

PHALLI AND BACULA OF EUROPEAN DORMICE: DESCRIPTION AND COMPARISON

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ABSTRACT – We examined the glans penis of 34 adult specimens belonging to five genera and six species of Myoxidae. Three measurements of phalli and 11 measurements of bacula were taken and nine ratios were calculated. The baculum of Myoxidae is simple and in all the species studied is fully expressed at the tip of the phallus and, excluding *Muscardinus*, lies beneath cavernous tissue. In *Myoxus*, the baculum is triangular, wide and flat and evident interpopulational variability is existing: North Italian specimens display shape differences in comparison with South Italian and Thracian populations. The baculum of *Dryomys* is relatively thick, wide on the base and narrow at the shaft. There are differences in size between Thracian and Israeli populations of *Dryomys nitedula*. The baculum of *Muscardinus* is short and thin, with a small base; the phallus is tubelike and shorter than the baculum. The baculum of *Myomimus* is very short and robust, with a relatively wide base; the phallus, in contrast to other species, has no pad-like structure. The baculum of *Eliomys* differs from that of *Dyoinsys* and resembles more that of *Myoxus*, being more curved, more triangular and flat in shape, with widening in the middle. There are marked differences between bacula of *E. quercinus* and *E. melanurus*. A cluster analysis showed high affinities between *Myoxus* and *Eliomys*, as well as *Myomimus* and *Dryomys*, reflecting possible phylogenetic relationships.

Key words: Glans penis, Phallus variation, Baculum variation, Myoxidae.

RIASSUNTO – *Falli e bacula di Mioxidi europei; descrizione e comparazione* – È stato esaminato il glans penis di 34 esemplari adulti appartenenti a cinque generi e sei specie di Myoxidae. Sono state rilevate tre misurazioni sul fallo, undici sul baculum e nove rapporti. Il baculum dei Myoxidae è semplice e in tutte le specie studiate è situato nella parte terminale del fallo e, tranne che nel moscardino, giace sotto il tessuto cavernoso. Il baculum di *Myoxus* è triangolare, ampio ed appiattito; è presente una evidente variabilità tra popolazioni. Esemplari dell'Italia settentrionale mostrano differenze nella forma del baculum rispetto a popolazioni dell'Italia meridionale e della Tracia. Il baculum di *Dryomys* è relativamente spesso, ampio alla base e sottile nella parte terminale. Esistono differenze nelle dimensioni tra popolazioni di *Dryomys nitedula* della Tracia e di Israele. Il baculum di *Muscardinus* è corto, sottile, con una piccola base; il fallo è tubolare e più corto del baculum. Il baculum di *Myomimus* è molto corto, robusto, con una base relativamente ampia; il fallo, contrariamente alle altre specie, è privo di protuberanze. Il baculum di *Eliomys* differisce da quello di *Dryomys* e ricorda più quello di *Myoxus*, avendo una forma più curvata, triangolare ed appiattita, con un allargamento nella parte mediana. Esistono marcate differenze tra il baculum di *E. quercinus* e quello di *E. melanurus*. Elevata affinità, che potrebbe indicare possibili

rapporti filogenetici, tra *Myoxus* e *Eliomys* e tra *Myomimus* e *Dryomys* e stata osservata inediante cluster analysis.

Parole chiave: Glans penis, Variazione fallica, Variazione baculum, Myoxidae.

INTRODUCTION

Morphologically the baculum of mammals is the most diverse bone found in vertebrates (Romer, 1962), varying greatly among groups while staying generally constant within a given species. Morphological analysis of this organ can be extremely useful in reconstructing the phylogeny of rodents (Wade & Gilbert, 1940; Blair, 1942; White, 1953; Dearden, 1958; Anderson, 1960; Best & Schnell, 1973; Burt, 1936, 1960; Hooper & Musser, 1964; Lidicker, 1968; Williams, 1982; Bradley & Shmidly, 1987; Lidicker & Brylski, 1987). However, only a few studies have dealt with interspecific and intraspecific variation among closely related species and their importance in speciation (Genoways, 1973; Williams et al., 1980; Kaya & Sitsek, 1986; Bradley et al., 1989; Lessa & Cook, 1989; Simson et al., 1993).

Several interpretations were given to the high variability of baculum morphology of mammals: adaptive correlation between baculum structure and copulatory behaviour (Cockrum, 1962; Dewsbury, 1975, 1979; Estep & Dewsbury, 1976; Kenney et al., 1977); adaptive mechanical function (Blandau, 1945; Long & Frank, 1968; Matthews & Adler, 1977); pleiotropic effect (Mayr, 1963); sexual selection by femal choice (Eberhard, 1985).

A detailed discussion of the correspondence of bacular and phyletic divergetice was given by Patterson & Thaeler (1982). Two non-exclusive hypotheses have been advanced to explain the remarkable pattern of bacular variation within and between species.

According to the first hypothesis (Burt, 1936; Mayr, 1963), the baculum is a pleiotropic by-product of phyletic divergence. The baculum lacks specific function but has a polygenic basis which, through pleiotropy, links it with the rest of the phenotype. By this view, changes in bacular morphology are products of indirect selection, caused by selection operating directly on other aspects of the phenotype. Bacular morphology is therefore distinctive but non-adaptive.

The second hypothesis suggests a precise function for the baculum and phallus as a whole in species-specific reproduction. The baculum (and phallus) is subject to direct selection because of its role in copulation as a reproductive isolating mechanism (Ruth, 1934; Long & Frank, 1968; Patterson & Thaeler, 1982). According to Patterson (1983), although continuous variation of the baculum strongly suggests a polygenic basis, and pleiotropic effects may be a universal property of genes, it is possible that genital morphology may be adaptive in the various interactions of males and females during copulations. Bacular and phallic modifications which lead to reproductive dysfunction in heterospecific crosses would be advantageous in reducing gametic wastage.

The family Myoxidae is an ancient one, which originated in the Early Eocene, but with disputed inter- and intrafamilial relations. Qualitative descriptions of bacula and phalli of Myoxidae were performed by Ognev (1947) on 5 genera, and

by Hrabe (1969) and Kratochvil (1973) through histomorphological analysis of male genitalia in 4 genera. Rossolimo & Pavlinov (1985) studied the external genital morphology of the genera *Myomimus* and *Glirulus*. Didier (1953) gave a description of the os penis for *E. melanurus*.

In the present study we tried a quantitative approach for describing phalli and bacula of Myoxidae, hoping to provide an additional data set that could be incorporated with others (morphological, karyological, electrophoretic) in any analysis of evolution within the group. Phallus and baculum variation and divergence were analysed among 15 populations representing the five western palaeartic genera of the family Myoxidae: *Myoxus glis* from Italy and Turkish Thrace; *Dryomys nitedula* from Israel and Turkish Thrace; different chromosomal forms of *Eliomys quercinus* from Spain ($2n = 48$), Germany ($2n = 50$), Italy ($2n = 48, 52, 54$) and Dalmatia ($2n = 48$); *Eliomys melanurus* from Israel ($2n = 48$) and Morocco ($2n = 46$); *Muscardinus avellanarius* from Italy; *Myomimus roachi* from Turkish Thrace.

MATERIALS AND METHODS

We examined phalli and bacula of 34 specimens belonging to six species and five genera of Myoxidae. The number of specimens examined for each population, their collecting sites and sample designations are shown in Table 1; sample localities and distribution are shown in Figure 1. Most of the animals were caught by the authors, except where otherwise mentioned. The measurements of Israeli *D. nitedula* were taken from a specimen kept in the Zoological Museum of Tel-Aviv University. Specimens of *E. quercinus* from Spain and Germany, were obtained from Dr. H. Meinig and Dr. S. Baasner.

Tab. 1 – Collecting site and number of specimens examined for each dormouse population analysed

POP. N.	SPECIES	LOCATION	N. SPEC.
1	<i>Dryomys nitedula</i>	Hurfesh, Upper Galilee, Israel	1
2	<i>Dryomys nitedula</i>	Edirne, Thrace, Turkey	5
3	<i>Eliomys melanurus</i>	Mizpe-Ramon, Negev Desert, Israel ($2n=48$)	4
4	<i>Eliomys melanurus</i>	Cap Spartel, Morocco ($2n=46$)	4
5	<i>Eliomys quercinus</i>	Cntreves, Valle d'Aosta, Italy ($2n=54$)	1
6	<i>Eliomys quercinus</i>	Altipiano d'Asiago, Venetia, Italy ($2n=52$)	2
7	<i>Eliomys quercinus</i>	Figueiras, Catalogna, Spain($2n=48$)	2
8	<i>Eliomys quercinus</i>	Firenze, Tuscany, Italy ($2n=48$)	3
9	<i>Eliomys quercinus</i>	Koblenz, Germany ($2n=50$)	3
10	<i>Eliomys</i>	Zivogosce, Dalmatia, Croatia ($2n=48$)	1
11	<i>Myoxus glis</i>	Altipiano d'Asiago, Venetia, Italy	3
12	<i>Myoxus glis</i>	Sila Mts., Calabria, Italy	1
13	<i>Myoxus glis</i>	Ycnicekoy, Istranca Mts., Thrace, Turkey	1
14	<i>Muscardinus avellanarius</i>	Muro Lucano, Basilicata, Italy	1
15	<i>Myomimus roachi</i>	Sütluce, Gelibolu, Thrace, Turkey	1

Phalli were removed from fresh or frozen dissected specimens. Phalli were cleared in 4% potassium hydroxide and stained with Alizarin Red S, following Lidicker (1968). Dehydration was achieved by transferring the red-coloured bacula to 25%, 50%, 75% and finally, 100% glycerin for final preservation. Three linear measurements were taken from each phallus, eleven measurements were taken and 9 ratios were calculated for each baculum. The linear measurements were taken with a calliper with an accuracy of up to 0.02 mm. The following measurements were taken (Fig. 2): body length (BDL), greatest skull length (GSL), phallus length (PHL), phallus width (PHW), phallus height (PHH), baculum length (BL), baculum height (BH), baculum base width (BaW), baculum base thickness (BaH), baculum tip width (BTW), baculum tip thickness (BTH), baculum middle width (MdW), baculum middle thickness (MdH).

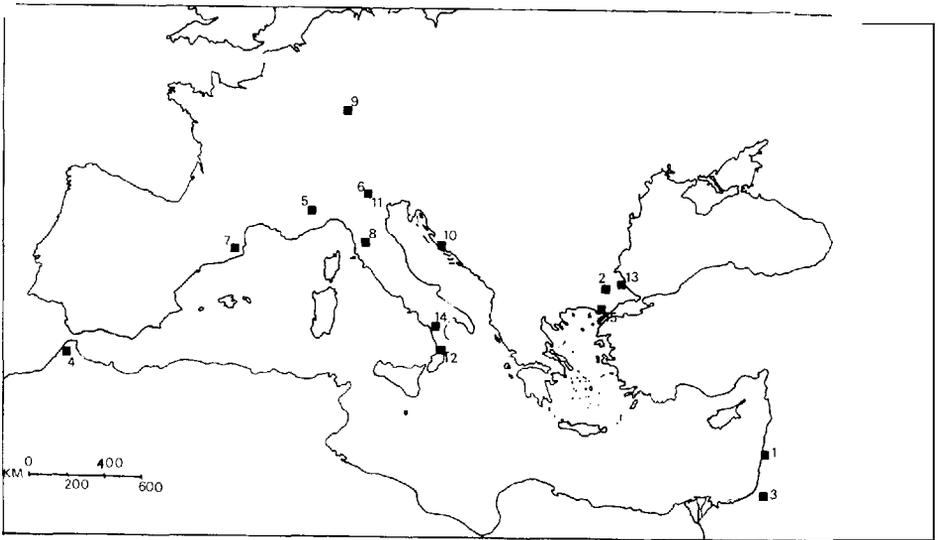


Fig. 1 – Map of distribution. numbers (1-15) are indicating populations. See Table 1 for details.

Three additional baculum measurements (total area: TOT; perimeter: PERIM; area of base: BASAR) and one ratio (roundness: ROUND) were taken using 'Quantimet 970', a computerized and integrated image analyzer by Cambridge Instruments. The subject of the analysis is captured by a high definition videocamera and displayed on two monitors (monochrome and color). It creates a digital image, resolved into 256 grey levels (level 0 = black, level 256 = white). Every portion of the image over or below a variable grey level can be isolated and subjected to morphometric analysis, using the specific software Clups vo. 700. Simple and complex parameters such as relative position, maximum and minimum length, perimeter, area, roundness, etc., can be directly selected, measured and expressed as absolute or relative values, or as histogram distributions.

The ratios calculated were: relative baculum/body length (RELBLD), relative baculum/greatest skull length (RELSSL), relative base width/baculum length

(RELBAW), relative baculum height/baculum length (RELBH), relative middle width/baculum length (RELMDW), relative total baculum area on body length (RELTOT), relative base area on total area (RELBAS), relative perimeter on baculum length (RELPERIM).

Drawings of the glans penis were made using a stereobinocular.

Statistical analysis was performed by the Systat package (Wilkinson, 1986). Descriptive statistics included means and standard deviations. Multivariate analysis included factor analysis, cluster, and canonical-discriminant analyses. The discriminant analysis was computed with multivariate general linear hypothesis, the residual correlation and residual covariance were pooled within-group matrices. The graphic presentation was performed by plotting canonical scores and Mahalanobis distances. The Cluster analysis was performed by a single linkage method, normalized data by using Euclidean distances.

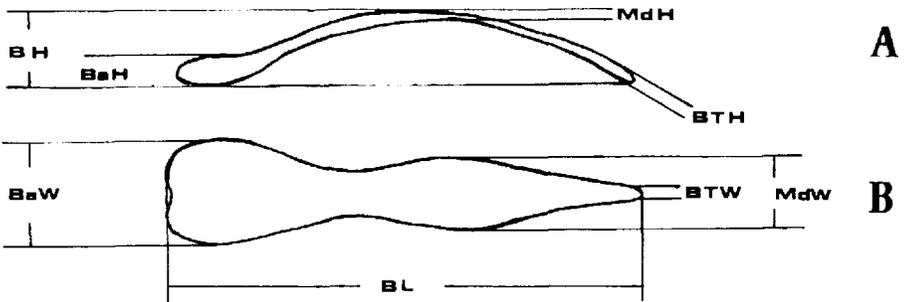


Fig. 2 – Measurements of baculum. For explanations and abbreviations see text. A-lateral view. B-dorsal view.

RESULTS

Means and standard deviations of the measurements taken and the calculated ratios are presented in Table 2. In *Eliomys* each population represents a different chromosomal form. Schematic drawings of phalli of five genera with relative position of the baculum are presented in Fig. 3.

Glans penis. The penis of *Myoxus glis* is club-shaped, with a small sharp protrusion; the ventral side is creased by longitudinal folds and covered with small spines. The penis of *Dryomys nitedula* is flattened dorsally (width 3.8 mm, height 3.2 mm), the ventral and lateral sides are covered with spines, and there are two pad-like structures. In the genus *Eliomys*, the penis is relatively narrow (width 3.5 mm, height 4.0 mm), with a long protrusion; spines cover the ventral and lateral sides, as well as four distinct regions of the dorsal side. *E. quercinus* and *E. melanurus* differ in length of protrusion (1.8-3.3 mm and 1.5-1.7 mm, respectively). The penis of *Myomimus roachi* is short (6.3 mm), expanded anteriorly, club-shaped (height 3.8 mm); the lateral sides are creased by longitudinal folds, most of the phallus surface is covered with short spines. Contrary to other species, the phallus of *Myomimus* has no pad-like structure. The

penis of *Muscardinus avellanarius* is very short (4.4 mm), cylindrical, very narrow (1.2 mm) and half of it is covered with small spines. It is unique in not covering all of the baculuin (baculum length 4.8 mm).

Baculum. The baculuin of Myoxidae is simple and in all the species studied is fully expressed at the tip of the phallus and, excluding *Muscardinus*, lies beneath cavernous tissue. The general shape of bacula of five genera and six species is presented in Fig. 4. All bacula studied are composed of a single proximal bone formed by a distal shaft and two basal expansions connected to the proximal corpus cavernosum penis, serving as a mechanical axis supporting soft tissues and covering the terminal portion of the urethra. Evident differences exist between the species. The baculum of *Myoxus glis* is the biggest, triangular, and most curved. The baculum of *Dryomys nitedula* has a big base and long narrow shaft. In *Eliomys* the sizes of the baculum are intermediate between *Dryomys* and *Myoxus*. The baculuin of *E. melanurus* is more delicate and less curved than in *E. quercinus*, with its tip curved dorsally. The bacula of *Myomimus roachi* and *Muscardinus avellanarius* differ from the others in being very small, not curved, with base and shaft delicate; that of *Myomimus* has two broad protuberances on the base and shallow longitudinal groove along the dorsal side.

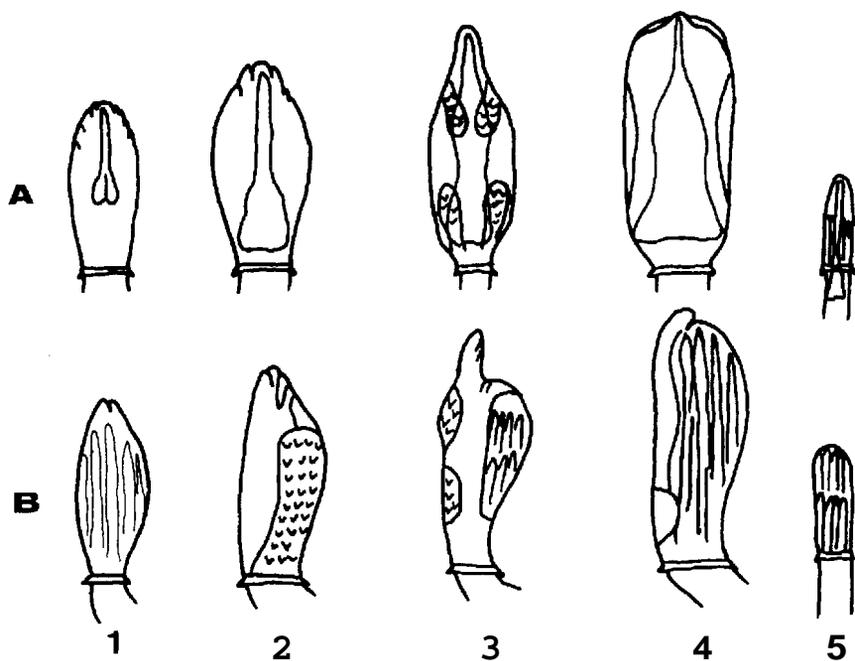


Fig. 3 – Schematic drawings of glans penis: 1-*Myomimus*; 2-*Dryomys*; 3-*Eliomys*; 4-*Myoxus*; 5-*Muscardinus*. A-dorsal view. B-lateral view.

Tab. 2 – Means and standard deviations (mm) of the considered measurements.

pop. n.	n. spec.	BDL	GSL	PHL	PHW	PHH	BL	BH	BaW
1	1	85.0	27.5	---	---	---	6.96	0.98	1.8
2	5	91.2± 9.5	25.8±0.2	8.8±0.6	3.86±0.5	3.2±0.2	7.53±0.5	0.90±0.1	1.88±0.3
3	4	107.0± 6.5	34.0±0.7	8.6±0.1	3.30±0.8	3.5±0.4	7.52±0.6	0.70±0.1	1.87±0.1
4	4	108.5± 7.4	32.0±1.5	9.3±1.2	3.85±0.7	3.9±0.6	7.12±0.1	0.95±0.3	1.98±0.2
5	1	121.0	34.0	10.5	3.60	4.0	8.00	0.98	2.46
6	2	142.0± 0.0	35.4±0.6	9.9±0.1	3.50±0.3	4.2±0.2	8.83±0.4	1.06±0.1	2.11±0.2
7	2	130.5±2.1	36.0±0.2	8.8±0.7	3.10±0.3	3.7±0.7	7.74±0.3	1.02±0.3	2.06±0.3
8	3	146.3± 5.5	38.9±0.5	10.7±0.6	3.90±0.2	4.1±0.4	8.86±0.5	1.16±0.1	2.23±0.2
9	3	135.3± 2.5	36.3±0.5	10.1±0.7	3.90±0.2	3.4±0.2	8.39±0.3	1.19±0.2	2.57±0.2
10	1	125.0	36.1	9.5	3.50	3.0	6.80	1.20	1.94
11	3	175.6±17.6	40.6±1.6	9.6±0.8	4.00±0.5	3.1±0.6	8.12±0.8	1.51±0.1	2.55±0.3
12	1	142.0	40.4	9.5	4.40	3.7	8.56	1.76	2.54
13	1	153.0	38.7	10.5	3.50	3.4	8.36	1.62	2.76
14	1	67.0	23.9	4.4	1.20	1.2	4.84	0.46	0.86
15	1	112.0	27.8	6.3	2.00	3.8	4.48	0.75	1.46

pop. n.	BaH	MDW	MDH	BTW	BTH	RELBLD	RELSL	RELBaW	RELMDW
1	0.95	0.62	0.50	0.42	0.35	0.80	0.25	0.258	0.089
2	0.78±0.3	0.56±0.0	0.36±0.1	0.37±0.1	0.38±0.10	0.80±0.1	0.29±0.0	0.247±0.00	0.075±0.01
3	0.50±0.1	1.22±0.2	0.29±0.0	0.28±0.0	0.26±0.03	0.70±0.1	0.22±0.01	0.249±0.01	0.162±0.02
4	0.78±0.2	1.27±0.1	0.29±0.0	0.29±0.0	0.31±0.07	0.65±0.1	0.22±0.01	0.277±0.03	0.177±0.01
5	0.86	1.76	0.30	0.30	0.30	0.66	0.23	0.307	0.220
6	0.89±0.1	1.57±0.0	0.32±0.0	0.29±0.0	0.32±0.00	0.60±0.0	0.25±0.00	0.239±0.03	0.177±0.01
7	0.42±0.1	1.37±0.3	0.31±0.1	0.33±0.1	0.32±0.10	0.60±0.0	0.21±0.01	0.266±0.02	0.179±0.04
8	0.86±0.1	1.45±0.2	0.31±0.0	0.29±0.0	0.31±0.01	0.59±0.0	0.24±0.00	0.252±0.02	0.163±0.01
9	0.69±0.2	1.49±0.1	0.25±0.0	0.25±0.0	0.22±0.20	0.60±0.0	0.23±0.01	0.307±0.04	0.177±0.02
10	0.52	1.26	0.34	0.30	0.28±	0.50	0.19	0.285	0.185
11	0.78±0.1	1.72±0.3	0.24±0.0	0.21±0.0	0.47±0.05	0.48±0.1	0.21±0.01	0.300±0.01	0.202±0.01
12	0.76	1.76	0.22	0.25	0.44	0.60	0.21	0.296	0.206
13	0.84	1.78	0.34	0.32	0.46	0.50	0.22	0.330	0.213
14	0.34	0.30	0.20	0.16	0.14	0.70	0.20	0.177	0.062
15	0.70	0.50	0.36	0.26	0.30	0.40	0.16	0.325	0.110

pop. n.	TOTAR	ROUND	PERIM	BASAR	RELTOT	RELBAS	RELPERIM	RELBH	RELMDH
1	---	---	---	---	---	---	---	0.14	0.81
2	6.9±1.6	3.9±0.2	18.8±1.7	3.6±1.0	0.074±0.011	0.52±0.02	2.72±0.38	0.12±0.010	0.65±0.2
3	6.9±1.0	3.6±0.1	18.2±1.4	2.4±0.5	0.064±0.006	0.35±0.13	2.66±0.20	0.09±0.005	0.24±0.0
4	7.2±0.2	3.3±0.1	17.7±0.2	2.3±0.3	0.066±0.005	0.32±0.03	2.48±0.07	0.12±0.003	0.29±0.0
5	10.5	3.3	21.6	2.9	0.085	0.28	2.05	0.12	0.17
6	10.0±1.1	3.4±0.6	21.1±3.3	2.9±0.5	0.071±0.001	0.30±0.09	2.10±0.10	0.12±0.005	0.20±0.0
7	8.4±1.6	3.2±0.3	18.9±1.4	2.4±0.5	0.077±0.008	0.28±0.05	2.10±0.42	0.13±0.070	0.22±0.0
8	10.8±1.1	3.4±0.3	22.0±0.4	3.8±0.7	0.074±0.006	0.35±0.03	2.05±0.19	0.13±0.020	0.21±0.0
9	10.5±0.9	3.6±0.8	22.3±1.7	2.7±0.7	0.077±0.008	0.26±0.01	2.14±0.31	0.14±0.020	0.17±0.0
10	10.1	2.9	21.2	2.7	0.082	0.22	1.92	0.18	0.26
11	15.0±3.4	2.5±0.1	22.2±2.1	4.7±0.7	0.085±0.017	0.33±0.03	1.52±0.24	0.18±0.020	0.14±0.0
12	16.1	2.6	21.2	4.9	0.113	0.30	1.320	0.21	0.13
13	16.9	2.7	22.3	3.4	0.110	0.20	1.32	0.19	0.19
14	2.2	4.7	11.5	1.0	0.033	0.47	5.25	0.09	0.67
15	3.8	2.6	11.5	1.4	0.034	0.35	3.03	0.17	0.72

There is no baculum/body length allometry. The relative baculum/body length (RELRLD) increases in the following order: *Myomimus* (0.4), *Myoxus* (0.55), *E. quercinus* (0.6), *Muscardinus* (0.7), *E. melanurus* (0.7), *Dryomys* (0.8).

The baculum height (BH) increases in the following order: *Muscardinus* (0.46), *Myomimus* (0.75), *E. melanurus* (0.83), *Dryomys* (0.91), *E. quercinus* (1.12), *Myoxus* (1.61).

Roundness (the bigger the number, the further is the shape from circle) decreases in the following order: *Muscardinus* (4.7), *Dryomys* (3.9), *E. melanurus* (3.45), *E. quercinus* (3.35), *Myoxus* (2.65), *Myomimus* (2.6).

Dryomys and *Muscardinus* have the biggest relative base (RELBAS), 0.52 and 0.47 respectively. The other genera display lower values in the following decreasing order: *Myomimus* (0.36), *E. melanurus* (0.33), *Myoxus* (0.33), *E. quercinus* (0.29).

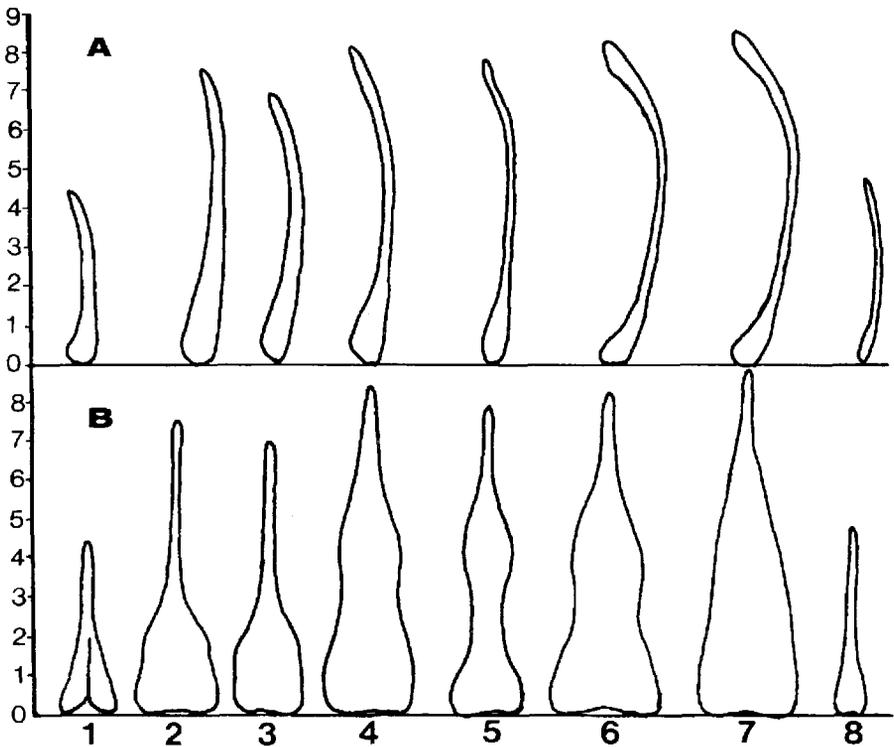


Fig. 4 – Drawings of bacula: 1-*Myomimus roachi*; 2-*Dryomys* (Thrace); 3-*Dryomys* (Israel); 4-*Eliomys quercinus* (Aosta); 5-*Eliomys melanurus* (Israel); 6-*Myoxus* (Thrace); 7-*Myoxus* (Asiago); 8-*Muscardinus*. A-lateral view, B- dorsal view. x10.

The highest value of relative baculum middle width (RELMDW) is displayed by *Myoxus* (0.20), whereas *Muscardinus* has the lowest value (0.06).

Marked interpopulation differences were observed in *Myoxus glis*, *Dryomys nitedula*, and *Eliomys*.

Specimens of *M. glis* from the Sila Mountains (Southern Italy) and Thrace (Turkey) look much more similar to one another than to *M. glis* from Asiago (Northern Italy).

Differences were observed between Israeli and Turkish populations of *Dryomys nitedula*. The Israeli population is characterized by a more robust, but shorter baculum. In the following measurements the Israeli sample was also bigger: greatest skull length (GSL), height of baculum base (BAH), height of the middle part of baculum (MDH), relative middle width (RELMDW).

In *Eliomys* it is difficult to distinguish between geographic and species-specific variation because each population represents a different chromosomal form and the number of specimens studied is small. Between *E. melanurus* and *E. quercinus* groups there are significant differences in the following six characters: relative baculum/body length (RELBDL); baculum height (BH); relative height (RELBH); total dorsal surface (TOTAR); perimeter (PERIM); relative thickness of the middle (RELMDH).

The differences within the *E. melanurus* group between $2n=48$ and $2n=46$ are greater than within the *E. quercinus* group. A higher differentiation among chromosomal forms of *E. melanurus* was also found by electrophoretic analysis (Filippucci & Kotzakis, 1995).

Statistical analysis. Results of canonical-discriminant analysis are presented in Fig. 5. The populations 1 and 2 (*Dryomys*) are separated mostly by discriminant function 1, which explains 62% of the variance. The populations 14 (*Muscardinus*) and 15 (*Myomimus*) are segregated from the others mostly by the second discriminant function which explained 32% of the variance. Populations 3 and 4 (*E. melanurus*) are clearly separated from other populations of *E. quercinus*. There is relatively big variance in population 9. Populations 11, 12 and 13 (*Myoxus*) are separated from *E. quercinus* mostly by discriminant function 2. Of the 34 specimens subjected to the discriminant function analysis based on raw data, 32 (i.e. 94%) were classified correctly, according to predicted frequencies.

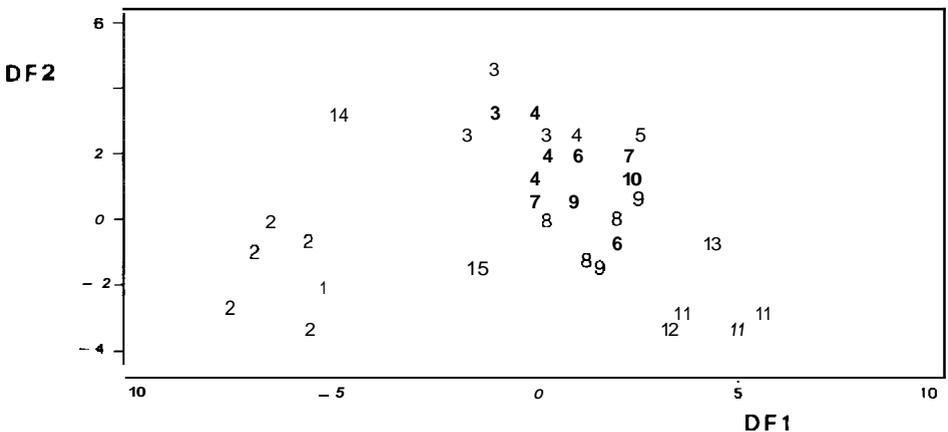


Fig. 5 – Plot of discriminant analysis for 5 genera. Symbols (1-15) are indicating populations. See Table 1 for details.

The principal component analysis was performed with the Systat module 'Factor'. The first component explained 47% of total variance, the second 20.5% and the third 10%. From the component loadings the variable that contributes greatly to the variance is the relative width of middle of the baculum MdW (0.875 on the first component and -0.107 on the second component), roundness ROUND contributing -0.874 and -0.213 on the first and second respectively. The width of tip of the baculum BTW contributes greatly to both of the components (-0.525 and 0.697).

The cluster analysis was performed with the Systat module 'Cluster'. The results are presented in Fig. 6. There is good separation between genera. The lowest values of Euclidean distance were observed between *Myomimus* and *Dryomys* (0.561) and *Myoxus* and *Eliomys* (0.567). Between these two groups the mean value of Euclidean distance was 0.799. The highest value of Euclidean distance was observed comparing *Muscardinus* with the other genera (1.271). Cluster analysis is less sensitive than discriminant analysis in separating chromosomal forms of *Eliomys*. There is no good separation between *E. quercinus* and *E. melanurus*.

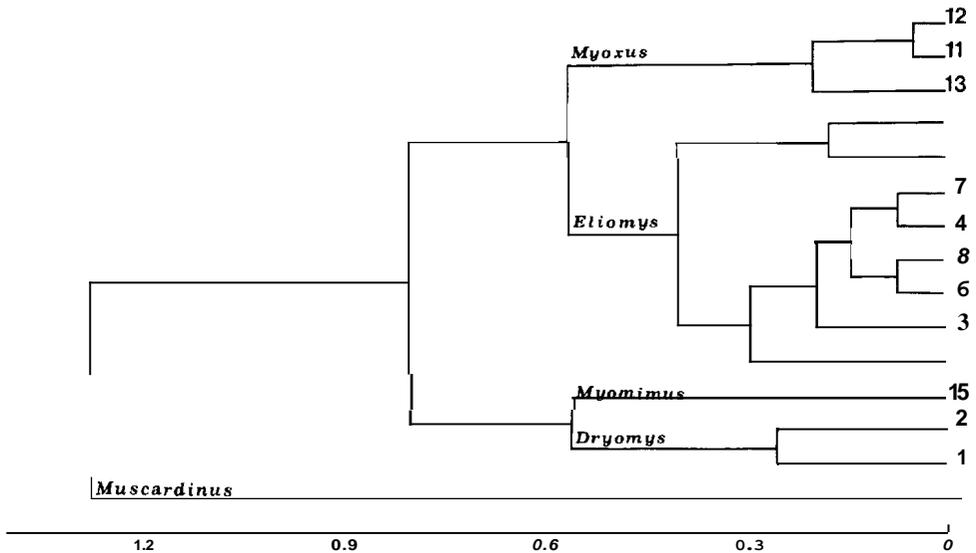


Fig. 6 – Cluster analysis for 5 genera. Clustering metrics is normalized Euclidean distances of means. Symbols (1-15) are indicating populations. See Table 1 for details.

DISCUSSION

The glans penis and baculum provide useful taxonomic characters in many groups of mammals, while also functioning as a mechanical reproductive isolating mechanism. We performed morphological analysis of the glans penis and baculum on representatives of Myoxidae, an ancient family of rodents. The number of specimens here analysed is small and did not allow real analysis of variances.

Nevertheless, between the species the differences are consistent.

Among Myomorpha, the bacula of Myoxidae resemble simple bacula of Geomyoidea, Spalacidae, Rhizomyidae and more primitive members of Cricetidae, while they differ from bacula of later radiated South-American Cricetidae and of Muridae, both characterized by a tridens os penis.

Patterson (1983) showed that when the baculum is placed at the tip of the glans, as in Myoxidae, its length evolves non-allometrically, and is dissociable from body size. Our data are in agreement with this. With respect to the baculum, the most distinct species is *Muscardinus avellanarius*. *Muscardinus* is the only genus in which the baculum is longer than the phallus and it is not covered completely by cavernous tissues. Nevertheless, considering the structure of phallus, the most distinctive species is *Myomimus roachi*. The glans penis of the genus *Myomimus* has no pad-like structure and, according to Rossolimo and Pavlinov (1985), it is the most primitive genus among Myoxidae.

There is clear interpopulational variability in *Myoxus*, comparing our results with those of Kratochvil (1973) and Ognev (1947). Bacula of specimens from North Italian (Asiago) and Czechoslovak populations are simple triangles in dorsal aspect; those of specimens from Southern Italy (Sila Mts.), European Turkey (Thrace) and Central Russia are closer in shape to the baculum of *Elionzys*: the baculum has a big base, then it becomes narrower and wide again in the middle part (Fig. 4).

There is relatively clear separation between European *E. quercinus* and *E. melanurus* from North Africa and Israel. The differences are the length of protrusion in the phallus and several baculum characters. The most significant differences in the baculum are in the following variables: RELMDH, RELBDL, TOTAR, PERIM. Because of the small sample size, little can be said about the existence of differences among chromosomal forms of *Elionzys*, but most of the populations are characterized by some variables. For example, the baculum of the Dalmatian specimen is outstanding in robustness and that of the specimen from Aosta is very wide. The specimens from Koblenz display a baculum with a very thin tip. In the specimens from Figueira it is thin, with total area and perimeter smaller than in other populations of *E. quercinus* and comparable with those of *E. melanurus*. The specimens from Firenze have a very big baculum base. Further studies will be necessary to explore inter- and intrapopulational variability.

An Israeli specimen of *Dryomys* was very different from those of Turkish Thrace. Differences between Israeli and European populations were also observed in biology (Nevo & Amir, 1961), biometric characters and allozymic analysis (Filippucci et al., 1995), suggesting the need of a revision for populations from Asia Minor, Middle East and Central Asia in order to clarify the taxonomic position of the Israeli population.

Noteworthy is the similarity between the results of cluster analysis of bacular characters and those coming from genetic data (Filippucci & Kotsakis, 1995). In both genetic and bacular studies the highest affinity was found between *Myoxus* and *Elionzys*, as well as between *Myomimus* and *Dryomys*. These results are in contrast with those deriving from other morphological analyses, mostly based on cranial and dental characters (De Bruijn, 1967; Daams, 1981; von Koenigswald,

1993; Wahlert et al., 1993).

CONCLUSIONS

Our data support the hypothesis of Patterson & Thaler (1982), Patterson (1983) and Lessa & Cook (1989) that penial characters are largely dissociable from other morphological characters. The dissociation of length of baculum, height of baculum base, and height of baculium from body size and skull size suggests that these Characters may evolve independently.

Our results, although preliminary, indicate the existence of variability among geographically distant conspecific populations, at least in those dormouse species for which several populations were available: *Myoxus*, *Eliomys*, and *Dryomys*.

It will be essential in the future to extend the studies on variation of phallic characters to other dormouse populations. The goal of future studies will be to determine the range of bacular variation within the species and the possibility of utilization of baculum characters in discrimination of chromosomal forms of *Eliomys*. The evaluation of the intraspecific range of bacular variation will allow the use of bacular characters as a more reliable and powerful tool for reconstructing the phylogeny of Myoxidae.

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