subsets formed in the SS-STP analysis. Condylobasal length had two non-overlapping subsets, one consisting of the samples from Posedarje, Rab, and Krk, the other consisting of sample Obrovac and Zagreb. Greatest width of the distal section of the glans also had two non-overlapping subsets, but the first subset consisted of only the sample from Krk. The only possible geographic trend noted is that individuals of samples from Krk and Posedarje tend to be generally larger than individuals of other samples of *A. sylvaticus*.

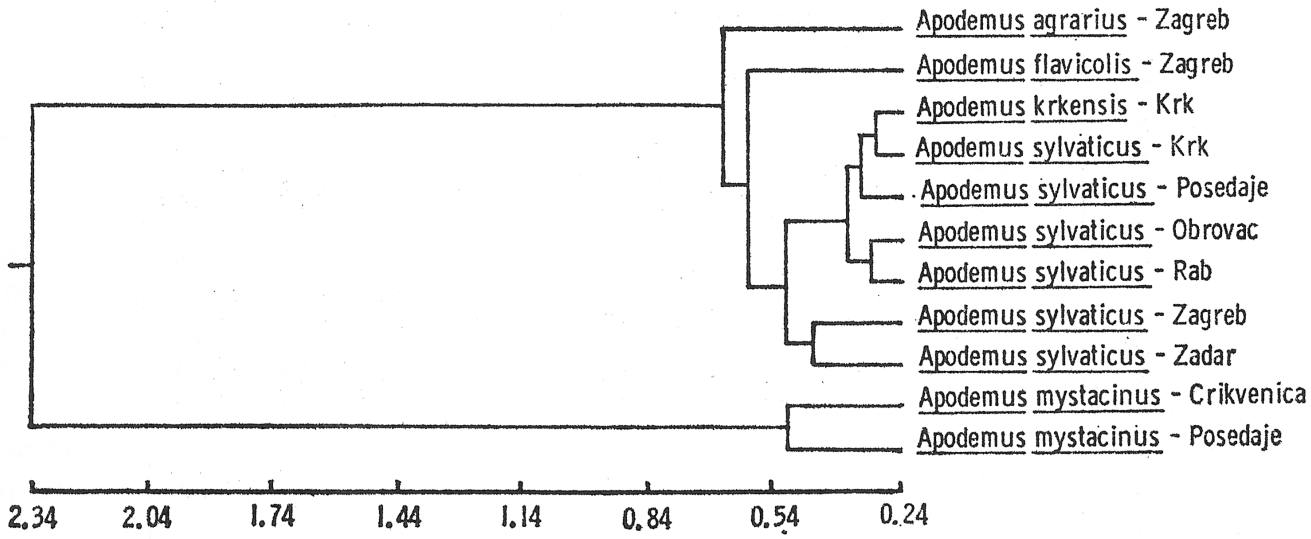

Fig. 6. — Distance phenogram resulting from cluster analysis of 11 samples of *Apodemus*.

Means of 10 characters, given in Table 1, were incorporated in a multivariate analysis of the 11 samples. Phenetic relationships of these samples were expressed by a phenogram (Fig. 6) which was computed by cluster analysis from a distance matrix. Two major groups were revealed in the phenogram. Samples of *A. mystacinus* formed one group, whereas the other group consisted of the remaining species. Within the latter group, three subdivisions were formed by *A. agrarius*, *A. flavicollis*, and a combination of *A. sylvaticus* and *A. krkensis*. This analysis indicated that *A. sylvaticus* and *A. krkensis* are more similar to each other than to any other species examined, with the sample of *A. sylvaticus* from Krk being more similar to *A. krkensis* than to other samples of *A. sylvaticus*. The coefficient of cophenetic correlation for the distance phenogram was 0.982.

TABLE 1. — Mean, range, and standard deviation of dimensions used in analyzing the glans and bacula of *Apodemus*.

Species	Locality	N	Mean	Min.	Max.	S.D.
		Hind foot length				
Apodemus agrarius	Zagreb	10	20.5	19	22	0.83
Apodemus flavicollis	Zagreb	6	25.6	25	26	0.49
Apodemus krkensis	Krk	2	23.5	23	24	0.71
Apodemus mystacinus	Crikvenica	2	29.0	29	29	0.00
Apodemus mystacinus	Posedarje	6	27.0	26	28	0.63
Apodemus sylvaticus	Krk	11	24.3	23	25	0.61
Apodemus sylvaticus	Obrovac	5	22.9	22	23.5	0.65
Apodemus sylvaticus	Posedarje	3	24.2	24	24.5	0.29
Apodemus sylvaticus	Rab	4	24.4	24	25.5	0.75
Apodemus sylvaticus	Zadar	2	23.0	23	23	0.00
Apodemus sylvaticus	Zagreb	6	22.2	21	23	0.75
		Condylobasal length				
Apodemus agrarius	Zagreb	9	25.9	24.2	27.0	0.89
Apodemus flavicollis	Zagreb	5	28.7	28.0	29.2	0.48
Apodemus krkensis	Krk	2	26.3	25.0	27.7	1.91
Apodemus mystacinus	Crikvenica	2	32.0	31.8	32.2	0.28
Apodemus mystacinus	Posedarje	6	31.8	31.5	32.2	0.26
Apodemus sylvaticus	Krk	11	24.2	23.4	25.0	0.55
Apodemus sylvaticus	Obrovac	4	23.4	23.1	23.6	0.21
Apodemus sylvaticus	Posedarje	3	24.5	24.4	24.6	0.11
Apodemus sylvaticus	Rab	4	24.4	24.1	24.9	0.36
Apodemus sylvaticus	Zadar	2	24.1	23.9	24.2	0.21
Apodemus sylvaticus	Zagreb	6	23.3	22.4	23.8	0.55
		Length of distal tract of glans				
Apodemus agrarius	Zagreb	9	6.10	5.63	6.72	0.33
Apodemus flavicollis	Zagreb	6	6.39	6.21	6.64	0.15
Apodemus krkensis	Krk	2	6.35	6.15	6.56	0.29
Apodemus mystacinus	Crikvenica	2	8.51	8.04	8.97	0.66
Apodemus mystacinus	Posedarje	6	8.04	7.71	8.34	0.23
Apodemus sylvaticus	Krk	10	6.63	6.11	7.15	0.27
Apodemus sylvaticus	Obrovac	5	6.36	6.22	6.57	0.15
Apodemus sylvaticus	Posedarje	3	6.34	6.09	6.63	0.27
Apodemus sylvaticus	Rab	4	6.45	6.38	6.50	0.05
Apodemus sylvaticus	Zadar	1	6.21	6.21	6.21	–
Apodemus sylvaticus	Zagreb	6	6.17	5.81	6.47	0.29
		Greatest width of proximal section of glans				
Apodemus agrarius	Zagreb	9	3.25	3.03	3.51	0.16
Apodemus flavicollis	Zagreb	6	3.12	2.89	3.50	0.22
Apodemus krkensis	Krk	2	3.12	3.03	3.21	0.13
Apodemus mystacinus	Crikvenica	2	4.77	4.59	4.94	0.25
Apodemus mystacinus	Posedarje	6	4.55	4.38	4.80	0.16
Apodemus sylvaticus	Krk	10	3.15	2.90	3.37	0.17
Apodemus sylvaticus	Obrovac	5	3.06	3.01	3.12	0.04
Apodemus sylvaticus	Posedarje	3	3.03	2.99	3.11	0.07
Apodemus sylvaticus	Rab	4	2.97	2.85	3.19	0.15
Apodemus sylvaticus	Zadar	1	3.16	3.16	3.16	–
Apodemus sylvaticus	Zagreb	6	3.00	2.90	3.28	0.14
		Greatest width of distal section of glans				
Apodemus agrarius	Zagreb	9	3.06	2.81	3.21	0.16
Apodemus flavicollis	Zagreb	6	3.03	2.91	3.34	0.16
Apodemus krkensis	Krk	2	3.11	3.08	3.13	0.03
Apodemus mystacinus	Crikvenica	2	4.19	4.07	4.31	0.17
Apodemus mystacinus	Posedarje	6	4.05	3.91	4.32	0.16
Apodemus sylvaticus	Krk	10	3.15	2.87	3.36	0.15
Apodemus sylvaticus	Obrovac	5	2.99	2.93	3.06	0.05
Apodemus sylvaticus	Posedarje	3	2.92	2.89	2.95	0.03
Apodemus sylvaticus	Rab	4	2.96	2.87	3.12	0.11
Apodemus sylvaticus	Zadar	1	3.02	3.02	3.02	–
Apodemus sylvaticus	Zagreb	6	2.99	2.86	3.19	0.11
		Lateral width of glans midsection				
Apodemus agrarius	Zagreb	9	2.94	2.73	3.20	0.15
Apodemus flavicollis	Zagreb	6	2.65	2.49	2.94	0.16
Apodemus krkensis	Krk	2	2.63	2.62	2.65	0.02
Apodemus mystacinus	Crikvenica	2	3.75	3.65	3.86	0.15
Apodemus mystacinus	Posedarje	6	3.67	3.47	3.90	0.17
Apodemus sylvaticus	Krk	10	2.68	2.32	2.91	0.17
Apodemus sylvaticus	Obrovac	5	2.60	2.51	2.68	0.08
Apodemus sylvaticus	Posedarje	3	2.54	2.52	2.55	0.02
Apodemus sylvaticus	Rab	4	2.55	2.48	2.69	0.10
Apodemus sylvaticus	Zadar	1	2.53	2.53	2.53	–
Apodemus sylvaticus	Zagreb	6	2.61	2.44	2.82	0.13
		Dorsoventral height of glans midsection				
Apodemus agrarius	Zagreb	9	2.61	2.41	2.91	0.15
Apodemus flavicollis	Zagreb	6	2.59	2.31	2.93	0.22
Apodemus krkensis	Krk	2	2.54	2.52	2.56	0.03
Apodemus mystacinus	Crikvenica	2	3.73	3.72	3.73	0.01
Apodemus mystacinus	Posedarje	6	3.43	3.21	3.77	0.19
Apodemus sylvaticus	Krk	10	2.62	2.43	2.74	0.09
Apodemus sylvaticus	Obrovac	5	2.49	2.38	2.67	0.11
Apodemus sylvaticus	Posedarje	3	2.46	2.40	2.55	0.08
Apodemus sylvaticus	Rab	4	2.50	2.30	2.64	0.15
Apodemus sylvaticus	Zadar	1	2.64	2.64	2.64	–
Apodemus sylvaticus	Zagreb	6	2.53	2.39	2.67	0.11
		Length of baculum				
Apodemus agrarius	Zagreb	9	5.43	4.85	6.01	0.49
Apodemus flavicollis	Zagreb	5	5.31	5.14	5.58	0.18
Apodemus krkensis	Krk	1	5.16	5.16	5.16	–
Apodemus mystacinus	Crikvenica	2	7.10	6.92	7.28	0.25
Apodemus mystacinus	Posedarje	3	6.65	6.39	7.10	0.39
Apodemus sylvaticus	Krk	9	5.40	4.73	5.79	0.37
Apodemus sylvaticus	Obrovac	5	4.81	4.68	4.99	0.12
Apodemus sylvaticus	Posedarje	3	5.22	5.06	5.45	0.20
Apodemus sylvaticus	Rab	4	5.11	4.96	5.34	0.18
Apodemus sylvaticus	Zadar	2	4.95	4.85	5.05	0.14
Apodemus sylvaticus	Zagreb	5	5.22	4.70	5.60	0.41
		Length of proximal section of baculum				
Apodemus agrarius	Zagreb	10	3.82	3.28	4.43	0.38
Apodemus flavicollis	Zagreb	5	3.78	3.57	3.95	0.13
Apodemus krkensis	Krk	2	3.81	3.78	3.84	0.04
Apodemus mystacinus	Crikvenica	2	5.33	5.31	5.36	0.03
Apodemus mystacinus	Posedarje	6	5.19	4.99	5.38	0.17
Apodemus sylvaticus	Krk	9	3.77	3.48	4.00	0.17
Apodemus sylvaticus	Obrovac	5	3.59	3.51	3.65	0.06
Apodemus sylvaticus	Posedarje	3	3.80	3.73	3.93	0.11
Apodemus sylvaticus	Rab	4	3.79	3.68	3.98	0.13
Apodemus sylvaticus	Zadar	2	3.74	3.69	3.79	0.07
Apodemus sylvaticus	Zagreb	4	3.62	3.14	3.90	0.33
		Lateral width of baculum base				
Apodemus agrarius	Zagreb	10	1.31	1.10	1.65	0.19
Apodemus flavicollis	Zagreb	6	1.25	1.13	1.48	0.13
Apodemus krkensis	Krk	2	1.31	1.24	1.37	0.09
Apodemus mystacinus	Crikvenica	2	1.69	1.61	1.77	0.11
Apodemus mystacinus	Posedarje	6	1.64	1.55	1.71	0.05
Apodemus sylvaticus	Krk	11	1.26	1.17	1.47	0.09
Apodemus sylvaticus	Obrovac	5	1.16	1.07	1.23	0.07
Apodemus sylvaticus	Posedarje	3	1.36	1.32	1.40	0.04
Apodemus sylvaticus	Rab	4	1.19	1.07	1.35	0.14
Apodemus sylvaticus	Zadar	2	1.07	0.95	1.19	0.17
Apodemus sylvaticus	Zagreb	6	1.17	1.04	1.28	0.11
		Dorsoventral height of baculum base				
Apodemus agrarius	Zagreb	10	0.75	0.63	0.88	0.10
Apodemus flavicollis	Zagreb	6	0.85	0.73	0.94	0.08
Apodemus krkensis	Krk	2	0.73	0.57	0.90	0.23
Apodemus mystacinus	Crikvenica	2	0.99	0.96	1.01	0.03
Apodemus mystacinus	Posedarje	6	0.93	0.79	1.04	0.08
Apodemus sylvaticus	Krk	11	0.79	0.68	0.98	0.09
Apodemus sylvaticus	Obrovac	5	0.72	0.64	0.79	0.06
Apodemus sylvaticus	Posedarje	3	0.92	0.87	0.99	0.06
Apodemus sylvaticus	Rab	4	0.67	0.63	0.72	0.05
Apodemus sylvaticus	Zadar	2	0.74	0.67	0.81	0.10
Apodemus sylvaticus	Zagreb	6	0.83	0.73	0.90	0.07

DISCUSSION

Based on samples of *A. agrarius* from Zagreb and *A. sylvaticus* from Krk, this study found that there was not an appreciable amount of variation within geographical samples of *Apodemus*, except for bacular measurements. It is surprising that a more durable portion of the phallus would show more variability. It is conceivable that such variation could be partially attributed to distortion caused during the dissection of the baculum. This study also found variation to occur among geographical samples of *Apodemus*, based on comparisons of five samples of *A. sylvaticus*. Because some sample sizes used in this study were small, comments concerning nongeographical and geographical variation should be considered as only preliminary observations.

General examination of the glans and baculum of the species of *Apodemus* used in this study clearly isolated *A. mystacinus* from the other species because of its larger size, general shape, and distinctive features such as the absence of a dorsal ridge, single set of urethral processes, and a proximal groove. The remaining species are similar in size and general shape, and must be differentiated according to more refined criteria. The glans of *A. agrarius* is unique from the other species by being somewhat larger, having a well-defined ventral groove and constriction, having a distinctive dorsal ridge which does not extend beyond the constriction, and having processes which extend beyond the terminal crater. The glans of *A. flavicollis* is very similar to that of *A. krkensis* and *A. sylvaticus*, but may be differentiated by a nonexisting or less conspicuous ventral groove, possessing more elaborate apical processes, and having slight differences in the dorsal ridge. For most general characters, *A. krkensis* and *A. sylvaticus* appear identical. However, slight differences may be detected if individual characters are examined. Because of the small sample size of *A. krkensis*, it is not possible to determine if these differences reflect characters that are unique to the species or to the individual specimen. Therefore, the value of these characters for differentiating *A. krkensis* and *A. sylvaticus* cannot be determined until more specimens of *A. krkensis* can be examined. Measurements of *A. krkensis* and *A. sylvaticus* were very similar to those of *A. flavicollis* and were usually overlapping. Therefore, any meaningful comparison, based on measurements, is difficult unless all characters are examined simultaneously, as was done in this study by multivariate analysis using NT-SYS (Fig. 6).

With respect to the relative size relationships of the glans and baculum, *A. agrarius* has a relatively large baculum as compared to the size of the glans, indicated by a ratio of 0.89 compared to ratios of 0.76 to 0.85. Comparing a ratio of 0.19 to ratios of 0.20 to 0.22 suggests that *A. flavicollis* is unique in having a relatively small baculum as compared to the body size. Comparisons of length of the glans to body size (as represented by condylobasal length) indicated that *A. mystacinus* (0.25-0.27) and *A. sylvaticus* (0.26-0.27) possess larger glans, followed by *A. krkensis* (0.24), *A. agrarius* (0.23), and *A. flavicollis* (0.22).

This study found the glans of *A. mystacinus* to be clearly distinct from the four other species. Although the phalli of the four other species were similar, *A. agrarius* and *A. flavicollis* could be differentiated from each other and from *A. krkensis* and *A. sylvaticus*. The similarities between characters and dimensions of *A. krkensis* and *A. sylvaticus* suggest a close systematic relationship between the two and not between *A. krkensis* and *A. mystacinus* as was stated by Miríc (1968). This close relationship is further exemplified by the level of correlation (98.2 percent) and the strong affinities between *A. krkensis* and *A. sylvaticus* from Krk, which were expressed

in the multivariate analysis, thus suggesting that the two species may represent a single species of *Apodemus*.

Based on collecting sites of specimens used in this study, *A. krkensis* is restricted to slopes of fractured Karst at the southern end of the island of Krk. *Apodemus krkensis* has been found to occur sympatrically with *A. sylvaticus* in such regions, but the latter is by far numerically dominant as indicated by trapping records. For instance specimens of both forms were collected in the same trap lines at 3.6 km S, 4.3 km E Krk, 100 m, and 4.7 km S, 5.4 km E Krk, 150 m. Based on these records the frequency of the lighter colored *Apodemus* is less than 20 percent.

The situation of *A. krkensis* may be best explained as being an example of local polymorphism in *A. sylvaticus* on the island. *Apodemus krkensis* is only able to survive in such dry Karst areas because of its cryptic coloration. The fact that *A. krkensis* is rare and not the dominant form of *Apodemus* in the rocks indicates that some sort of pleiotropic effect, associated with the gray pelage color, is preventing the light-colored form (*A. krkensis*) from becoming dominant. An example of this situation, which may be quite similar to the color variation observed in *Apodemus* on the island of Krk, has been observed in *Microtus californicus* (Lidicker, 1963).

Because systematic and taxonomic relationships of any group of mammals should be based on a total assessment of all aspects of the group, the findings of this study alone may not reflect the actual interrelations among species of *Apodemus*. However it is hoped that this work will serve as a contribution to the knowledge of the group and be of use in determining the systematics of the genus.

Specimens examined.

Specimens used in this study are currently being maintained in the mammal collection of The Museum, Texas Tech University. Museum catalog numbers have not been assigned because of plans to divide specimens between the University of Zagreb and Texas Tech University upon completion of the project funded by the Smithsonian Foreign Currency Program. Therefore, individual specimens examined in this study are identified below by the collector's initials and field number which appear in parentheses following the locality. The total number of specimens examined from each locality precedes the field numbers. All specimens are from the Republic of Croatia, Yugoslavia.

Apodemus agrarius (23). — 12 km N, 3.5 km E Labin, 25 m, 1 (NT 115); 6 km N, 1 km E Lekenik, 100 m, 15 (SLW 1474, 1475, 1485, 1486, 1488, 1489, 1506-1508, 1574-1577, 1579; JCH 463); 5 km N Lekenik, 100 m, 1 (SLW 1563); 7 km N, 6 km S Pazin, 260 m, 2 (NT 101, 102); 22 km S, 17 km E Zagreb, 100 m, 4 (PGD 143-146).

Apodemus flavicollis (22). — 6 km N, 1 km E. Lekenik, 100 m, 1 (JCH 460); 5 km N Lekenik, 100 m, 4 (SLW 1561, 1562, 1566, 1583); 8 km W Lekenik, 150 m, 10 (SLW 1593-1595, 1597, 1599, 1601-1604, 1608); 3 km S, 2 km W Rude, 700 m, 3 (SLW 1529, 1535, 1536); 1.5 km N, 3 km N, 3 km E Sljeme, 700 m, 3 (SLW 1448, 1453, 1454); 1 km S, 1 km W Sljeme, 500 m, 1 (SLW 1513).

Apodemus krkensis (2). — 2.2 km N, 5.4 km E, Krk, 175 m, 1 (PGD 298); 3.6 km S, 4.3 km E Krk, 100 m, 1 (JCH 916).

Apodemus mystacinus (9). — 1.5 km N, 3 km E. Crikvenica, 300 m, 2 (SLW 1784, 1786); 2 km N, 11 km E Posedarje, 120 m, 5 (PGD 43, 79, 80, 89, 90); 4 km S, 2.5 km E Posedarje, 50 m, 1 (PGD 85); 18 km S, 25 km E. Zadar, 100 m, 1 (PGD 71).

Apodemus sylvaticus (66). — : 2.7 km N, 2.9 km E Biograd, 10 m, 1 (PGD 278); 2.6 km N, 2 km E Biograd, 10 m, 1 (PGD 286); 3 km N Karlovac, 100 m, 2 (SLW 1736, 1737); 16.1 km N, 1 km W Krk, 10 m, 3 (PGD 318, 320, 348); 13.5 km N, 0.8 km E Krk, 70 m, 1 (PGD 314); 4.5 km N, 0.6 km W Krk, 20 m, 6 (PGD 305, 308, 309, 311, 314; JCH 894); 4.0 km N, 6 km E Krk, 175 m, 2 (JCH 886, 887); 3.3 km N, 6.3 km W Krk, 70 m, 2 (PGD 339, 340); 2.2 km N, 5.4 km E Krk, 175 m, 2 (PGD 297; JCH 889); 0.3 km S, 8.2 km E Krk, 300 m, 1 (PGD 291); 2.6 km S, 9.8 km E Krk, 150 m, 1 (JCH 880); 3.6 km S, 4.3 km E Krk, 100 m, 3 (PGD 327, 328, 333); 4.5 km S, 11.8 km E Krk, 50 m, 1 (PGD 293); 6 km N, 1 km E Lekenik, 100 m, 6 (SLW 1460-

1464, 1496); 5 km N Lekenik, 100 m, 1 (SLW 1584); 6 km S, 11 km E Pazin, 25 m, 1 (NT 105); 5.5 km N, 26 km E, Posedarje, 750 m, 6 (PGD 229; NT 453, 456, 457, 459; JJ 1); 4 km N, 26.5 km E Posedarje, 66 m, 1 (NT 463); 3 km N, 5 km W Posedarje, 150 m, 4 (PGD 61-63; NT 458); 2 km N, 11 km E Posedarje, 120 m, 2 (PGD 46, 47); 2 km S, 5 km W Posedarje, 50 m, 1 (PGD 37); 3 km S, 19.5 km W Posedarje, 20 m, 6 (PGD 107, 108, 124, 250; NT 418, 419); 7.1 km N, 2.8 km W Rab, 20 m, 3 (PGD 369; JCH 963, 964); 3.4 km N, 2.4 km W Rab, 20 m, 2 (PGD 365; JCH 960); 0.9 km N, 1.9 km E, Rab, 175 m, 2 (JCH 954, 955); 5.2 km S, 6.2 km W Rab, 75 m, 3 (PGD 372-374); 2 km S, 8 km W Samobor, 400 m, 1 (SLW 1713); 15 km N, 10 km E Zagreb 275 m, 1 (SLW 1670).

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SUMMARY

The glans penis and baculum of five species of *Apodemus* were examined. Basically the glans of this genus is cylindrical in shape and possesses a dorsal ridge, ventral groove, apical processes, and constriction near the midsection of the glans. The baculum consists of a trilobed cartilagenous tip and a proximal osseous portion. The osseous portion of the baculum consists of a shaft with an expanded base.

Analysis of physical characters and measurements revealed no distinct differences which could be attributed to nongeographical variation. However, there are some indications that geographical variation may occur in *A. sylvaticus*. Distinct differences were noted among most of the species. *Apodemus mystacinus* was easily separable from the other species because of its size among other features. Although the four other species were similar, *A. agrarius* and *A. flavicollis* could be differentiated from each other and from *A. krkensis* and *A. sylvaticus*. The similarities between *A. krkensis* and *A. sylvaticus*, in addition to other factors, makes the taxonomic and systematic relationship of these two forms highly questionable. This study indicates that *A. krkensis* and *A. sylvaticus* are synonymous.

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